

**Putting intermittent rivers on the map:
integrating non-perennial rivers and streams
in the sustainable management of freshwater ecosystems**

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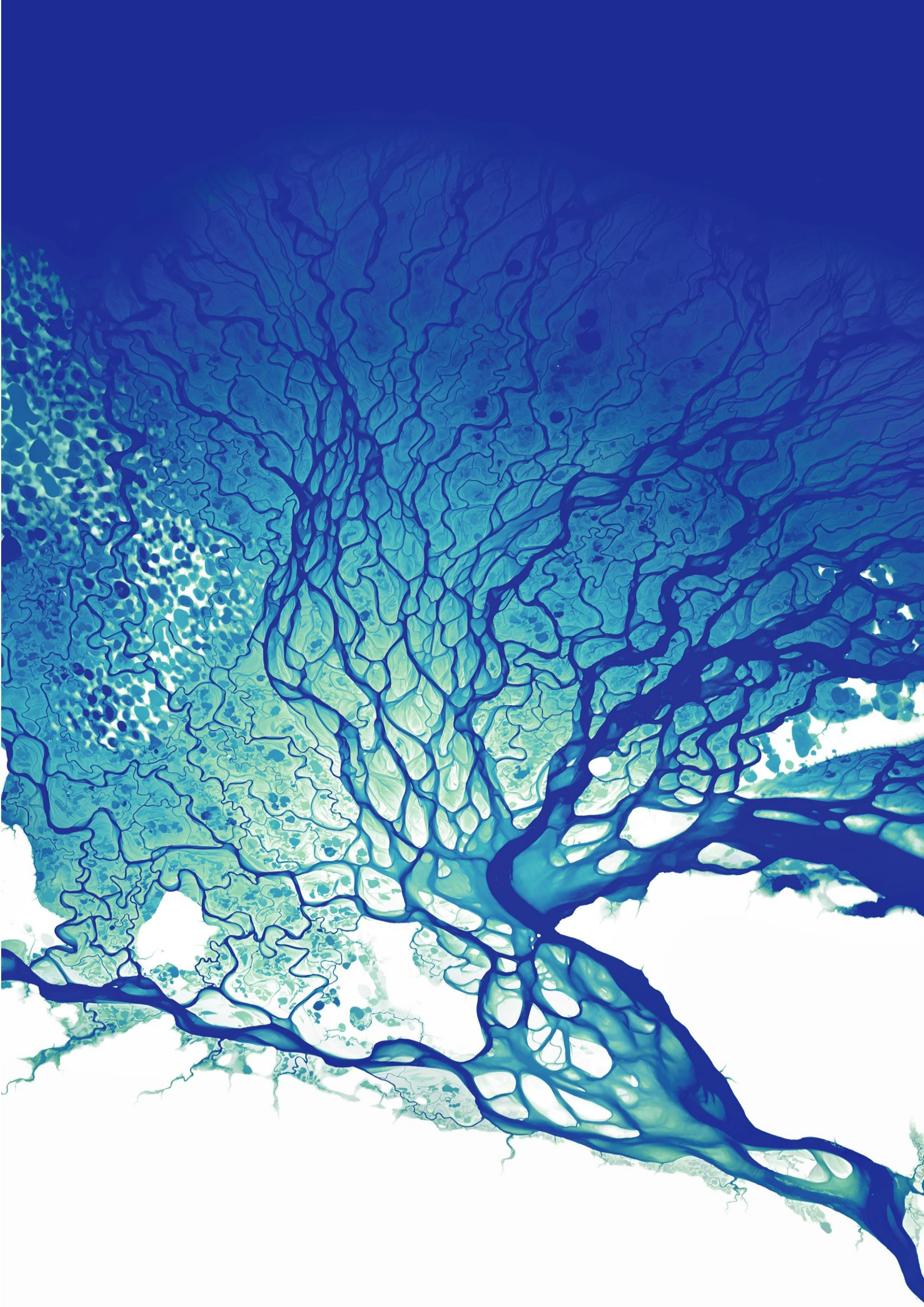
I'm grateful to my friends in France, Canada and elsewhere. I may be the worst long-distance correspondent, but I know our friendship is unwavering. It's hard to even begin listing you, but thank you for being you Maïlys (merci pour cette super relecture), Luc, Manu, Héloïsa, Teresa, Romain, Dom, Jake, Nuria et Camille, Sophie, Juliette, Luca, Thomas, Floriand et Clemence, la colloc et ses satellites!!, Meije, Lucille, Julie, Paka, Marina, Mike, Elliot, Natalie, Anna, Flaam, Sarah, Vincent, Aaron, Janine (thank you so much for welcoming me into your life and apartment; this was a precious time I will cherish), Daviken, Steven. Thank you, Molly, too; for your presence, top-notch editing, and for seeing me, always.

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Now that it comes an end, this PhD feels like whirlwind. It started in confinement, away from home, with all my classes at McGill done remotely, and involved moving, between Quebec and France, five times. Yet it has been a grounding element of my life for the past four years and I would not have done it otherwise; it literally makes sense for me. Besides, there is so much more to do, it's only the beginning!



Abstract

Virtually every river network on Earth includes non-perennial rivers and streams (NPRs) that periodically cease to flow or dry. The recurrence of flowing, non-flowing and dry phases that characterize NPRs uniquely supports high biodiversity and biogeochemical cycles in entire river networks. Consequently, changing these hydrological cycles can threaten the integrity of riverine ecosystems and the people that depend on them for their livelihood and culture. Despite their prevalence and importance, NPRs are largely excluded from management practices, conservation laws, and scientific research that have been tailored to perennial rivers. This bias, which stems from a historical lack of consideration for the value and distinctiveness of NPRs, is resulting in their rapid degradation. **The aim of this thesis is to advance our understanding of the global prevalence and diversity of NPRs, and to improve their integration in river policy and sustainable management.** Leveraging an interdisciplinary perspective integrating hydrology, ecology, geography, and data science, this thesis addresses three main objectives through four articles (Chapters 2 to 5).

- i) Chapter 2 and 3 provide the first robust quantitative estimate of the prevalence, distribution, and diversity of NPRs worldwide. Using a machine learning model informed by global data on hydrology, climate, geology, and land cover, Chapter 2 reveals that water ceases to flow for at least one day per year along 51%–60% of the world's rivers by length. This finding demonstrates that non-perennial rivers and streams are the rule rather than the exception on Earth, and that they occur within all climates and biomes, and on every continent. Chapter 3 identifies nine hydrological types of NPRs globally which differ in how often, how long, when and why they stop to flow.
- ii) Chapter 4 highlights the inadequate protection of NPRs by environmental protection laws. Through a case study of regulatory maps defining which watercourses are protected under the Water Law in France, this chapter sheds light on the socio-political factors influencing regulatory cartography, exposes the disproportionate exclusion of NPRs from regulatory frameworks, and discusses the implications of this exclusion for river network integrity.
- iii) Chapter 5 introduces a novel conceptual and operational framework to enhance the effectiveness of flow management programs to sustain freshwater ecosystems (i.e., environmental flows) in river networks with a high prevalence of NPRs. It proposes to broaden the set of ecological processes integrated into the design, implementation, and monitoring of environmental flows with the end goal of better protecting the distinct ecological structure and dynamics of NPRs.

This thesis challenges the prevailing conceptual models of river ecosystems by demonstrating the global prevalence and diversity of NPRs, and by supporting their integration into science, policy, and management frameworks. In doing so, it contributes to an ongoing paradigm shift towards an integrated view of river networks. This integrated view involves studying and managing all reaches, their floodplain, and contributing catchment as a dynamically interconnected meta-ecosystem whose components span the aquatic-terrestrial continuum.

Résumé

Pratiquement tous les réseaux fluviaux de la planète comprennent des rivières et des ruisseaux non pérennes (RNP) qui cessent périodiquement de couler ou s'assèchent. Les cycles répétés de phases d'écoulement, de non-écoulement et d'assèchement qui caractérisent les RNP est un facteur clef contribuant à la grande biodiversité et cycles biogéochimiques des réseaux fluviaux. Par conséquent, la modification de ces cycles hydrologiques peut menacer l'intégrité des écosystèmes fluviaux, leur biodiversité et les populations humaines qui en dépendent pour leur subsistance et leur culture. Malgré leur prévalence et leur importance, les RNP sont souvent exclus des pratiques de gestion, des lois sur la conservation et de la recherche scientifique, qui sont basées sur le fonctionnement des rivières pérennes. Ce biais provient d'une perception négative des RNP chez les gestionnaires et le public, et d'un manque historique de considération de leurs spécificités. En conséquence, les RNP souffrent d'une mauvaise gestion chronique et se dégradent à un rythme alarmant. **L'objectif de cette thèse est de faire progresser notre compréhension de la prévalence et de la diversité des RNP à l'échelle mondiale, et d'améliorer leur intégration dans les politiques publiques et dans les mesures de gestion durable de l'eau.** S'appuyant sur une perspective interdisciplinaire intégrant l'hydrologie, l'écologie, la géographie, et la science des données, cette thèse aborde trois objectifs principaux en quatre articles (Chapitres 2 à 5).

- i) Les Chapitres 2 and 3 fournissent la première estimation quantitative robuste de la prévalence, de la distribution et de la diversité des RNP dans le monde. En utilisant un modèle de *machine learning* basé sur des données mondiales sur l'hydrologie, le climat, la géologie et l'occupation des sols, le Chapitre 2 révèle que l'eau cesse de couler au moins un jour par an dans 51 % à 60 % des cours d'eau du monde. Ce résultat démontre que les rivières et les ruisseaux non pérennes sont la règle plutôt que l'exception sur Terre, et qu'ils sont présents dans tous les climats et biomes, et sur tous les continents. En outre, le Chapitre 3 identifie neuf types hydrologiques de RNP à l'échelle mondiale, qui diffèrent par la fréquence, la durée, la saisonnalité et la raison de l'arrêt de l'écoulement.
- ii) Le Chapitre 4 met en évidence la protection inadéquate des RNP dans la législation environnementale. À travers une étude de cas portant sur les cartes réglementaires définissant les cours d'eau protégés par la Loi sur l'eau en France, ce chapitre révèle une exclusion disproportionnée des RNP des cadres réglementaires, les facteurs sociopolitiques qui influencent la cartographie réglementaire et ses implications pour l'intégrité du réseau hydrographique.
- iii) Le Chapitre 5 développe un cadre conceptuel et opérationnel pour améliorer l'efficacité des programmes de gestion des débits écologiques (*e-flows*) qui visent à protéger les écosystèmes d'eau douce, particulièrement dans les réseaux fluviaux avec une forte prévalence de RNP. Dans ce chapitre, je propose d'élargir le panel de processus écologiques intégrés dans la conception, la mise en œuvre et le suivi des débits écologiques dans le but de mieux protéger la structure et la dynamique particulières des écosystèmes de RNP.

En conclusion, cette thèse remet en question les modèles conceptuels dominants des écosystèmes fluviaux en démontrant la prévalence et la diversité mondiale des RNP et en promouvant leur intégration dans les cadres scientifiques, de politiques publiques et de gestion. Ce faisant, elle contribue à un changement de paradigme vers une vision intégrée des réseaux fluviaux. Ce nouveau paradigme repose sur l'étude et la gestion de tous les segments, de leur plaine d'inondation et des bassins versants qui y contribuent comme un méta-écosystème dynamiquement interconnecté dont les composants couvrent le continuum aquatique-terrestre.

Keywords

Sustainable water resource management; Intermittent Rivers and Ephemeral Streams (IRES), metacommunity ecology; lotic ecosystems; environmental governance, policy and legislation; river network integrity and connectivity

Mots-clefs

Gestion durable des ressources en eau; rivières intermittentes et cours d'eau éphémères (IRES), écologie des métacommunautés; écosystèmes lotiques; gouvernance, politique et législation environnementales; intégrité et connectivité des réseaux fluviaux.

Résumé substantiel

Chapitre 1: Introduction

Les fleuves, rivières et ruisseaux ne couvrent à eux tous que 0,15 % de la surface de notre planète et contiennent seulement 0,005 % de ses réserves d'eau douce (G. H. Allen & Pavelsky, 2018; Oki & Kanae, 2006). Pourtant, ces écosystèmes d'eau courante sont essentiels à la vie sur Terre. Avec les lacs et les zones humides, les cours d'eau soutiennent un tiers des espèces de vertébrés et 10 % de toutes les espèces animales connues (Balian et al., 2008). Nonobstant leur petite superficie, les cours d'eau s'étendent sur des millions de kilomètres (Linke et al., 2019). Ils forment ainsi la plus grande interface sur Terre entre les continents, les océans et l'atmosphère, contribuant de manière critique aux cycles biogéochimiques mondiaux (Aufdenkampe et al., 2011; Battin et al., 2023).

Les civilisations humaines ont co-évolué avec les réseaux hydrographiques qui maillent les continents, et dépendent toujours fondamentalement d'eux (Anderson et al., 2019; WWAP, 2015). Cette interconnexion entre sociétés et rivières découle des innombrables façons dont les eaux courantes et leur biodiversité favorisent le bien-être humain ; à travers non seulement des contributions matérielles telles que l'eau potable ou les sédiments pour le ciment, mais aussi des contributions non matérielles telles que des activités récréatives, et la régulation du climat et des cycles des nutriments (Lynch et al., 2023).

Au cours des 50 dernières années, la science des rivières a mis en lumière la structure et le fonctionnement uniques des écosystèmes d'eau courante, ainsi que leur contribution disproportionnée à la biodiversité, à la biogéochimie et aux sociétés humaines. Nous savons également que les écosystèmes fluviaux subissent une pression extrême par les activités humaines et le changement climatique, compromettant leur intégrité écologique et les services écosystémiques associés (Dudgeon et al., 2006; Reid et al., 2019; Tickner et al., 2020). Jusqu'à récemment, cependant, la recherche et la gestion des rivières étaient axées sur les cours d'eau pérennes, négligeant les rivières et ruisseaux non pérennes (RNP) qui cessent périodiquement de couler (Acuña et al., 2017; Datry et al., 2023). Les RNP ont été sous-étudiés et sous-protégés, entraînant leur mauvaise gestion allant de la pollution et de la destruction du lit à une gestion inadéquate de leur débit (Acuña et al., 2017; Datry et al.,

2023). Dans de nombreux pays, par exemple, les définitions réglementaires des cours d'eau qui établissent la portée des lois de protection environnementale excluent la plupart des RNP (Acuña et al., 2014; Sullivan et al., 2020); les pratiques courantes de gestion durable comme le suivi de l'état écologique et les débits écologiques ne sont pas adaptées à leur fonctionnement particulier (Acuña et al., 2020; Stubbington et al., 2018). Même leur prévalence dans le monde reste largement non quantifiée (Datry et al., 2014).

Le but de cette thèse est de faire progresser notre compréhension de la prévalence et de la diversité des RNP à l'échelle mondiale, et d'améliorer leur intégration dans les cadres réglementaires et dans les mesures de gestion durable de l'eau. J'ai spécifiquement cherché à résoudre trois principaux verrous en ce sens à travers quatre articles (Chapitres 2 à 5) :

- Le manque de base de connaissance hydrologique mondial pour la science et la gestion des RNP (Chapitres 2 et 3).
- La représentation inégale des RNP dans les cartographies réglementaires définissant quels cours d'eau sont protégés par les lois sur l'environnement (Chapitre 4).
- L'inadéquation des cadres pour la conception et la mise en œuvre de débits écologiques dans les réseaux fluviaux présentant une forte prévalence de tronçons non pérennes (Chapitre 5).

Les Chapitres 2 et 3 font exclusivement progresser notre compréhension de la géographie et de l'hydrologie des RNP, tandis que les Chapitres 3 et 4 adoptent une perspective plus large applicable à tous les écosystèmes de rivières. J'ai intentionnellement opté pour cette portée inclusive pour les deux derniers Chapitres afin éviter de passer d'un biais en faveur des cours d'eau pérennes avec un traitement anecdotique des RNP à une compartimentalisation tout aussi peu productive de l'étude et de la gestion des écosystèmes d'eau courante entre les cours d'eau pérennes et non pérennes. Le message sous-jacent à cette approche est que les RNP sont présents et font partie intégrante de tous les réseaux fluviaux à l'échelle mondiale, même quand ils sont confinés aux têtes de bassin. En tant que tel, une meilleure prise en compte de leur hydrologie et écologie particulières améliorera l'efficacité des mesures de protection et de restauration pour l'ensemble du réseau fluvial.

Chapitre 2: Prévalence mondiale des rivières et ruisseaux non-pérennes

Dans cette étude, j'ai développé un modèle statistique *random forest* pour produire la première estimation mondiale de la distribution des RNP à l'échelle des tronçons. J'ai appliqué ce modèle aux 23 millions de kilomètres de cours d'eau cartographiés à travers le monde (à l'exception de l'Antarctique) dont le débit naturel moyen (module) dépasse $0,1 \text{ m}^3 \text{ s}^{-1}$. J'ai ensuite extrapolé ces estimations aux 64 millions de kilomètres de cours d'eau avec un module supérieur à $0,01 \text{ m}^3 \text{ s}^{-1}$. Dans ce but, j'ai associé des données de débit provenant de 5615 stations de jaugeage (4428 tronçons pérennes et 1187 tronçons non pérennes) à 113 variables hydro-environnementales potentiellement prédictives de l'intermittence de l'écoulement. Ces variables décrivent le climat, la physiographie, l'occupation des sols, la nature des sols, la géologie et les eaux souterraines en amont de chaque tronçon de rivière dans le monde (Linke et al., 2019). Elles incluent également des estimations des débits mensuels moyens et débits annuels moyens, dérivées d'un modèle hydrologique mondial (Water-GAP 2.2 ; Müller Schmied et al., 2014). Après l'entraînement et la validation du modèle, j'ai prédit la probabilité d'intermittence pour tous les tronçons de rivière dans la base de données RiverATLAS (Linke et al., 2019), une représentation numérique du réseau fluvial mondial à haute résolution spatiale. Dans cette thèse, je considère l'intermittence comme incluant tous les phénomènes pouvant conduire à l'absence de débit, y compris l'assèchement ou le gel total du lit de la rivière, ainsi que l'arrêt de l'écoulement sans perte complète de l'eau liquide en surface (c'est-à-dire, avec une présence continue de mouilles dans le lit du cours d'eau).

Cette étude révèle que l'eau cesse de couler pendant au moins un jour par an, en moyenne interannuelle, le long de 41 % de la longueur du réseau fluvial mondial cartographié (module $\geq 0,1 \text{ m}^3 \text{ s}^{-1}$). En extrapolant aux cours d'eau avec un débit moyen supérieur à $0,01 \text{ m}^3 \text{ s}^{-1}$, j'estime que 60 % de toutes les rivières et ruisseaux dans le monde sont des RNP. En outre, l'application d'une approche d'extrapolation alternative, plus conservatrice, résulte en une limite inférieure de cette estimation à 51 %. J'estime également que pour 52 % de la population mondiale en 2020, la rivière ou le cours d'eau le plus proche est non pérenne. Ce résultat démontre que les rivières et les ruisseaux non pérennes sont naturellement la règle

plutôt que l'exception sur Terre et qu'ils sont présents dans tous les climats et biomes, et sur tous les continents.

Le jeu de données résultant de cette étude représente une base hydrographique cruciale pour la gestion des RNP ainsi que pour l'évaluation de leur rôle et destin futur dans le système terrestre. Sa haute résolution en particulier permet de relier les prévisions d'intermittence à d'autres sources de données à l'échelle des tronçons, ce qui permet d'évaluer et de suivre de manière spatialement explicite les contributions des RNP aux cycles biogéochimiques et hydrologiques, ainsi que leur rôle pour la biodiversité et les sociétés humaines.

Chapitre 3: Diversité hydrologique globale des cours d'eau non-pérennes

Le Chapitre 2 démontre que la plupart des rivières et des cours d'eau sur Terre cessent périodiquement de couler. Le Chapitre 3 va plus loin pour répondre au manque de base hydrologique mondial sur les RNP et quantifie la diversité des régimes d'intermittence en produisant la première classification mondiale de l'hydrologie des RNP.

A partir des chroniques long-termes de débits journaliers provenant d'un réseau mondial de 10740 stations de jaugeage, j'ai d'abord identifié les périodes d'enregistrements hydrométriques fiables, avec une influence humaine limitée, sur des RNP. Ces critères m'ont permis de sélectionner 690 chroniques d'une durée minimale de 15 ans pour analyser l'hydrologie des RNP. Grâce à une classification hiérarchique multivariée, j'ai ensuite délimité neuf groupes distincts de RNP en termes de durée, de fréquence, de saisonnalité et de dépendance climatique des événements d'intermittence, ainsi que de la variabilité générale des débits, aux échelles intra- et interannuel. J'ai ensuite analysé les caractéristiques environnementales associées à chaque groupe en fonction du climat, de la physiographie, de la lithologie, de l'hydrographie et de l'occupation des sols en amont des stations de jaugeage. Cette dernière analyse est une première étape vers le développement d'un modèle prédictif qui inférerait l'appartenance de tous les RNP non jaugés à l'échelle mondiale à un groupe hydrologique. À cette fin, j'ai également identifié les régions sous-représentées par les stations de jaugeage utilisées pour mon analyse afin d'aider à cibler les futures additions à cet échantillon du réseau hydrométrique mondial.

La délimitation de classes distinctes d'intermittence favorise une compréhension plus nuancée des RNP. Ces écosystèmes couvrent en effet un large spectre, des rivières quasi pérennes qui ne s'assèchent jamais en dehors de sécheresses sévères, aux écosystèmes principalement terrestres façonnés par des écoulements d'eau occasionnels et de courte durée. En quantifiant comment deux rivières peuvent cesser de couler pendant la même période mais pour des raisons différentes, cette analyse souligne aussi l'importance de dépasser une caractérisation unidimensionnelle de l'intermittence pour comprendre la diversité des façons dont elle influence la biodiversité, la biogéochimie et les services écosystémiques. Enfin, le fait que des cours d'eau appartenant au même bassin hydrographique puissent appartenir à différentes classes d'intermittence montre la pertinence de mener des analyses à l'échelle des tronçons de rivière pour mieux saisir la variabilité subrégionale dans les régimes hydrologiques.

En termes d'applications scientifiques, cette classification permettra de générer des hypothèses concernant les processus hydrologiques communs caractérisant les RNP au sein et entre les classes (Shanafield et al., 2021), et leurs conséquences sur la faune et la flore, les processus écosystémiques et les sociétés. En termes de gestion, cette classification pourrait guider l'établissement de conditions de référence adaptées à l'hydrologie des RNP dans le suivi de leur état écologique, par exemple pour la Directive Cadre sur l'Eau (DCE) de l'Union Européenne (Stubbington et al., 2018). Enfin, une telle classification hydrologique est l'un des prérequis pour déterminer et mettre en œuvre des débits écologiques à l'échelle régionale : en supposant que les classes hydrologiques représentent des cours d'eau dans lesquels les écosystèmes répondent de manière similaire aux changements hydrologiques, les relations entre l'altération anthropique des écoulements et les métriques écologiques déterminées pour un ensemble limité de rivières pourraient donc être appliquées de manière présomptive à d'autres rivières du même type (Arthington et al., 2006; Harris et al., 2000; Poff et al., 2010).

Chapitre 4: La cartographie réglementaire des cours d'eau menace l'intégrité des réseaux fluviaux

À travers le monde, les législations environnementales protègent la santé des écosystèmes d'eau douce et des populations humaines qui en dépendent en régulant les activités pouvant les impacter, imposant des permis pour certaines activités et en interdisant

d'autres. Un aspect critique de ce cadre réglementaire est la définition et la cartographie de ce qui constitue un cours d'eau aux yeux de la loi, car cela dicte l'étendue des protections légales pour les écosystèmes d'eau douce. L'insuffisance des lois environnementales pour la protection des RNP a été évoquée auparavant (Acuña et al., 2014, 2017; Doyle & Bernhardt, 2011; Larned et al., 2010; Taylor & Stokes, 2007). En utilisant la France comme étude de cas, le Chapitre 4 est la première évaluation de l'implication d'une définition juridique des cours d'eau et de son interprétation sur l'étendue réelle des cours d'eau protégés à l'échelle d'un pays.

Ce qui caractérise un cours d'eau aux yeux de la loi en France était indéfini jusqu'à récemment. Ce n'est qu'avec *l'instruction du gouvernement du 3 Juin 2015 relative à la cartographie et l'identification des cours d'eau et à leur entretien* qu'une définition est donnée et désormais inscrite dans le droit français ; ainsi, « constitue un cours d'eau, un écoulement d'eaux courantes dans un lit naturel à l'origine, alimenté par une source et présentant un débit suffisant une majeure partie de l'année » (Article L215-7-1 - Code de l'environnement). Basé sur cette définition nationale nouvellement établie, chaque département a été missionné d'élaborer et de mettre en œuvre un protocole de cartographie en collaboration avec les parties prenantes locales.

L'objectif du Chapitre 4 était donc d'évaluer les implications de la définition légale et de la cartographie décentralisée des cours d'eau au titre de la loi sur l'eau (« police de l'eau ») en France sur l'intégrité des réseaux fluviaux grâce à des analyses cartographiques. La portée de cette cartographie est considérable, puisque la loi sur l'eau régule toutes « les installations, les ouvrages, travaux et activités réalisés à des fins non domestiques entraînant des prélèvements sur les eaux superficielles ou souterraines, restitués ou non, une modification du niveau ou du mode d'écoulement des eaux, la destruction de frayères, de zones de croissance ou d'alimentation de la faune piscicole ou des déversements, écoulements, rejets ou dépôts directs ou indirects, chroniques ou épisodiques, même non polluants. »

J'ai d'abord compilé et harmonisé les cartes des cours d'eau de tous les départements de France métropolitaine, à l'exception de la région parisienne et de la Corse. Cet effort m'a permis de constituer la première carte nationale des cours d'eau au titre de la loi sur l'eau en France. Ensuite, j'ai évalué la cohérence des cartes entre les départements et au sein de ces derniers. Pour ce faire, j'ai comparé la longueur des cours d'eau cartographiés par unité

de surface (c'est-à-dire la densité de drainage) dans ces cartes à la base hydrographique BD TOPO de l'Institut national de l'information géographique et forestière (IGN) utilisée par les départements pour cartographier les cours d'eau (ONEMA & IGN, 2015). J'ai également évalué si cette densité de drainage relative était corrélée à divers facteurs socio-environnementaux, y compris les utilisations des sols anthropiques (ex : agriculture et zones artificialisées), l'irrigation et l'aridité climatique par exemple. Enfin, j'ai évalué les implications potentielles des cartes pour l'efficacité de la loi sur l'eau dans la protection de l'intégrité des réseaux fluviaux en France, en mettant l'accent sur les cours d'eau non pérennes et ceux en tête de bassin versant, ainsi que sur la connectivité du réseau.

A travers cette analyse couvrant 93% du territoire métropolitain et plus de 2 millions de tronçons, j'estime qu'environ un quart des tronçons hydrographiques précédemment cartographiés, en termes de longueur, ont été qualifiés de non-cours d'eau, et constate des variations géographiques marquées dans l'étendue des cours d'eau protégés. Les RNP représentent près de 60 % de la longueur du réseau hydrographique cartographié en France mais constituent environ 80 % des segments hydrographiques qui ont été disqualifiés en tant que non-cours d'eau (c'est-à-dire exclus de la protection au titre de la police de l'eau).

L'exclusion disproportionnée des RNP dans de nombreux départements n'est pas surprenante compte tenu de la stipulation ambiguë dans la nouvelle définition selon laquelle un cours d'eau doit avoir un débit "suffisant" à partir d'une source la plupart de l'année pour être considéré comme un cours d'eau. La définition précise également que le « l'écoulement peut ne pas être permanent compte tenu des conditions hydrologiques et géologiques locales » (Article L215-7-1 - Code de l'environnement), laissant ainsi une marge d'interprétation importante. Mon objectif n'était pas d'évaluer quels segments je jugerai être des cours d'eau ou non-cours d'eau, ou de critiquer des cartes départementales spécifiques. Néanmoins, compte tenu des différences cartographiques entre les départements et de la variabilité géographique des corrélats identifiés, il est probable que de nombreux ruisseaux écologiquement importants et sensibles manquent désormais de protection en vertu de la loi sur l'eau. Enfin, je démontre que les cadres réglementaires dans d'autres pays tels que les États-Unis ou l'Australie présentent des biais similaires (Doyle & Bernhardt, 2011; Greenhill et al., 2024; Taylor & Stokes, 2007), ce qui rend les réseaux fluviaux et les populations humaines qui en dépendent vulnérables à l'échelle mondiale. Ces

résultats soulignent la nécessité d'une meilleure gouvernance des réseaux fluviaux qui inclut la protection des têtes de bassins versants et des RNP.

Chapitre 5: Une approche métasystémique pour la conception des débits écologiques.

Les débits environnementaux (*e-flows* en anglais) ont émergé comme un outil central de gestion durable des ressources en eau pour contrer le déclin de la biodiversité des eaux douces et des services écosystémiques associés (Horne et al., 2017; Tickner et al., 2020). Les *e-flows* sont définis comme « la quantité, la saisonnalité et la qualité des débits nécessaires à la durabilité des écosystèmes d'eau douce et estuariens ainsi qu'aux besoins et au bien-être des hommes qui dépendent de ces écosystèmes » (Arthington et al., 2018). Malgré leur importance, l'efficacité des efforts actuels pour concevoir et mettre en œuvre des *e-flows* restent souvent limitée par une compréhension insuffisante des processus écologiques à grande échelle dans les réseaux fluviaux (e.g., Brooks et al., 2011; Chester et al., 2014).

Historiquement, les *e-flows* se sont concentrés sur le maintien de débits minimums dans les rivières en aval des barrages (Poff et al., 2017). Cependant, une transition vers des normes d'*e-flows* régionales intégrant plusieurs aspects du régime hydrologique a été observée récemment (Poff et al., 2010). Malgré cela, les planifications régionales des *e-flows* continuent souvent de se concentrer sur les réponses des espèces au régime local des débits. Cette approche ignore les preuves croissantes selon lesquelles les réseaux fluviaux sont des métasystèmes dans lesquels la variabilité de la biodiversité et du fonctionnement des écosystèmes à l'échelle du paysage résulte de l'interaction des processus à l'échelle régionale et locale (Cid et al., 2022; Gounand et al., 2018; Poff, 2018).

La structure « régionale » du réseau fluvial régule les flux de matériaux, d'énergie et d'organismes parmi ses sous-composantes (par exemple, les sites, les patchs d'habitat). Chaque sous-composante est à son tour caractérisée par des dynamiques locales gouvernées par ses conditions abiotiques (débit, température, etc.) et les interactions biotiques. Les processus écologiques à l'échelle locale (par exemple, au sein d'un tronçon de rivière) sont donc influencés par les processus écologiques opérant à l'échelle régionale (par exemple, à travers de multiples tronçons dans un réseau de rivières) et vice versa, de sorte

que les deux échelles nécessitent une considération simultanée pour comprendre les métasystèmes.

Ces dynamiques existent à travers tous les niveaux d'organisation biologique, des populations aux écosystèmes. Ainsi, une métapopulation se compose de multiples populations d'une seule espèce connectées par la dispersion (Hanski, 1998). De telles populations spatialement structurées peuvent former des métacommunautés, où un ensemble de communautés locales sont connectées par la dispersion de plusieurs espèces potentiellement en interaction (Leibold et al., 2004). Enfin, l'énergie et les matériaux, tels que la matière inorganique et organique ou les nutriments, se déplacent également à travers les métaécosystèmes dans lesquels les patches présentent des fonctions écosystémiques hétérogènes (Gounand et al., 2018). L'interaction des processus locaux et régionaux est particulièrement déterminante pour la structure écologique et le fonctionnement des RNP présentant une forte variabilité spatiotemporelle des conditions hydrologiques. Cette variabilité crée une mosaïque dynamique d'habitats où la dispersion et les interactions biotiques régissent l'abondance et la distribution des espèces (Cid et al., 2020; Datry et al., 2016; Sarremejane et al., 2017).

L'adoption d'une perspective métasystémique qui considérerait les liens entre les débits des rivières et une large gamme de processus écologiques à différentes échelles spatiales pourrait améliorer la gestion, la conservation et la restauration des réseaux fluviaux. Cependant, il n'existe pas de cadre pour guider la conception des e-flows à partir de cette perspective et combler l'écart actuel entre la théorie et la pratique. Dans cet article, je propose d'incorporer les concepts et outils scientifiques en rapport aux métasystèmes dans la mise en œuvre des e-flows. Je démontre comment les processus de métasystèmes fluviaux influencent les réponses des espèces à l'altération des débits. Grâce à ces fondements conceptuels, je fournis ensuite un cadre opérationnel de gestion adaptative pour la conception, la mise en œuvre et le suivi des programmes d'e-flows visant à conserver ou à restaurer les dynamiques métasystémiques, en mettant l'accent sur les échelles de métapopulation et métacommunauté. J'illustre mes propos en prenant pour exemple le bassin du fleuve Murray-Darling en Australie, où le programme de gestion des e-flows s'approche le plus d'une gestion métasystémique. Par exemple, les débits sont couramment modulés pour promouvoir la connectivité et la dispersion des espèces de poissons,

notamment pour permettre l'accès à des refuges pendant les périodes d'étiage, pour submerger les obstacles et ainsi permettre leur franchissement, pour déclencher les mouvements migratoires, pour permettre la recolonisation des tronçons de rivière à partir de tronçons voisins après une perturbation locale, pour faciliter le flux génétique entre les sous-populations par le biais de dispersion à longue distance et pour reconnecter les îlots et les plaines inondables lors de crues importantes (Commonwealth Environmental Water Office, 2022; Gawne et al., 2018).

Dans ce chapitre, les recommandations sont nuancées en réfléchissant à quelles mesures peuvent être plus réalisables dans différents contextes réglementaires, en lien avec le Chapitre 4, et peuvent être adaptées même dans les réseaux fluviaux où le manque de données est limitant. En synthétisant les connaissances actuelles en écologie des métasystèmes et en s'appuyant sur un ensemble étendu d'études de cas, ce chapitre crée un point de rencontre entre les scientifiques et les gestionnaires, et à travers les disciplines, pour améliorer la gestion des RNP.

Chapitre 6: Discussion

Un modèle est une abstraction de la réalité, une manière de saisir la complexité inextricable du monde en se concentrant sur les patrons et les processus essentiels qui sont pertinents pour notre objectif. En écologie et en science des rivières, les modèles conceptuels cherchent la généralité, guident la formulation d'hypothèses et permettent de faire des prédictions, façonnant ainsi notre compréhension collective et la gestion des écosystèmes fluviaux. Cependant, dans le processus de simplification de la réalité pour gagner en compréhension, certains éléments importants peuvent être erronément considérés comme anecdotiques. L'intermittence, et les rivières non pérennes par extension, sont l'un de ces éléments qui ont historiquement été omis des modèles conceptuels dominants.

Chaque chapitre de cette thèse remet en cause les modèles conceptuels encadrant la science, les politiques publiques et la gestion des rivières, qui étaient adaptés aux tronçons pérennes considérés de manière isolée du reste du réseau fluvial. Le Chapitre 2 a démontré qu'il est impossible de faire abstraction des RNP dans notre modèle des écosystèmes fluviaux car ils sont la règle plutôt que l'exception sur Terre. Le Chapitre 3 nuance notre modèle des RNP en tant qu'écosystèmes se situant sur un continuum entre les

environnements aquatiques et terrestres. Le Chapitre 4 remet en question le modèle sous-jacent à la définition légale des cours d'eau dans les cadres réglementaires, qui établit une ligne artificielle entre tronçons pérennes et non-pérennes et néglige la connectivité des réseaux fluviaux. Le Chapitre 5 remet également en question le modèle conceptuel des rivières sous-tendant les programmes d'e-flows, soutenant plutôt une perspective à l'échelle du réseau qui prend en compte divers processus écologiques et des mesures de gestion complémentaires.

Cette thèse a contribué à un changement de paradigme en cours. Plusieurs programmes de recherche coordonnés à grande échelle sur les RNP ont été lancés juste avant le début de ma thèse en septembre 2020. Ces programmes mobilisent des équipes multidisciplinaires dans plusieurs pays pour collecter, analyser et modéliser des données dans différents réseaux fluviaux dominés par les RNP. Ils visent à étudier la biodiversité, les processus écologiques et les services écosystémiques des RNP. En outre, des initiatives de synthèse conceptuelle et analytique sur les RNP, telles que le Dry Rivers Research Coordination Network dont j'ai fait partie, ont permis de réunir des chercheur.euses de divers domaines et continents pour promouvoir la reconnaissance et la gestion appropriée de ces rivières.

Cela dit, à mesure que la prévalence et l'importance des RNP sont de plus en plus reconnues, une intégration est désormais nécessaire pour s'éloigner d'un modèle dualiste des écosystèmes pérennes versus non pérennes. Une vision intégrée des réseaux fluviaux implique d'étudier et de gérer l'ensemble des tronçons, de leurs plaines d'inondation et du bassin versant comme un continuum aquatique-terrestre dynamiquement interconnecté, un méta-écosystème avec des degrés variables d'inondation et de flux d'eau (D. C. Allen et al., 2020; Datry et al., 2023; O'Sullivan et al., 2022; Stegen et al., 2024; Wohl, 2015). De plus, cela implique une considération des connexions parmi les composantes d'un réseau fluvial comme étant tout aussi importantes pour son fonctionnement et sa résilience que les composantes elles-mêmes (Datry et al., 2023). Cette perspective n'est pas entièrement nouvelle ; la connectivité et le dynamisme hydrologique des réseaux fluviaux faisaient déjà partie du concept de *flood pulse* (Junk, 1989; Tockner et al., 2000) et de la perspective en 4 dimensions de Ward (Ward, 1989), entre autres. Elle est également au centre de l'écologie des métacommunautés et des métaécosystèmes modernes (Cid et al., 2022; Sarremejane et al., 2024). Cependant, ce développement récent intègre plus pleinement les assèchements

par rapport aux modèles précédents qui les considéraient largement inertes, sur le plan écologique et biogéochimique (Datry et al., 2023).

Une perspective intégrée du réseau encourage les scientifiques et les gestionnaires à penser aux écosystèmes à travers les processus et les échelles les plus pertinents pour leur application plutôt que par des catégories. Par exemple, des flux d'énergie réciproques importants relient les rivières et leur zone riveraine, avec des grandes variations temporelles et spatiales entre les phases humides et sèches, brouillant la frontière entre ces milieux d'habitude étudiés et gérés séparément (D. C. Allen et al., 2024; Baxter et al., 2005). Les Chapitres 4 et 5 de ma thèse ont été intentionnellement rédigés pour mettre en avant cette perspective intégrée du réseau. Ils sont étayés par des travaux antérieurs sur la connectivité du réseau fluvial (Fritz et al., 2018; Leibowitz et al., 2018) pour le premier et sur la théorie des métacommunautés (Leibold & Chase, 2017) pour le second, tout en mettant en évidence la spécificité et la vulnérabilité des RNP. Le Chapitre 3, qui catégorise actuellement les RNP pour comprendre leur diversité hydrologique, sera élargi pour communiquer et promouvoir l'étude représentative et la gestion de l'ensemble de la diversité des régimes de débit des cours d'eau mondiaux - à la fois pérennes et non pérennes.

En conclusion, cette thèse a contribué à augmenter la visibilité des RNP, à la fois littéralement et conceptuellement. Littéralement, en créant une base cartographique pour leur étude et leur gestion, et en mettant concrètement en lumière leur exclusion des cartographies réglementaires. Conceptuellement, en attirant l'attention sur leur prévalence, leur distribution et leur diversité, et en créant un cadre opérationnel pour atténuer plus efficacement l'effet délétère des altérations anthropiques du débit sur ces écosystèmes uniques. Une telle reconnaissance devrait, j'espère, déclencher des efforts pour les étudier et les gérer adéquatement, et pour pallier leur exclusion des cadres réglementaires.

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Preface

Context

This thesis results from a PhD in cotutelle between Université Claude Bernard Lyon 1 (UCBL) in Lyon (France) and McGill University in Montreal (Canada) from September 2020 to April 2024. During this time, I was jointly supervised by Dr. Bernhard Lehner (McGill University) and Dr. Thibault Datry (National Research Institute for Agriculture, Food and Environment – INRAE). I was primarily registered at McGill University from 09/20 to 01/22 and from 09/23 to 01/23 whereas I was hosted at INRAE from 01/22 to 09/23 and from 01/23 to 04/23. This thesis was written to meet the requirements of both UCBL and McGill University in terms of formatting and content, to the extent that they were not mutually exclusive.

Two of my chapters were developed as part of collaborative research programs:

- Chapter 2 was conceived as part of the European H2020 DRYvER project (Securing biodiversity, functional integrity and ecosystem services in DRYing riVER networks; <https://www.dryver.eu/>). DRYvER mobilized multidisciplinary teams from 11 countries in 2020-2025 to collect, analyse and model data in nine river networks with a high prevalence of non-perennial reaches. Its goal is to investigate the impacts of climate change on the biodiversity, ecosystem functions and ecosystem services of non-perennial rivers and streams.
- Chapter 5 was conceived as part of the Dry Rivers Research Coordination Network (RCN) funded by the National Science Foundation, a synthesis program on non-perennial rivers formed by over 40 ecologists, hydrologists and biogeochemists.

My contributions and those of my co-authors are described in the CRediT (Contributor Roles Taxonomy) section below for each chapter of the thesis. For more information on CRediT roles, see <https://credit.niso.org/>.

CRediT (Contributor Roles Taxonomy)

Chapter 2: Global prevalence of non-perennial rivers and streams

- Conceptualization: K. Tockner, T. Datry, B. Lehner, **M.L.M.**
- Methodology: **M.L.M.**, B. Lehner, T. Snelder, N. Lamouroux
- Data curation: **M.L.M.**, B. Lehner, Caitlin Watt, C. Cockburn, H. Pella
- Software, validation, visualization: **M.L.M.**
- Formal analysis: **M.L.M.**, C. Cockburn
- Writing - original draft: **M.L.M.** with contributions from T. Datry & B. Lehner
- Writing - review and editing: **all authors**
- Project administration: **M.L.M.**
- Supervision: B. Lehner, T. Datry

Chapter 3: Global hydrological diversity of non-perennial rivers and streams

- Conceptualization: **M.L.M.**, T. Datry, B. Lehner
- Methodology: **M.L.M.**
- Data curation: **M.L.M.**
- Software, validation, visualization: **M.L.M.**
- Formal analysis: **M.L.M.**
- Writing - original draft: **M.L.M.**
- Writing - review and editing: **all authors**
- Project administration: **M.L.M.**
- Supervision: B. Lehner, T. Datry

Chapter 4: Inconsistent regulatory mapping quietly threatens rivers and streams

- Conceptualization: **M.L.M.**, T. Datry, H. Pella
- Methodology: **M.L.M.**, H. Pella
- Data curation: **M.L.M.**, H. Pella
- Software, validation, visualization: **M.L.M.**
- Formal analysis: **M.L.M.**
- Writing - original draft: **M.L.M.**
- Writing - review and editing: **M.L.M.**, T. Datry
- Project administration: **M.L.M.**
- Supervision: T. Datry

Chapter 5: A metasytem approach to designing environmental flows

- Conceptualization: led by **M.L.M.** with primary contributions from T. Datry, J. D. Olden, and J. Tonkin, and secondary contributions from all authors
- Methodology: **M.L.M.**
- Investigation: led by **M.L.M.** with contributions from J. S. Rogosch, M. H. Busch, C. J. Little, S. Yu, and R. H. Walker
- Software, formal analysis, validation, visualization: **M.L.M.**
- Writing - original draft: **M.L.M.** with contributions from M. Shanafield, M. H. Busch, C. J. Lytle, and S. Yu.
- Writing - review and editing: **all authors**
- Copy-editing: R. Stubbington
- Project administration: **M.L.M.**
- Supervision: Thibault Datry

Positionality statement

The following statement is an acknowledgement of my epistemological position in writing this thesis. Although positionality statements are near-inexistent in hydrology and ecology, they are commonplace in geography. I believe that they are relevant to all disciplines that deal with socio-ecological systems. In writing this thesis, I primarily tried to advance scientific scholarship while also placing myself as what Pielke (2007) defines as an “honest broker”. When a scientist acts as an honest broker, they help policymakers make informed decisions based on the best available scientific knowledge and a clear understanding of the policy implication. They act as an intermediary between the scientific community and policy makers, and facilitate a transparent and impartial discussion of scientific information by acknowledging uncertainties and different perspectives. In other words, I do not seek knowledge for its own sake, yet I am not trying to influence what management decisions are made either. Ultimately, my objective is to allow trade-offs among management options to be acknowledged and to support evidence-based decision-making. Nonetheless, I acknowledge the potential influence of my personal ecocentric philosophy, which emphasizes the intrinsic value of all living things and their environment, and considers humans as integral to ecosystems. I also acknowledge my position as a Western scientist working within a Eurocentric knowledge system. As such, I enjoin those who may use these findings in a management context to do so in partnership with all concerned. In particular, I advise all who apply knowledge from this thesis to be cautious in trying to “integrate” Indigenous knowledges within a Western paradigm. I instead encourage them to seek “pairing”, or “adopting a Two-Eyed Seeing approach” (Reid et al., 2020), a conceptual framework developed by Mi’kmaw Elder Albert Marshall in 2004 for unifying knowledge systems. It is described as “learning to see from one eye with the strengths of Indigenous knowledges and ways of knowing, and from the other eye with the strengths of Western knowledges and ways of knowing, and to use both these eyes together, for the benefit of all” (Bartlett et al., 2012).

Bartlett, C., Marshall, M., & Marshall, A. (2012). Two-Eyed Seeing and other lessons learned within a co-learning journey of bringing together indigenous and mainstream knowledges and ways of knowing. *Journal of Environmental Studies and Sciences*, 2(4), 331–340.

Pielke, R. A. (2007). *The Honest Broker: Making Sense of Science in Policy and Politics*. Cambridge University Press.

Reid, A. J., Eckert, L. E., Lane, J.-F., Young, N., Hinch, S. G., Darimont, C. T., Cooke, S. J., Ban, N. C., & Marshall, A. (2021). “Two-Eyed Seeing”: An Indigenous framework to transform fisheries research and management. *Fish and Fisheries*, 22(2), 243–261.

Open science: data, code and manuscript availability

All source code associated with this thesis is free and available for re-use under the GNU General Public License v3.0. All data, when shareable, are available and shared under a Creative Commons Attribution 4.0 International License (CC-BY-4.0 License). All manuscripts are (or will be) available in their accepted format on my HAL repository:

<http://cv.hal.science/mathis-loic-messenger>

Chapter 2

Research compendium: <https://messamat.github.io/globalRmap/>

Data repository: <https://doi.org/10.6084/m9.figshare.14633022>

Geospatial analysis - python code: https://github.com/messamat/globalRmap_py

Data wrangling and machine learning - R code: <https://github.com/messamat/globalRmap>

Pre-processing code: https://github.com/messamat/globalRmap_HydroATLAS_py

Chapitre 3

Geospatial analysis – python code: https://github.com/messamat/gloric_hydro_v2_py

Data wrangling and statistics – R code: https://github.com/messamat/gloric_hydro_v2_R

Custom Shiny app *hydrocleanR*: <https://github.com/messamat/hydrocleanR>

Data will be shared once project is finalized.

Chapitre 4

Geospatial analysis – python code: https://github.com/messamat/cartographie_cours_deau

Data wrangling & statistics – R code: https://github.com/messamat/cartographie_cours_deau_R

Data will be shared once project is published.

Chapitre 5

Simulation model: https://github.com/messamat/metacom_EF_sim

No associated data

Prerequisites: Most GIS (python) analyses in this thesis require an ESRI ArcGIS license including the Spatial Analyst extension, which itself requires a Windows OS.

The R code is most compatible with R ≥ 4.0 and incompatible with versions prior to version 3.6.0.

R Workflow: all projects are setup with a [drake](#) or [targets workflow](#), ensuring reproducibility.

Dependency management: the R library of all projects is managed by [renv](#). This makes sure that the exact same package versions are used when recreating the project. When calling `renv::restore()`, all required packages will be installed with their specific version.

For any inquiries on the code or data, or for a publisher-formatted version of the articles, please email mathis.messenger@mail.mcgill.ca.

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- 2020/2021: Tomlinson Doctoral Fellowship (\$35,000) from McGill University
- 2021/2024: Vanier Canada Graduate Scholarship (\$150,000) from the Natural Science and Engineering Research Council of Canada (NSERC)
- 2021/2023: Fellowship (€50,000) from the H₂O'Lyon Doctoral School

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2023 McGill University · Geography graduate stimulus travel initiative
2022 McGill University · GREAT Travel Award
McGill University · International Graduate Mobility Award
2021 McGill University · Rathlyn Fellowship in Geographic Information Systems
McGill University · GREAT Travel Award
2020 Mackenzie King Scholarship Trust · Mackenzie King Open Scholarship – declined
McGill University · Delta Upsilon Scholarship
McGill University · Graduate Excellence Award

Publications during thesis

Included in this manuscript

Chapter 2:

Messenger, M. L., Lehner, B., Cockburn, C., Lamouroux, N., Pella, H., Snelder, T., Tockner, K., Trautmann, T., Watt, C., & Datry, T. (2021). Global prevalence of non-perennial rivers and streams. *Nature*, 594(7863), 391–397. <https://doi.org/10.1038/s41586-021-03565-5>

Chapter 4:

Messenger, M. L., Pella, H., & Datry, T. (*in review*). Inconsistent regulatory mapping quietly threatens rivers and streams. *Environmental Science & Technology*.

Chapter 5:

Messenger, M. L., Olden, J. D., Tonkin, J. D., Stubbington, R., Rogosch, J. S., Busch, M. H., Little, C. J., Walters, A. W., Atkinson, C. L., Shanafield, M., Yu, S., Boersma, K. S., Lytle, D. A., Walker, R. H., Burrows, R. M., & Datry, T. (2023). A metasystem approach to designing environmental flows. *BioScience*, 73(9), 643–662. <https://doi.org/10.1093/biosci/biad067>

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Peer-reviewed articles

In review

Price, A. N., Zimmer, M. A., Bergstrom, A. J., Krabbenhoft, C. A., Zipper, S., Busch, M. H., Dodds, W. K., Datry, T., Walters, A. W., Rogosch, J. S., Stubbington, R., Walker, R. H., Stegen, J. C., Kaiser, K. E., **Messenger, M. L.**, Olden, J. D., Godsey, S., Shanafield, M., Lytle, D. A., Allen, G. H., Mims, M. C., Tonkin, J. D., Bogan, M., Burrows, R. M., Hammond, J., Boersma, K. S., DelVecchia, A. G., Allen, D. C., Yu, S., & Ward, A. (*in review*). Biogeochemical and community ecology responses to the wetting of non-perennial streams. *Nature Water*.

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Datry, T., Truchy, A., Olden, J. D., Busch, M. H., Stubbington, R., Dodds, W. K., Zipper, S., Yu, S., **Messenger, M. L.**, Tonkin, J. D., Kaiser, K. E., Hammond, J. C., Moody, E. K., Burrows, R. M., Sarremejane, R., DelVecchia, A. G., Fork, M. L., Little, C. J., Walker, R. H., ... Allen, D. (2023). Causes, Responses, and Implications of Anthropogenic versus Natural Flow Intermittence in River Networks. *BioScience*, 73(1), 9–22.
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Presentations, panels, workshops

2023

- Symposium for European Freshwater Science (SEFS) 13 · Newcastle, UK · invited session organizer and presentation
- Global Conference on Biodiversity and Monitoring (GEO-BON) · Montreal, QC, Canada · presentation
- Dry Rivers Research Coordination Network (RCN) · Ichauway, GA, USA · Fall workshop participant

2022

- Virtual Summit: Incorporating Data Science and Open Science in Aquatic Research (DSOS) · online · invited panelist
- JASM (Joint Aquatic Sciences Meeting) · Grand Rapids, MI, USA · session organizer and presentation
- Zone Atelier Bassin du Rhône (ZABR) scientific seminar · Lyon, France · presentation and workshop participant
- Dry Rivers Research Coordination Network (RCN) · Flathead Lake, MT, USA · Fall workshop participant
- Dry Rivers Research Coordination Network (RCN) · online · Winter virtual workshop participant
- INRAE Lyon-Villeurbanne Journée des thèses · Lyon, France · presentation
- H2O'Lyon 4th Annual Meeting · Lyon, France · poster
- Institute of Physical Geography at Goethe University Frankfurt · online · invited 1h-seminar
- Trent University Temporary Rivers Meeting · Nottingham, UK · invited presentation

2021

- AGU (American Geophysical Union) · online · invited presentation
- H2O'Lyon 3rd Annual Meeting · Lyon, France · invited presentation
- Réseaux Rivières TV, Graie, EUR H2O'Lyon live discussion · online · invited panelist
- FMA (Floodplain Managers Association) annual meeting · online · invited panelist
- INRAE Lyon-Villeurbanne Journée des thèses · Lyon, France · presentation
- CGU (Canadian Geophysical Union) annual meeting · online · presentation
- ASLO (Association for the Sciences of Limnology and Oceanography) aquatic sciences meeting · online · presentation
- SFS (Society for Freshwater Science) annual meeting · online · presentation + discussion moderator
- McGill University Three Minute Thesis competition · online · presentation

2020

- H2O'Lyon Annual Meeting · Lyon, France · poster
- FAO (Food and Agriculture Organization) expert workshop on environmental flows and SDGs · online · invited expert

Peer reviews

Nature (2), Nature Sustainability (1), Nature Communications (3), Geophysical Research Letters (1), Earth System Science and Data (1), Functional Ecology (1), Science of the Total Environment (1), Water Research (1), Canadian Water Resources Journal (1), Bioinvasions record (2), Northwest Science (1), Anthropocene (1)



Chapter 1

Introduction

1.1. Background

1.1.1. Global significance of river ecosystems

Rivers and streams cover only 0.15% of our planet and contain a mere 0.005% of its freshwater stock (**Figure 1.1**; G. H. Allen & Pavelsky, 2018; Oki & Kanae, 2006), yet running water ecosystems are essential to much of life and play a disproportionate role in the Earth system. Together with lakes and wetlands, rivers and streams support one-third of vertebrate species and 10% of all known animal species (Balian et al., 2008). This disproportionate level of species richness is associated with high levels of endemism (Strayer, 2006; Tedesco et al., 2012). Most riverine species are distributed over narrow geographic ranges, sometimes in a single drainage basin and exceptionally in a single waterhole (C. H. Martin et al., 2016). Rivers also determine biodiversity patterns beyond the freshwater realm by shaping continents over millennia, by forming ecological gradients along their margin, and as dynamic barriers to dispersal (Harcourt & Wood, 2012; C. He et al., 2024; Musher et al., 2022; Naka et al., 2022).

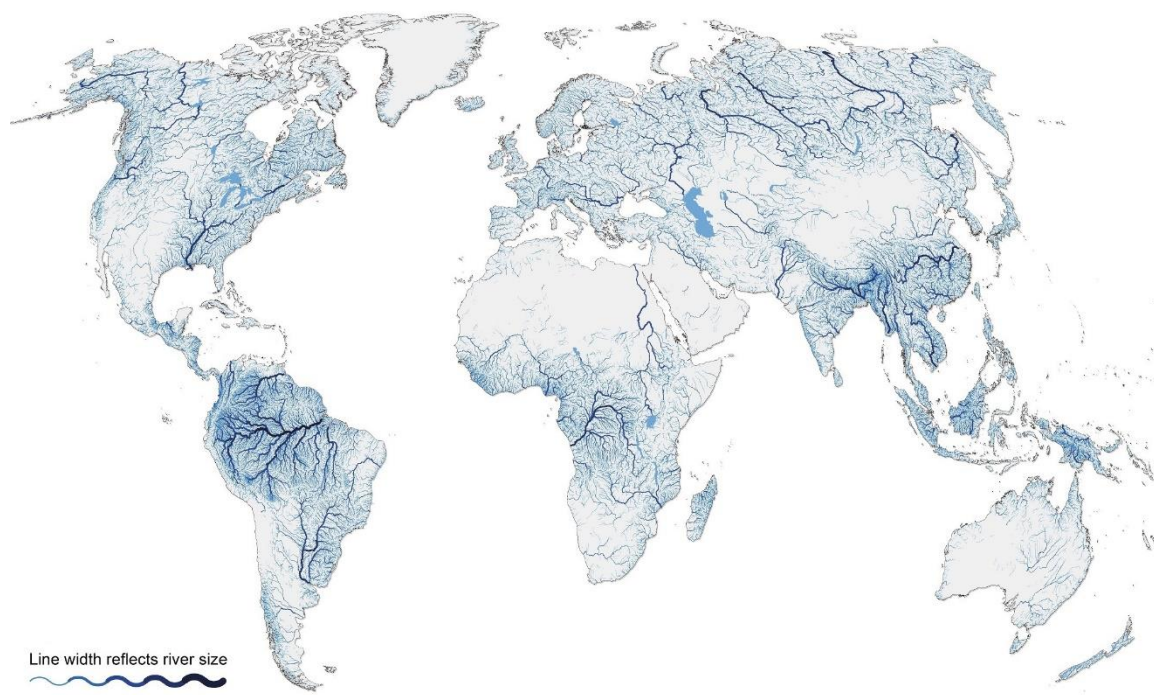


Figure 1.1. Global distribution of rivers.

Advances in remote sensing and mapping technology at the beginning of the 21st century have accelerated the study of river ecosystems at the global scale. Data from Linke et al. (2019) and Messenger et al. (2016).

Notwithstanding their small surface area, river and stream channels cumulatively span millions of kilometers (Linke et al., 2019). River networks form the largest interface between the land, ocean, and atmosphere, critically contributing to global biogeochemical cycles

(Aufdenkampe et al., 2011; Battin et al., 2023). By eroding, transporting, and depositing sediments and nutrients across the landscape, rivers naturally transfer over 2×10^{13} kg of sediment every year from continents to the coastal ocean (Syvitski et al., 2022). And while long thought to passively transport carbon and other bioactive elements from the terrestrial to the marine environment like a “pipe”, running water ecosystems are now considered biogeochemical reactors that not only bury N, P, S, C and other elements into sediment but also metabolize them (Aufdenkampe et al., 2011; Cole et al., 2007; Fowler et al., 2013; Raymond et al., 2013; Xia et al., 2018). In fact, rivers are among the most heterotrophic ecosystems on Earth (Battin et al., 2023; Gounand, Little, et al., 2018) and emit an estimated 2×10^{12} kg C yr⁻¹ as CO₂ to the atmosphere (Liu et al., 2022; Raymond et al., 2013).

Civilizations have evolved from and are still fundamentally dependent on the river networks that dissect continents (Anderson et al., 2019; WWAP, 2015). Humans have lived along rivers for so long that global settlements follow fractal patterns congruent with those of river networks (Fang et al., 2018; Kummu et al., 2011). This intertwining of societies and rivers stems from the myriad ways that running waters and their biodiversity promote human well-being through material, non-material, and regulating contributions (**Figure 1.2**; (IPBES, 2019; Lynch, Cooke, et al., 2023). Proximity to rivers affords people water for human consumption, irrigation, industry and hydroelectricity; sediment for building materials, glass and electronics; navigation pathways for movement and trade; and nutrients for floodplain agriculture. Sand and gravel, for example, are globally the most extracted group of materials in terms of volume, exceeding fossil fuels and biomass, and largely come from river channels (Bendixen et al., 2019; Koehnken et al., 2020). Riverine ecosystems also provide food, genetic resources, and recreational opportunities; they regulate climate, nutrient cycling and water quality, and figure prominently in cultures around the world (Lynch, Cooke, et al., 2023; Wantzen, 2022).

Material		Production/harvest of food/nutritional resources from wild, managed, or domesticated organisms. Includes a wide range of finfish, invertebrates, waterbirds, freshwater algae, and more. Extends beyond nutritional security support (and associated health and wellness benefits) to include livelihood support from those that are involved with production, harvest, processing, preparation or other aspects of freshwater food production systems.
		Production of materials derived from organisms in cultivated or wild ecosystems, for construction, clothing, printing, and ornamental purposes. Live organisms being directly used for decoration (e.g., fish or turtles in households and public spaces, aquatic plants) and company (e.g., pets).
		Production of materials derived from organisms used for medicinal, veterinary, and pharmacological (e.g., poisonous, psychoactive) purposes. Production of genes and genetic information used for plant and animal breeding and biotechnology.
Non-material		Provision, by freshwater ecosystems, habitats, or organisms, of opportunities for physically and psychologically beneficial activities, healing, relaxation, recreation, leisure, tourism, and aesthetic enjoyment based on the close contact with nature (e.g., swimming, fishing, birdwatching, snorkeling).
		Water, freshwater ecosystems, habitats or organisms being the basis for religious, spiritual, and social-cohesion experiences. Provisioning of opportunities by nature for people to develop a sense of place, belonging, rootedness, or connectedness, associated and servings as basis for narratives, rituals, and celebrations provided by water, freshwater ecosystems, habitats, species, or organisms.
		Provision, by freshwater ecosystems, habitats, or organisms, of opportunities for the development of the capabilities that allow humans to prosper through education, acquisition of knowledge and development of skills for well-being, information, and inspiration for art and technological design (e.g., biomimicry).
Regulating		Climate regulation by ecosystems (including regulation of global warming). Positive or negative effects on emissions of greenhouse gases (e.g., biological carbon storage and sequestration; methane emissions from wetlands).
		Regulation, by ecosystems, of the quantity, location, and timing of the flow of surface and groundwater used for drinking, irrigation, transport, hydropower, and as the support of non-material contributions. Amelioration, by ecosystems, of the impacts on humans or their infrastructure caused by floods, drought, and other geophysical hazards.
		Regulation – through filtration of particles, pathogens, excess nutrients, and other chemicals – by freshwater ecosystems or particular organisms of the quality of water used directly (e.g., drinking, swimming) or indirectly (e.g., aquatic foods, irrigated food and fiber crops, freshwater habitats of heritage value). Regulation, by organisms, of pests, pathogens, predators, or competitors that affect humans (materially and nonmaterially), or freshwater plants or animals of importance for humans. Also the direct detrimental effect of organisms on humans or their plants, animals, or infrastructure.

Figure 1.2. People need freshwater biodiversity: ecosystem services dependent on freshwater biodiversity by categories of ‘Nature's Contributions to People (NCP)’.

Reproduced from Lynch, Cooke, et al. (2023).

1.1.2. River ecosystem structure and functioning

How can rivers and streams so disproportionately contribute to global biodiversity, biogeochemical cycles, and human well-being? A watercourse could simply be defined as the unidirectional movement of water in response to gravity along the slope of a linear topographic depression on the land surface (Lehner, 2024). By extension, a lotic ecosystem (i.e., of flowing water, as opposed to *lentic* ecosystems of standing water) would encompass this physical template and the associated biotic community. Yet such a definition is reductive. Rivers are dynamic hierarchical systems operating in four dimensions (J. V. Ward, 1989). At the reach scale, most watercourses are spatially connected in three dimensions: longitudinally with upstream and downstream reaches; laterally with adjacent channels, banks, and the floodplain; and vertically with groundwater and the atmosphere. The fourth, temporal dimension also dominates processes in flowing waters. Discharge, for example, the amount of water flowing through a given channel cross-section per unit time, can vary across multiple orders of magnitude over short periods and impacts ecological processes on the short and long-term (Poff et al., 1997). Beyond the reach scale, rivers form dendritic networks that expand and contract over time (Gao et al., 2021; Godsey & Kirchner, 2014; Prancevic & Kirchner, 2019). River channels receive large amounts of material from their surrounding landscape such that water flow also drives the transport and cycling of sediments, nutrients, and energy downstream, fueling lotic food webs (Ensign & Doyle, 2006; Ripl, 2003; Sponseller et al., 2013; Vannote et al., 1980). This network structure and its four-way connectedness together create a mosaic of habitats, govern organism movements and biotic community structures, and drive the biogeochemistry of rivers (Covino, 2017; Erős & Lowe, 2019; Tonkin, Heino, et al., 2018; J. V. Ward, 1989).

Running waters fundamentally differ from marine, terrestrial, and lentic ecosystems. For example, even if variations in temperature are buffered by the thermal inertia of water on a daily basis, the physico-chemistry of riverine waters greatly fluctuates in space and time compared to marine or terrestrial media. Aquatic primary producers differ from their terrestrial counterparts in terms of size (e.g., smaller, unicellular) and structure, with higher growth rates and nutritional quality than land plants (Shurin et al., 2005). Primarily lotic ecosystems also differ from primarily lentic ecosystems in their unidirectional flow of water, which results in short water residence times and characteristic habitat geometry, hydraulic forces exerted on organisms, and longitudinal gradients in conditions (Lehner, 2024;

Vannote et al., 1980). This physical template is reflected in the form, function, and diversity of organisms that inhabit river ecosystems.

River systems are at once connected and isolated, dynamic and long-lived. Despite interpenetrating all terrestrial ecosystems, river channels and their floodplains form confined environments limiting the dispersal of obligate aquatic species within their branches, making river drainage basins a specific island-like system, like “fish archipelagoes” (Rosenzweig, 1995; Tedesco et al., 2012). Other species vary in their mode (e.g., swimming, crawling, flying) and strength of dispersal, which in turn determines the respective influence the river network and surrounding basin structure on their distribution (**Figure 1.3**; Cañedo-Argüelles et al., 2015; Tonkin, Altermatt, et al., 2018).

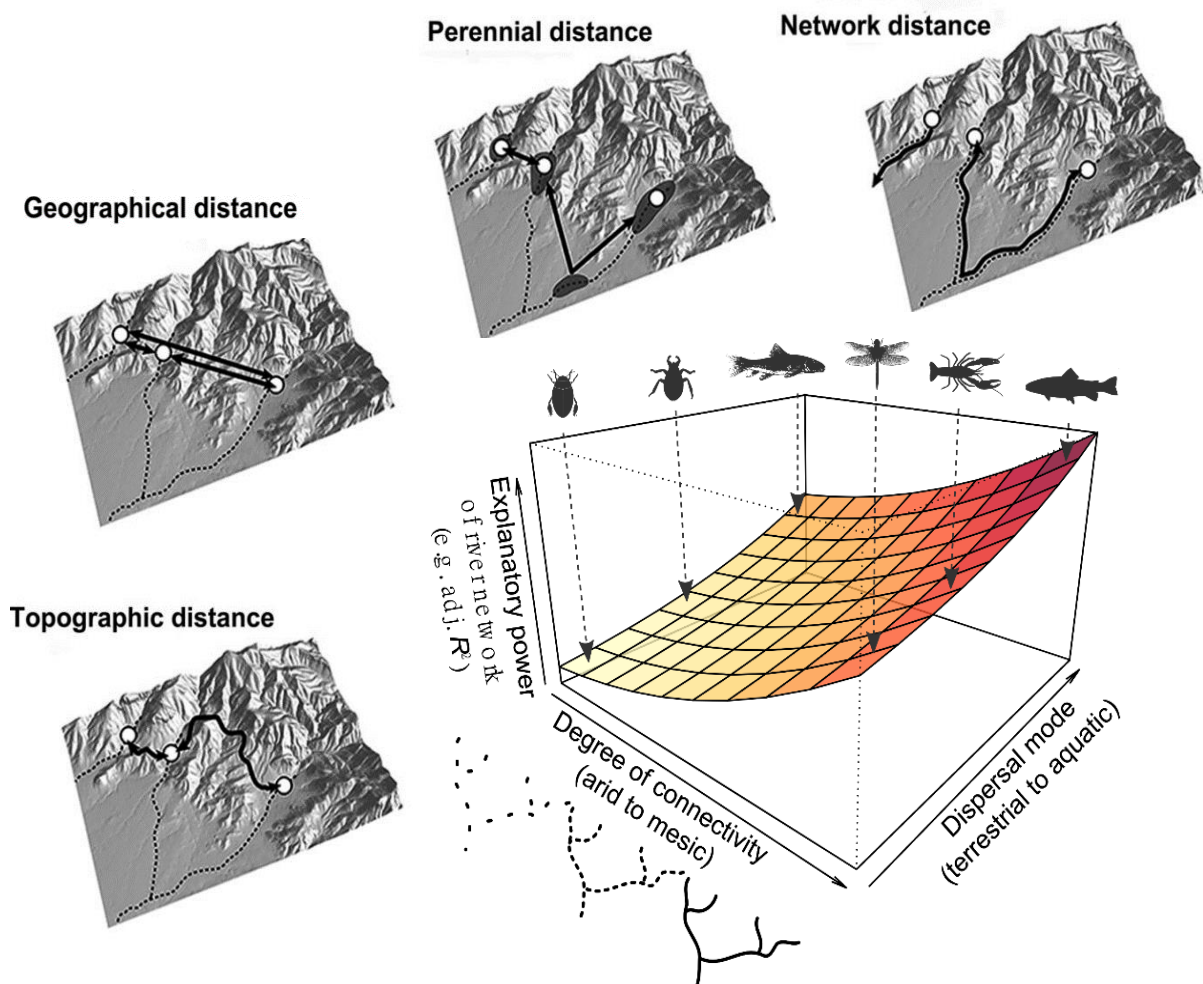


Figure 1.3. Interactions between species dispersal models and riverscape structure.

Examples of species dispersal paths (black lines) among sites (white points) in river networks depending on different dispersal mode, and resulting conceptual relationship (graph) between the degree of physical connectivity of river networks in the landscape, dispersal mode, and the explanatory power of the river network for explaining patterns of biodiversity. Adapted from Cañedo-Argüelles et al. (2015; distance panels) and Tonkin, Altermatt, et al. (2018; graph panel).

While constantly morphing, rivers are relatively old features of the landscape in geological terms, compared to most lakes for example, and thus carry the mark of both current and past environments. Only a few dozen lakes on Earth have existed for a full glacial cycle (Hampton et al., 2018) whereas the location, size, shape, and orientation of large modern river basins was long ago determined by plate tectonics (Seybold et al., 2021; Tandon & Sinha, 2022). Therefore, the observed biogeography of riverine species is the product of the insularity of river basins modulated by major events like orogenesis, glaciation and sea intrusions — whether merging previously isolated habitat or separating them (Boschman et al., 2023; Carvajal-Quintero et al., 2019; Dijkstra et al., 2014; Su et al., 2022). In conclusion, river networks are characterized by distinctive structures and processes, both in terms of physical environment, the biotic communities they support, and the services they provide to society, making them a unique ecosystem to study and manage.

1.1.3. Threats to biodiversity and sustainable management of river ecosystems

Despite, and because of their pivotal role in the landscape and for human societies, rivers are uniquely threatened by anthropogenic pressures, leading to rapid biodiversity loss and reorganization of biotic communities (Danet et al., 2024; Dudgeon et al., 2006; Harrison et al., 2018; Reid et al., 2019; Tickner et al., 2020). No river or stream ecosystem on Earth is free from the effects of environmental changes occurring at the global scale (**Figure 1.4**): over-exploitation, water pollution, water flow modification, destruction or degradation of habitat, invasion by exotic species, and climate change (Dudgeon et al., 2006; Reid et al., 2019). In fact, most rivers are exposed to several of these stressors, often with synergistic impacts (Craig et al., 2017; Jackson et al., 2016).

What makes river ecosystems unique also renders them vulnerable to human activities (Dudgeon et al., 2006). Their tight coupling with the terrestrial environment and interconnectedness means that physical disturbance and pollution in one part of the drainage basin can have ripple effects across the river network (Fritz et al., 2018; Leibowitz et al., 2018). Freshwater biodiversity critically relies on clean water (i.e., in natural condition) whose availability is compromised by widespread withdrawal, diversion, storage, and contamination (Grill et al., 2019; Vörösmarty et al., 2010). Moreover, the fact that many species are restricted to the channel and can only disperse within a given basin increases their risk of extinction, a risk further exacerbated by artificial barriers like dams (Olden et al.,

2010). Dispersal limitation means that these species can only marginally adjust their range to adapt to climate change (Comte & Grenouillet, 2013) and other human stressors, and that their population is smaller, isolated, and thus more vulnerable (Gido et al., 2016). Low gene flow among drainage basins, high levels of endemism, and the rarity of many species further amplify the vulnerability of freshwater biodiversity (Dudgeon et al., 2006). Those organisms that can disperse, like macroinvertebrates with an aerial life stage, can more easily shift their range, leading to the assembly of novel biotic communities (Mouton et al., 2022).

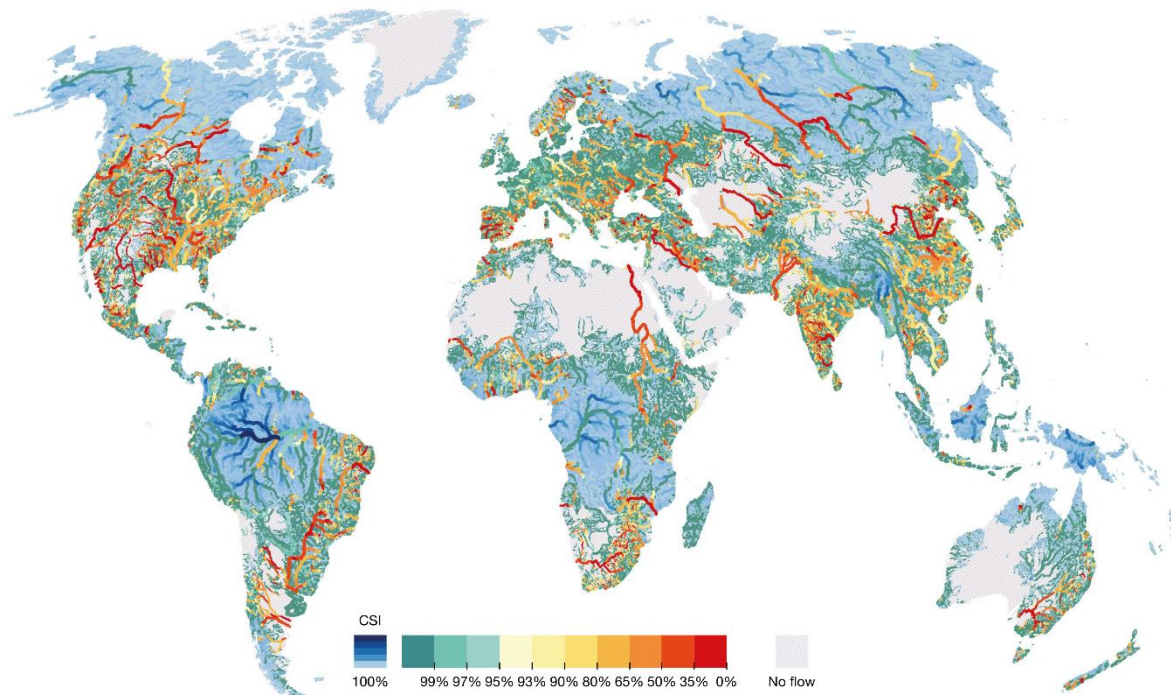


Figure 1.4. Of all mapped river reaches globally, 48.2% are impaired by diminished river connectivity to various degrees (Connectivity Status Index < 100%).

Climate change affects all rivers; the CSI accounts for (1) river fragmentation (longitudinal); (2) flow regulation (lateral and temporal); (3) sediment trapping (longitudinal, lateral and vertical); (4) water consumption (lateral, vertical and temporal); and (5) infrastructure development in riparian areas and floodplains (lateral and longitudinal). The blue shades represent the magnitude of river discharge for river reaches with CSI = 100% (that is, darker shades for larger rivers). Reproduced from Grill et al. (2019).

The acute vulnerability of freshwater biodiversity implies more drastic decreases in population sizes and higher extinction rates than in other ecosystems (Tickner et al., 2020; WWF, 2020). The abundances of freshwater vertebrate populations have declined by more than 80% since 1970 (WWF, 2020). Populations of freshwater animals over 30 kg have plummeted by 88% in just four decades (F. He et al., 2019); the modern extinction rate for freshwater fishes is over 100 times greater than the background extinction rate for freshwater fishes in Europe and the USA (Burkhead, 2012; Dias et al., 2017); and the fungal chytridiomycosis panzootic is causing mass die-offs and extinctions of amphibians worldwide

(Scheele et al., 2019). By contrast, global trends in freshwater macroinvertebrate abundance and diversity exhibit more variability over time, and among taxa, regions, and metrics (Feio et al., 2023; Haase et al., 2023; Powell et al., 2023; Rumschlag et al., 2023).

Numerous efforts are already underway from the national to the global scale to protect ecosystems and their contribution to people (IPBES, 2019; Kim, 2013), including flagship agreements like the Kunming-Montreal Global Biodiversity Framework (GBF) and the Sustainable Development Goals (SDGs). However, freshwater ecosystems are usually under- and misrepresented in these global conservation actions, which often fail to recognize the specificities of their structure and functioning (Darwall et al., 2018; Tickner et al., 2020). For instance, indicators of conservation are usually static and area- or pixel-based — thus overlooking the dynamic, networked, structurally linear, and watershed-based character of rivers (Abell et al., 2007; Leal et al., 2020). The IPBES 2019 global assessment report on biodiversity and ecosystem services, for example, only included “permanent surface water extent” and “Wetland Extent Trends (WET) index” as indicators of freshwater ecosystem structure, overlooking rivers and streams altogether, and did not include any indicator of ecosystem function for freshwaters (IPBES, 2019). The SDG number 14 for ‘life below water’ exclusively covers marine environment, and none of the targets include inland waters or the productive fisheries they support (Reid et al., 2017). Therefore, coordinated efforts are needed to increase recognition of river ecosystems and devise measures to protect their unique characteristics (Darwall et al., 2018; Tickner et al., 2020).

Six priority actions have been suggested as part of an “Emergency Recovery Plan” to curb the ongoing loss of global freshwater biodiversity (Tickner et al., 2020). The proposed actions focus on each of the major threats to river ecosystems identified in the literature (Dudgeon et al., 2006; Reid et al., 2019) and include: (i) accelerating the implementation of environmental flows; (ii) improving water quality; (iii) protecting and restoring critical habitats; (iv) managing the exploitation of freshwater ecosystem resources; (v) preventing and controlling non-native species invasions; and (vi) safeguarding and restoring river connectivity (Tickner et al., 2020). This call to action is gaining traction in the scientific literature (Arthington, 2021; Birnie-Gauvin et al., 2023; Lynch, Hyman, et al., 2023; Twardek et al., 2021) and has contributed, with other efforts, to elevate the status of freshwater ecosystems in global policies like the GBF (Cooke et al., 2023).

1.1.4. Environmental flows (e-flows)

A particular focus of this thesis is the first item of the Emergency Recovery Plan, which advocates for the provision of environmental flows (e-flows). Environmental flows are defined as “the quantity, timing, and quality of freshwater flows and levels necessary to sustain aquatic ecosystems that, in turn, support human cultures, economies, sustainable livelihoods, and well-being” (Arthington et al., 2018). The conservation and restoration of e-flows is globally accepted as a centerpiece of sustainable water resource management mandated by national and international environmental policies to mitigate anthropogenic alterations of the hydrology of rivers and streams (Arthington et al., 2018; Dourado et al., 2023). The guiding principle of e-flows is that streamflow is correlated with and critically contributes to sustaining rivers’ habitats and physiochemical characteristics (e.g. water temperature, channel geomorphology, and habitat diversity). It can thus be considered a "master variable" that limits the distribution and abundance of riverine species and regulates the ecological integrity of lotic ecosystems (Poff et al., 1997). The goal of e-flows, then, is to identify and protect the characteristic patterns of a given river’s flow in time — its “flow regime” — that regulate its ecological processes (**Figure 1.5**; Acreman, 2016). This flow regime is usually divided in five critical components: magnitude, frequency, duration, timing, and rate of change of hydrologic conditions over various time scales, from hours to years (Arthington et al., 2018; Poff et al., 2017).

Protecting or restoring e-flows can involve regulating dam releases, managing surface water and groundwater withdrawals, improving conveyance or irrigation efficiency, releasing wastewater treatment plant effluents, or even occasionally diverting domestic water from urban or suburban water supply networks (Hamdhani et al., 2020; McCoy et al., 2018; Norton et al., 2010; Opperman et al., 2019).

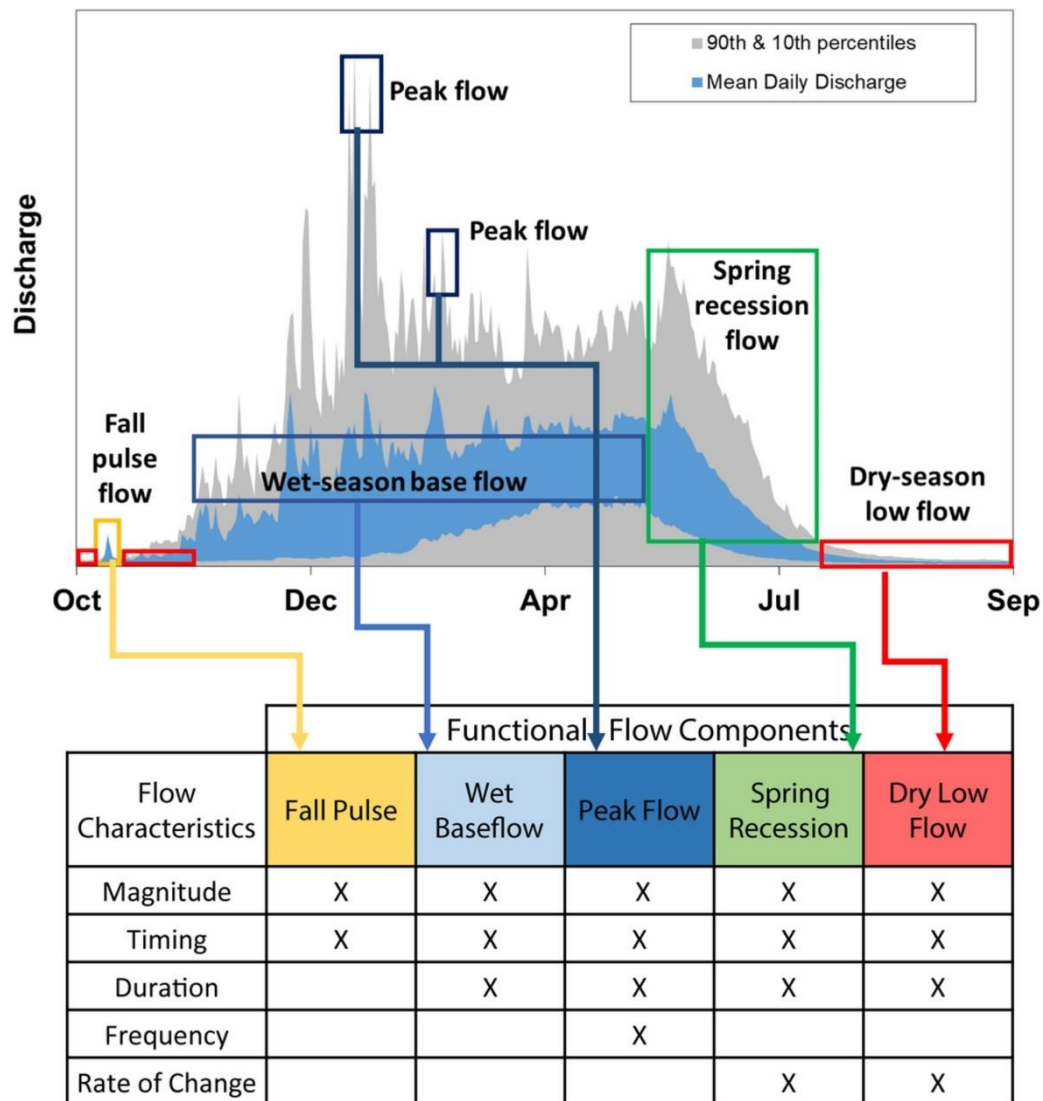


Figure 1.5. Example of natural flow regime components to targeted for protection in a mixed rain-snowmelt runoff system (hydrograph) typical to rivers in California, with characteristics for each flow component (table).

Reproduced from Yarnell et al. (2020).

Various techniques have been developed for assessing flow regimes required to sustain the ecosystem at a given site. They are called frameworks because they rely on different sets of principles and practices, with well-defined protocols. E-flow assessment frameworks are usually classified in four categories, which require increasing amounts of resources, time, and expert knowledge for implementation (Tharme, 2003):

- i. **Hydrological Analysis:** leverage historical flow data or models of natural discharge to identify simple indices that reflect crucial aspects of the flow regime to conserve, like low-flow levels and duration (Pastor et al., 2014; Salinas-Rodríguez et al., 2020). This approach is the least costly to implement because it is desktop-based and only requires long-term discharge time series and/or hydrological modelling.

- ii. Hydraulic rating: analyse the relationship between discharge and simple hydraulic variables (i.e., wetted width, depth, and water velocity) which define the quantity of habitat available to species in a river (Loar et al., 1986). This approach is seldom used today and has been largely replaced by habitat modelling.
- iii. Physical habitat modelling: develop biological response models to assess changes in the physical habitat available for specific target species based on discharge. This is more specific than hydraulic assessments because it accounts for the traits of target species (Lamouroux et al., 2017; Lamouroux & Jowett, 2005).
- iv. Holistic frameworks: evaluate river flow regime through expert workshops to recommend flow levels that accommodate all aspects of the river ecosystem, including societal and recreational needs. This approach is widely regarded as the optimal standard when sufficient resources and data are available (Arthington et al., 2003; Poff et al., 2010).

While I focus on e-flows in this thesis, measures to protect or restore e-flows must be considered in tandem with complementary actions such as those outlined in the Emergency Recovery Plan as part of an integrated basin management approach for maximizing the benefits to freshwater biodiversity (Nicol et al., 2021; Stewardson et al., 2017).

1.1.5. River science: conceptual developments and limitations

Owing to their characteristic structure and processes, river ecosystems have inspired a rich interdisciplinary field of research at the interface of natural sciences, engineering, and social sciences (Gilvear et al., 2016). River science aims to understand and predict the patterns and processes governing the interactions between the physical, chemical, biological, and social components of riverine landscapes across multiple scales, from the microhabitat to the global scale (Dunham et al., 2018; Thoms & Parsons, 2002). Despite its relative youth as a field of inquiry and the enduring gap in communication between scientists across realms (Menge et al., 2009), river science has co-evolved with its disciplinary roots in natural sciences. It has both drawn from and informed theoretical advances in hydrology and hydraulics, geomorphology, ecology, and biogeochemistry. In ecology for example, fluvial ecosystems are commonly used as models for testing and refining general theories, notably on disturbance and succession, ecosystem metabolism and biodiversity-ecosystem functioning, reciprocal subsidies among ecosystems, and more recently, meta-community

and meta-ecosystem concepts (Brown et al., 2011; Gounand, Harvey, et al., 2018; Milner & Tockner, 2010; Thompson & Lake, 2010).

Many conceptual models of river ecosystems have been developed over the past 50 years to synthesize our understanding and find generalities in the patterns and processes observed in lotic environments. Beginning with seminal works in geomorphology (Leopold et al., 1964) and ecology (Hynes, 1970), successive conceptual models brought new perspectives to the inquiry of river ecosystems. For instance, Hynes (1975) first formalized the view that river ecosystems are inextricable from their catchment and emphasized the tight coupling between their physical template, flow regime, and ecology. Maybe the most widely taught conceptual model of rivers is the River Continuum Concept (Vannote et al., 1980), which sought to describe predictable patterns along the longitudinal dimension of rivers. It links gradients in hydrology, geomorphology, and canopy cover to multiple resultant abiotic variables, energy inputs, ecological processes, and macroinvertebrate community structure from headwaters to the river mouth. This gradient-based perspective, while stimulating river science to shift from a descriptive to a prescriptive approach, has nonetheless been extensively critiqued since then (Doretto et al., 2020; Thorp et al., 2023). The flood pulse concept and its extensions, for example, underlined the importance of river-floodplain interactions and the broader role of episodic changes in flow magnitude (Junk, 1989; Tockner et al., 2000). Patch- and network-based conceptual models have also gained prominence (Benda et al., 2004; Erős & Lowe, 2019; Pringle et al., 1988; Townsend, 1989). In general, successive models have increasingly aimed for integration, across multiple spatial dimensions (longitudinal, lateral, vertical), between general gradients and discontinuous patterns, and across spatial and temporal scales (**Figure 1.6**; Brown et al., 2011; Cid et al., 2022; Gilvear et al., 2016; Poff et al., 1997; Stanford & Ward, 1993; Thorp et al., 2023; J. V. Ward, 1989). These models underpin our understanding of river ecosystems, guide scientific inquiry and hypothesis testing, and provide an essential foundation to inform river policy, management, and conservation.

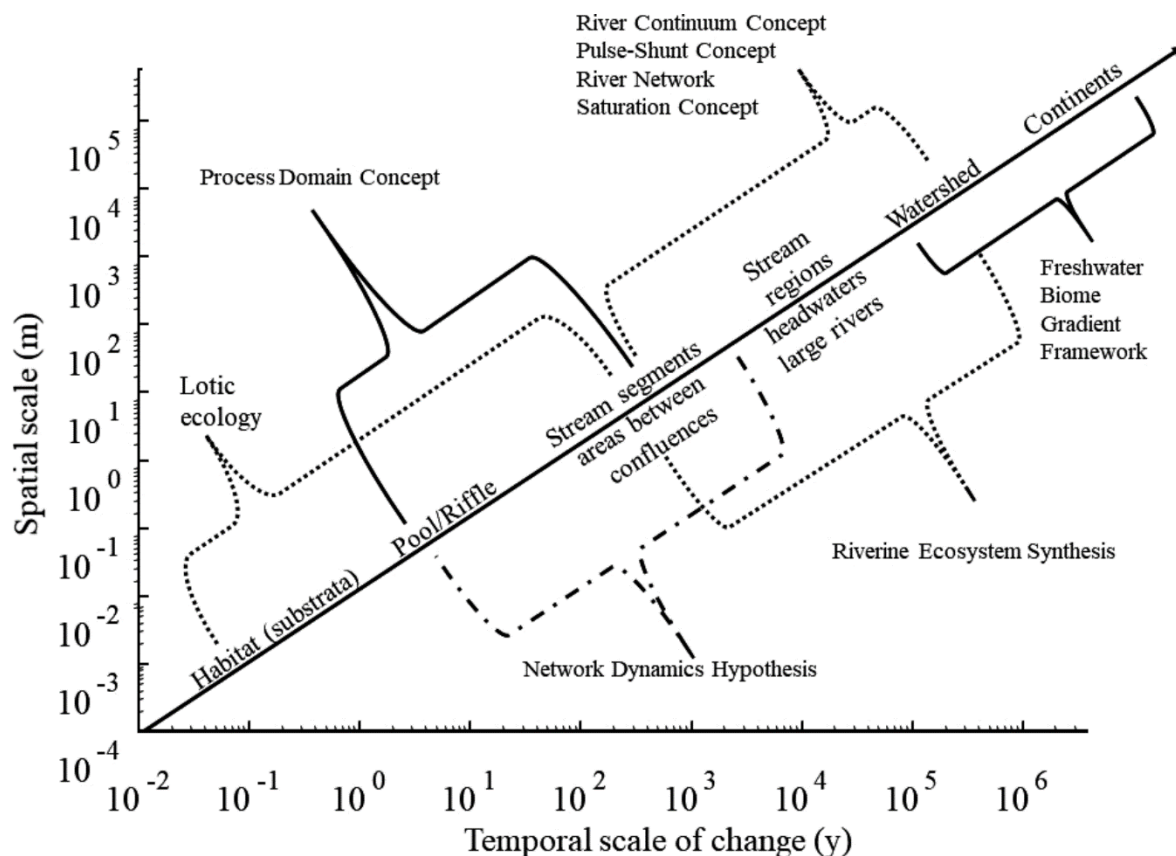


Figure 1.6. River ecosystems can be understood at multiple spatial and temporal scales. Numerous ecological conceptual models have been developed to synthesize our understanding and hypotheses on their structure and functioning at different scales.
Reproduced from Thorp et al. (2021).

Our understanding of ecosystems is rooted in the geoclimatic and cultural contexts in which published scientists conduct research (Hughes et al., 2021; L. J. Martin et al., 2012). As a result, conceptual models are biased towards a subset of ecosystems, usually in temperate climates, and may thus ascribe disproportionate importance to specific patterns and processes over others that may dominate less-studied systems. As an illustration, the River Continuum Concept has been heralded as a general model of river ecology but was developed from observations in temperate, near-pristine, and forested low- to medium-order streams, a limitation that drew critiques shortly after its publication (Doretto et al., 2020). For example, nowhere did it mention the central importance of flooding in large river-floodplain systems that abound in the tropics (Junk, 1989). Bias exists outside of ecology as well. In hydrology, author affiliation is the primary predictor of which hydrological model is used in a study, implying that “legacy, rather than adequacy” motivates model selection (Addor & Melsen, 2019).

1.1.6. *Non-perennial rivers and streams (NPRs)*

One major bias of river science and management that has come under the spotlight in the past decade is the outsized focus on perennial watercourses, which flow year-round (Acuña et al., 2014; D. Allen & Datry, 2020; Larned et al., 2010; Tooth, 2000). A review of 18 conceptual models in river science concluded that most were designed for and derived from research on perennial rivers (D. Allen & Datry, 2020). By and large, they fail to adequately represent the hydrology, geomorphology, ecology, and biogeochemistry of non-perennial rivers and streams (NPRs) that cease to flow at some point in time or space. This is despite the fact that many early studies in fluvial geomorphology were set in semi-arid and arid rivers of the US southwest and Australia (Tooth, 2000). Considering preliminary evidence that these ecosystems make up from 30% to over 50% of global river network length (Datry, Larned, & Tockner, 2014; FAO, 2014; Pekel et al., 2016; Raymond et al., 2013; Schneider et al., 2017) and that conceptual models strongly influence river policy and management, such an oversight has far-reaching implications for our understanding of river ecosystems and for their conservation worldwide (Acuña et al., 2017).

Terminology

The key feature that distinguishes NPRs from other lotic environments is the temporary absence of surface water movement, often accompanied by the partial or complete loss of surface liquid water in the channel (Datry, Boulton, et al., 2023). NPRs encompass hydrologically diverse lotic ecosystems along the aquatic-terrestrial spectrum (Shanafield et al., 2021). In some river reaches, water may stop to flow once every few years and for a short period of time, such that surface water persists in pools until flow resumption. Other systems are almost always dry and disconnected from groundwater, but prone to flash floods in response to episodic precipitation.

Considering their diversity and ubiquity, numerous terms have been used in the scientific literature to designate NPRs, with little consistency (Busch et al., 2020; Uys & O’Keeffe, 1997). I prefer to use the term *non-perennial*, following Busch et al. (2020), because it is the broadest term, yet easily understood with minimal ambiguity. Other common epithets include seasonal, irregular, temporary, non-permanent, discontinuous, intermittent, ephemeral, episodic, or simply “dry” rivers (Busch et al., 2020). Terminology is not benign because a consistent lexicon helps to standardize a field of research, which promotes clearer

communication among scientists as well as with non-scientists, underpins policies and regulations, and enables more effective searches and syntheses of the literature. Further, some descriptors are reductive in the type of flow regime they describe. For instance, not all NPRs exhibit pronounced seasonality in flow cessation while others may dry like clockwork and can thus not be deemed “irregular”. Likewise, not all flow cessation results in drying or discontinuity in surface water. Another term that is often meant to cover all NPRs is *intermittent*, due to its association with the general term flow intermittence (or intermittency). However, intermittent watercourses can be thought to imply a greater connection to the groundwater table and more durable flow compared to ephemeral and episodic watercourses — which flow for shorter periods, typically only after precipitation events, and lose surface water to groundwater the majority of the time (Busch et al., 2020; Costigan et al., 2016). No universal criterion quantitatively differentiates these categories though.

This terminology and the associated acronyms keep evolving, which is reflected in this thesis. At its onset in 2020, Intermittent Rivers and Ephemeral Streams (IRES) was a common term (and acronym), popularized by Datry et al. (2017b). Like intermittent and ephemeral, the distinction between rivers and streams is qualitative, with no definite threshold in drainage area, discharge, or width and depth. A river is simply thought of as larger than a stream. The term IRES hints at the fact that larger watercourses tend to exhibit greater flow permanence so that a stream is more likely to be ephemeral and a river intermittent (Datry et al., 2017a). This is the term used in much of **Chapter 2** of this thesis. Nevertheless, elsewhere in the thesis, I try to favor the term non-perennial rivers and streams and the acronym NPRs. I often opt for non-perennial *watercourses* or non-perennial *reaches* as well, which do not make a distinction in size. Finally, I sometimes use *river* as a generic term (i.e., *river* ecosystem) to improve the flow of the prose but do not imply a size criterion in doing so unless specifically stated or obviously implied by the context.

Below, I provide a brief review of the hydrology, ecology, and biogeochemistry of NPRs with particular emphasis on their hydrology.

Hydrology of NPRs

Most hydrological research has historically focused on perennial watercourses but several recent reviews, which I draw upon here, provide a robust foundation to understand the mechanisms driving flow generation and cessation (Costigan et al., 2016, 2017; Price et al., *In review*; Shanafield et al., 2021).

Flow cessation is fundamentally a matter of water balance: do water outputs exceed inputs? Climate and geology, and the resulting catchment lithology, topography, soil, and vegetation are the dominant external controls on this water balance (Costigan et al., 2016; Padrón et al., 2017). Together, these factors exert control on the spatiotemporal dynamics of flow intermittence across scales, from the individual flow cessation event to the seasonal and interannual scales, and from the individual pool or riffle (i.e., mesohabitat) to the reach, basin, and global scales (**Figure 1.7**; Costigan et al., 2016). At the global scale, the overarching drivers of the prevalence and flow permanence of NPRs are climatic aridity (the ratio of precipitation and evapotranspiration, ET) and winter temperatures (Eng et al., 2016; Hammond et al., 2021; Sauquet et al., 2021; Schneider et al., 2017). NPRs are found in all climates, continents, and biomes (Datry, Larned, & Tockner, 2014; Stubbington, England, et al., 2017), but aridity essentially determines the largest watercourse that can stop to flow in a region. Flow cessation is mainly confined to first- and second-order streams in humid and cool climates whereas whole river networks may dry in hot and arid climates (Shanafield et al., 2021; Stubbington, England, et al., 2017). At high latitudes and elevations, frozen ground and water, as well as the absence of liquid precipitation can result in long periods without flow (Buttle et al., 2012; Tolonen et al., 2019). Beyond these two overarching factors, the natural mechanisms controlling flow vary at finer temporal and spatial scales, resulting in an array of natural flow intermittence regimes (Costigan et al., 2016; Poff et al., 1997; Price et al., 2021).

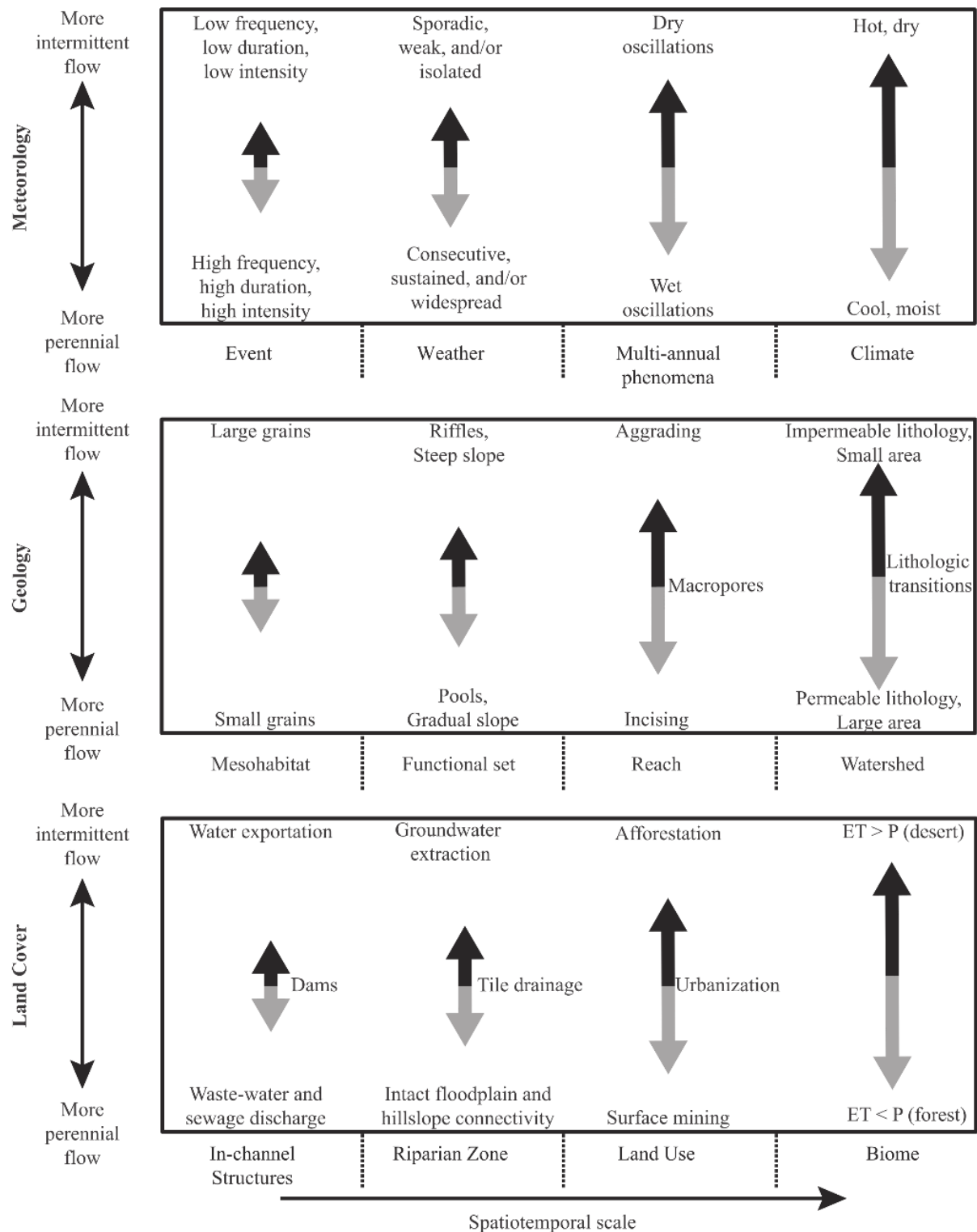


Figure 1.7. Spatial and temporal factors related to (A) climate/weather, (B) geology, and (C) land cover that govern flow intermittence regimes.

The diagram depicts how these factors promote either flow permanence (upper portion with black arrows) or flow cessation (lower portion with grey arrows). It acknowledges the presence of other scenarios and uncertain influences, indicated along the central line where arrows diverge. The x-axis represents hierarchical nesting, while the tendency towards promoting continuous or intermittent flows is shown along the y-axis. Reproduced from Costigan et al. (2016).

At the reach scale, flow is initiated and sustained by a combination of surface water and ground water inputs, whose relative contributions fluctuate in space and time (Gutiérrez-Jurado et al., 2019; Shanafield et al., 2021). Surface water comes from precipitation falling directly in the channel, from upstream by flowing along the channel, or from the reach catchment as overland runoff (either due to infiltration- or saturation-excess; **Figure 1.8**). Groundwater can also have multiple origins with more variable residence times. At the mesohabitat scale, water may infiltrate in the channel substrate when flowing out of a pool into a riffle head and shortly after re-surface at the downstream end of the riffle. Interflow may reach the channel by the banks and bed at variable speeds after a storm, moving along hydraulic gradients through saturated or unsaturated soils. Finally, groundwater may outflow into the river or be expelled from the banks into the bed — either from the regional water table, if high enough, or from a perched aquifer (free ground water above a low-permeability layer above the regional water table; Gutiérrez-Jurado et al., 2019; Nadeau & Rains, 2007; Shanafield et al., 2021). Water stops to flow in a reach once those sources are inferior to “transmission losses” along the reach, evapotranspiration and seepage through the channel bed and banks, or the rate of freezing (Shanafield & Cook, 2014). Flow cessation is usually driven by the combination of both, decreasing inputs and increasing outputs. In most warm temperate climates, for example, rainfall events are less frequent during the summer. After a storm, hillslope and upstream runoff decrease quickly after an initial peak while groundwater inputs may keep increasing for longer. Without additional inputs, only baseflow (i.e., flow originating from groundwater) remains and starts decreasing as the water table subsides, until the channel eventually starts losing surface water to groundwater. Inputs from melting snow or ice upstream may cease once all frozen stocks are depleted; those from standing water bodies like lakes and wetlands decrease as their water level falls. In parallel, increased evapotranspiration resulting from solar radiation during longer days, rising temperatures, and growing vegetation decrease interflow and lower groundwater levels, ultimately causing flow cessation. Outside of arid landscapes where rivers may never be connected to groundwater, a major determinant of the flow intermittence regime of a reach is whether and when groundwater inputs cease because flow cessation mechanically requires the absence of baseflow. Just as drying may take place through diverse processes, rewetting mechanisms also vary, from sudden and highly erosive flooding and debris flow to groundwater upwelling slowly progressing upstream, with

substantial implications on ecosystem structure and function (Price et al., *In review*). Nonetheless, the event-scale hydrology of drying and rewetting was little explored until recently (Price et al., *In review*; Price et al., 2021).

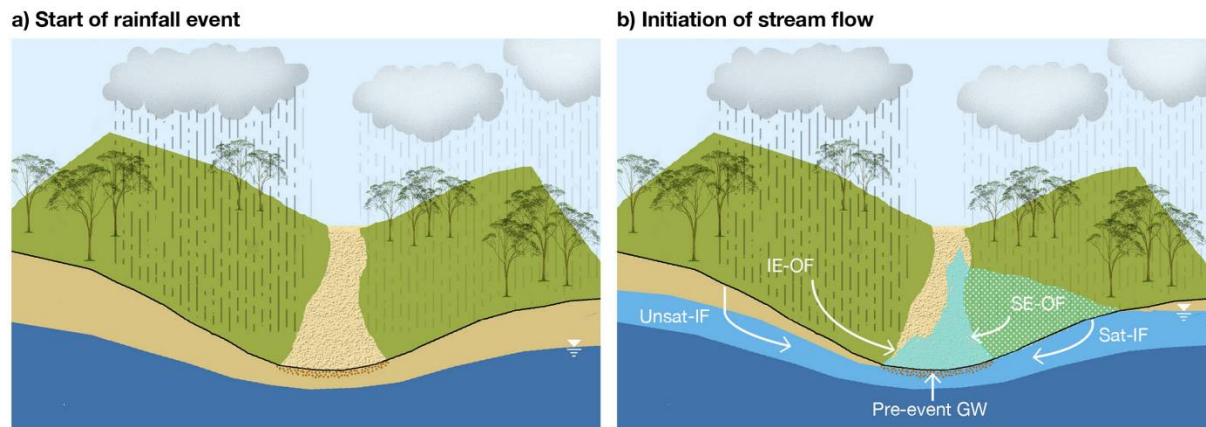


Figure 1.8. Conceptual diagram showing the transition from a dry (a) to a flowing stream (b).

The main processes contributing to the initiation of streamflow typical of NPRs are shown, although additional processes occur within the hydrologic cycle. Flow generation mechanisms include infiltration excess overland flow (IE-OF), saturation excess overland flow (SE-OF), interflow generated from saturated and unsaturated soil profiles (unsaturated interflow [Unsat-IF]/saturated interflow [Sat-IF]) and pre-event groundwater (GW). Reproduced from (Gutiérrez-Jurado et al., 2019).

Local lithology, soils, topography, and vegetation form a complex interplay that mediates the partitioning of climatic water inputs and outputs (Costigan et al., 2016; Edwards et al., 2015). In general, greater soil and rock permeability in the catchment will increase flow permanence by enabling the storage and gradual release of infiltrated water, whereas hydraulic conductivity of channel substrate increases transmission losses in losing watercourses, hence promoting flow cessation (Jencso & McGlynn, 2011). NPRs are widespread in regions underlain by karst, which exhibit complex surface-groundwater interactions to the point that entire rivers may disappear into a sinkhole and resurface elsewhere (Bonacci, 2015). Despite their importance, geologic controls on flow intermittence and groundwater-surface water interactions are the least understood and measured processes in NPR hydrology (Shanafield et al., 2021). In many arid landscapes, snowmelt from distant mountain ranges can create periods of flow, whereas local and brief convective precipitation events on hydrophobic and unvegetated soils result in infiltration-excess overland flow causing short-lived peaks in discharge (Kalma & Franks, 2003; Shanafield et al., 2021). Steeper catchment and channels decrease infiltration and increase flashiness. River gradients steeper than the water table may draw groundwater inflow

(Konrad, 2006) while longitudinal changes in river slope can result in two-way convective movement between ground- and surface water, causing alternating stretches of wet and dry bed (Harvey & Bencala, 1993; Shanafield et al., 2021). Plant cover in the catchment simultaneously increases evapotranspiration and decreases flow flashiness via enhanced infiltration through soil macropores created by roots and soil fauna (Beven & Germann, 1982).

The presence or absence of flow is a crucial binary distinction, but the consequences of flow cessation on the ecology and biogeochemistry of a watercourse very much depend on what happens next. Once flow stops, a river reach can experience a succession of aquatic states, which are not captured by measures of streamflow alone (Gallart et al., 2016). All mesohabitats may temporarily remain inundated (“eurheic”). Soon, however, riffles dry and surface water is limited to connected pools (“oligorheic”). Without water inputs, the pools become isolated (“arheic”) and slowly shrink until flow only remains in the substrate (“hyporheic”). Eventually, all water disappears and the entire bed and hyporheos is dry (“edaphic”). Whether a reach will undergo these transitions and the speed at which it will do so depend on the level of hydrologic imbalance at that location. Even the fate of adjacent pools can differ, depending on their geometry, linkage to groundwater, turbidity, and shading from overhanging vegetation (Hwan & Carlson, 2016; Yu (于松延) et al., 2022).

At broader scales, spatial and temporal variability in drying and rewetting leads to distinctive dynamics among branches of the river network. In temperate climates, the hydrographic network expands and contracts in its upper end as headwater streams cycle through flowing, non-flowing, and dry phases, both seasonally and following individual rainfall events (de Vries, 1995; Godsey & Kirchner, 2014; A. S. Ward et al., 2018). In other systems, the downstream end of the network may dry for longer and be rewetted from upstream (e.g., in arid landscapes where water comes from high elevation areas or local storms), or reaches may asynchronously cycle through aquatic states across the network, creating a dynamic mosaic of lotic, lentic, and terrestrial habitats (Larned et al., 2010).

Anthropogenic activities have already had profound impacts on the hydrology of global rivers and streams (Gudmundsson et al., 2021; Porkka et al., 2024; Wang et al., 2024). As previously perennial rivers dry out due to climate change, land use change, and water abstractions by humans, NPRs are becoming increasingly widespread (Datry, Foulquier, et

al., 2018; de Graaf et al., 2019; Eng et al., 2016). At the same time, the prevalence of freezing NPR will decrease in the Arctic because of the rapid transition from a snow-dominated to a rain-dominated precipitation regime (Bintanja & Andry, 2017). Coarse models have identified regions where NPRs may become more or less prevalent under future climates (Döll & Schmied, 2012), and there is extensive evidence of increased drying caused by human alterations of streamflow (Carey et al., 2023; Datry, Truchy, et al., 2023; Trambly et al., 2021; Zipper et al., 2021). However, the complexity of modeling global human impacts on hydrology (Döll et al., 2016) and the scale of hydrological processes driving streamflow cessation imply that even the current extent of anthropogenic flow intermittence has not been reliably quantified (Datry, Truchy, et al., 2023).

Ecology, biogeochemistry and ecosystem services of NPRs

The presence and movement of water in river and stream networks drives ecosystem metabolism and the abiotic conditions that organisms experience; it regulates the transport of energy, sediments, and organisms across the landscape, and sculpts landforms through erosional and depositional processes, hence creating or resetting habitat for species (Sponseller et al., 2013). Consequently, the absence of flowing water is a primary determinant of biotic communities, ecosystem processes, and ecosystem services in NPRs from the river reach to the network scale (Datry, Boulton, et al., 2023).

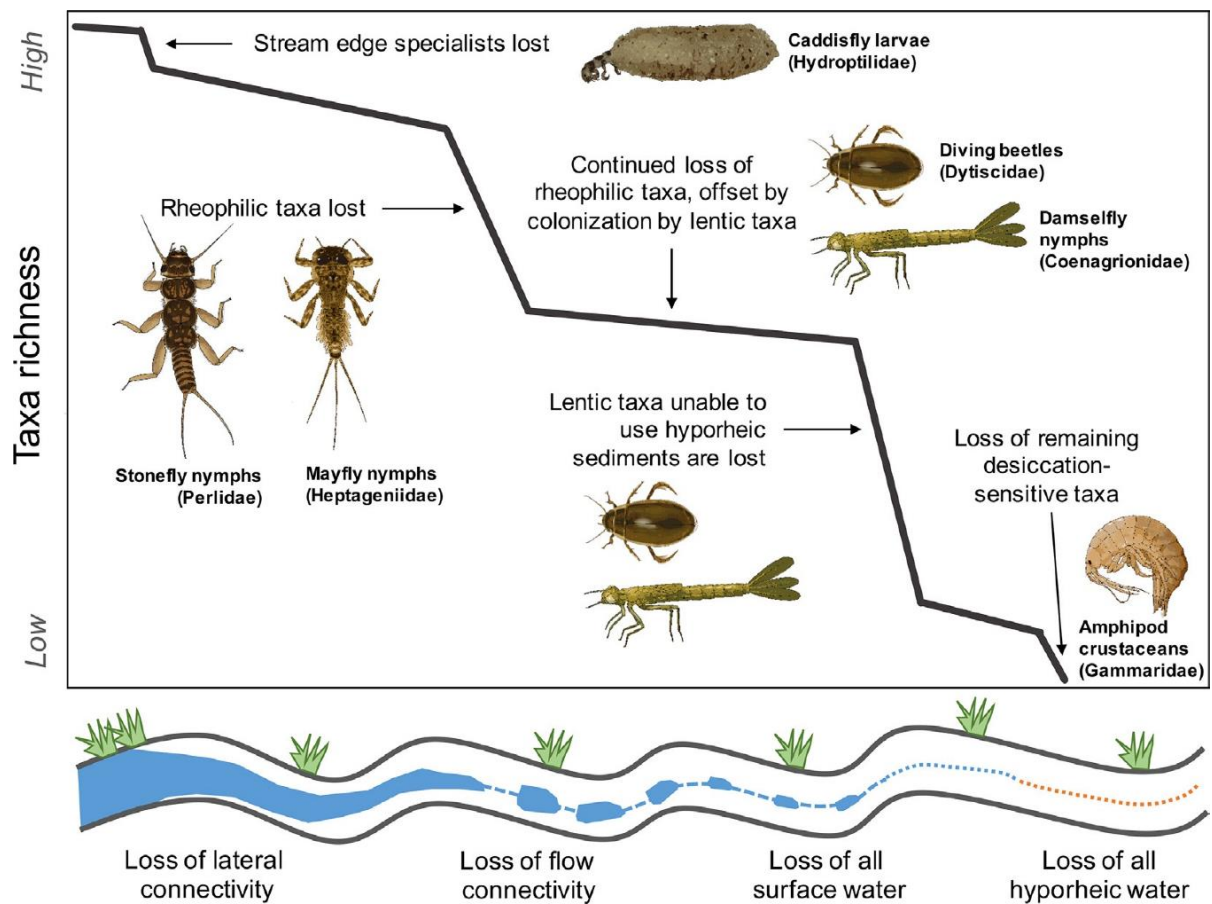


Figure 1.9. Decrease in local species diversity (taxa richness) of aquatic macroinvertebrates with successive stages of flow cessation, indicating critical thresholds in relation to habitat types and availability.

Rheophilic taxa require habitat with high flow conditions and clear water. Lentic taxa thrive in standing water. Reproduced from Stubbington, Bogan, et al. (2017), originally adapted from Boulton (2003). Invertebrate drawings from Pau Fortuño Estrada. Not to scale.

At the reach scale, the transitions from flowing conditions to successive aquatic states and rewetting create a cascade of impacts on the abiotic conditions within NPRs (Gómez et al., 2017). These temporal sequences impose strong environmental constraints on aquatic organisms, impacting their habitat, food source and interactions (**Figure 1.9**; Boulton, 2003). After flow cessation, drying is first felt as the aquatic disconnection of the main channel and riparian habitat, followed by a shift from flowing to stagnant conditions. With continued drying comes the loss of longitudinal connectivity and pools become isolated and gradually shrink over time. As flow stops, pools experience elevated and fluctuating water temperatures, increased nutrient concentrations and salinity, and reduced oxygen availability (Acuña et al., 2005; von Schiller et al., 2011). Once pools become disconnected, each pool may follow a separate trajectory and abiotic conditions become longitudinally differentiated, depending on the hydrology, microhabitat, and species composition within

each pool (Hopper et al., 2020; Larsen & Woelfle-Erskine, 2018). As the pools contract, biotic interactions such as predation and competition intensify, further affecting the ecosystem dynamics (Magoulick & Kobza, 2003; Matthews & Marsh-Matthews, 2003). As channels shift from flowing to stagnant conditions, biological communities undergo abrupt changes towards pond-like communities (Bonada, Rieradevall, et al., 2006). However, disconnected pools can become inhospitable (Gómez et al., 2017). The complete disappearance of surface water represents the most critical stage for aquatic organisms, with many dying and their remains providing food for terrestrial scavengers (Steward et al., 2012).

Organisms in NPRs have diverse traits and strategies to cope with the disturbance caused by hydrological variability (Bogan et al., 2017). The species that survive flow cessation rely on a combination of resistance (the ability to withstand flow cessation and drying in place) and/or resilience (the capacity for the population to recover after flow resumes) to flow intermittence (Lake, 2000; Leigh et al., 2016; Stanley et al., 1994). Adaptations to flow cessation may affect their anatomy and physiology (e.g., tolerance to low-oxygen and high temperatures in pools, resistance to desiccation) as well as multiple aspects of their life history – dispersal (e.g., strong swimming or flying ability), reproduction (e.g., cohort splitting), synchronization (e.g., migratory timing), and development (e.g., asynchronous emergence; **Figure 1.10**; Bonada et al., 2007; Kerezszy et al., 2017; Robson et al., 2011; Vander Vorste et al., 2020; Verberk et al., 2008). Resilient species disperse to a variety of temporary refuges depending on their mode of locomotion and resistance to desiccation (Boulton, 1989; Chester & Robson, 2011; Davis et al., 2013). Such refuges include perennial flowing-water reaches upstream and downstream of intermittent sections, nearby rivers, persistent pools and springs, and other perennial standing water bodies. Additionally, various moist microhabitats such as leaf litter, algal mats, woody debris, and damp sediment beneath large stones serve as localized refuges within surface channels. True resistance to prolonged drying is the exception rather than the rule despite the existence of specialist species with adapted traits that only exist in drying rivers and streams (Bogan et al., 2013). Most biodiversity found in NPRs is comprised of generalist species also found in perennial freshwaters that can inhabit a broad range of ecosystems (Datry, Larned, Fritz, et al., 2014).

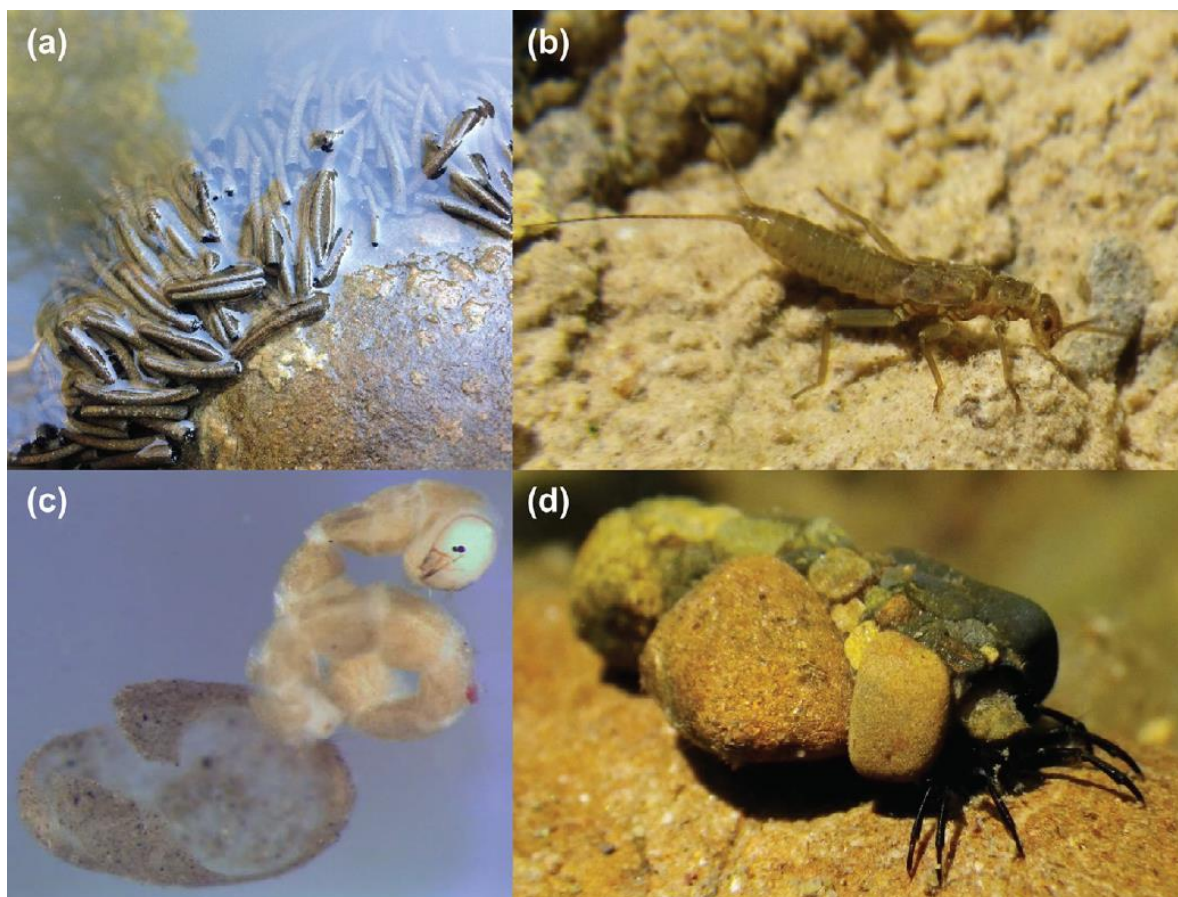
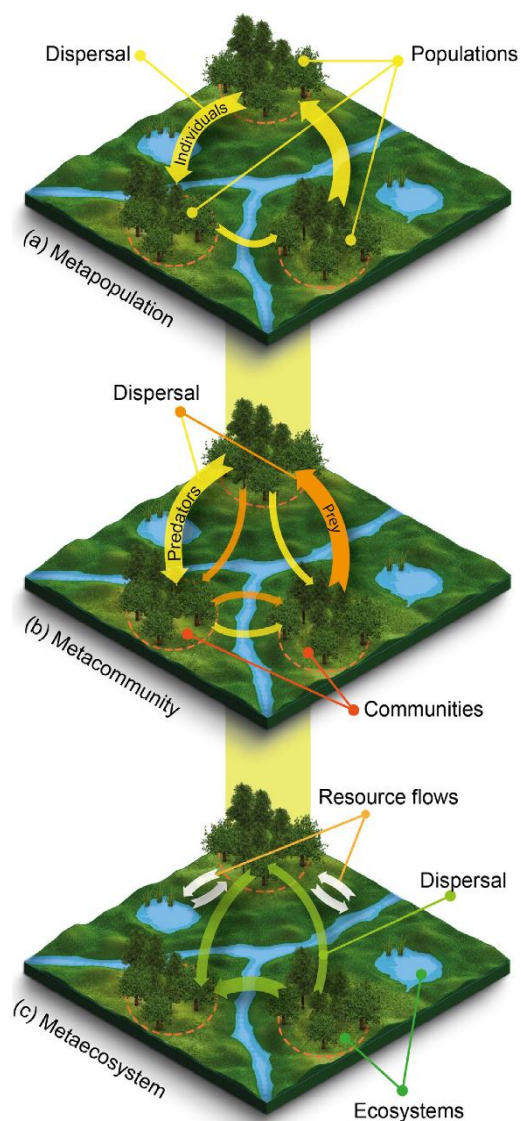


Figure 1.10. Invertebrates with traits promoting resistance in non-perennial rivers and streams.

(a) sedentary *Gumaga* caddisfly larvae congregate in pools; (b) the stonefly *Mesocapnia arizonensis* enters dormancy as nymphs; (c) dormant *Hydrobaenus* chironomid larvae inhabit protective cases; (d) *Limnephilidae* caddisfly larvae enter dormancy in humidity-trapping cases. Reproduced from Stubbington, Bogan, et al. (2017). Photo courtesy of M. Bogan (a, b, and d) and R. Vander Vorste (c).

The harshness resulting from flow cessation and ensuing habitat changes in NPRs significantly limits the reach-scale abundance and diversity of species (Fritz & Dodds, 2005). Local taxonomic and functional richness (alpha diversity) are generally lower in non-perennial than perennial streams at a given time, even in the same basin (Crabot et al., 2021; Leigh & Datry, 2017). At the river network scale, on the other hand, diversity among sites and over time (i.e. spatial and temporal beta-diversity, respectively) is higher in river networks with non-perennial reaches; the habitat heterogeneity and temporal cycles between lotic, lentic, and terrestrial phases result in diverse species with a gamut of resistance and resilience traits (Corti & Datry, 2016; Crabot et al., 2020; Leigh & Datry, 2017; Soria et al., 2017). Notably, there is growing acknowledgement that dry river channels provide crucial habitat and dispersal routes for many terrestrial species and thus contribute to ecological functioning across the entire catchment (Sánchez-Montoya et al., 2023; Steward et al., 2012, 2022).



Owing to their spatiotemporal dynamism and the resulting primacy of dispersal in the abundance and distribution of species, river networks with many NPRs have become a textbook example for the study of metacommunity dynamics (**Figure 1.11**; Cañedo-Argüelles et al., 2015; Datry, Bonada, et al., 2016; Sarremejane et al., 2017). Whereas a metapopulation is a set of local populations of a single species that are linked by dispersal (Hanski, 1998), a metacommunity is a set of local communities that are linked by dispersal of multiple interacting species (Wilson, 1992). Transitions between aquatic states lead to repeated local extirpation and recolonization by multiple species (Datry, Bonada, et al., 2016). These cycles, largely fueled by dispersal among patches of habitat across the basin, promote beta diversity and create local and network-wide community structures that deviate from what would be expected under constant conditions (Tonkin, Heino, et al., 2018).

Figure 1.11. Schematic representation of metacommunity entities in terrestrial ecosystems.

(a) a metapopulation, (b) a metacommunity, and (c) a metaecosystem. In each landscape, the orange dashed circle indicates local populations, communities or ecosystems in forest patches connected through the flow of organisms (colored arrows) and resources (white arrows). Note that flow rate (arrow thickness) may vary across the landscape. Reproduced from Schiesari et al. (2019).

In terms of biogeochemistry, the successive periods of drying and rewetting of NPRs promote much higher temporal variabilities in process rates than in perennial river ecosystems, which has earned them the qualifier of punctuated biogeochemical reactors (Datry, Foulquier, et al., 2018). When a reach ceases to flow and dry, photosynthetic activity comes to a halt while ecosystem respiration proceeds (Sabater et al., 2016). Sediment respiration then increases substantially upon rewetting, causing a large pulse in CO₂ that significantly contributes to the annual carbon emissions of the whole river network (von Schiller et al., 2019). Few studies have quantified the biogeochemical dynamics of lotic

ecosystems at the river network scale (Silverthorn et al., 2024). Most that do exclude emissions in dry reaches from the CO₂ budget and overlook the importance of the rewetting phase (Conroy et al., 2023; Raymond et al., 2013, p. 200). No study to date has modeled the biogeochemical dynamics of NPRs beyond a single network despite evidence that global carbon emissions from river ecosystems may be underestimated because of this oversight (Battin et al., 2023; Datry, Foulquier, et al., 2018; Keller et al., 2020).

The provision of ecosystem services by NPRs is also distinctly dependent on flow state and is likely enhanced by the spatiotemporal arrangement of non-perennial and perennial reaches at the river basin scale (Datry, Boulton, et al., 2018; Stubbington et al., 2020). For instance, dry channels are used as routes and crossing points for nomadic livestock herding, support many recreational activities, and provide a source of high-quality yet easily accessible subterranean water in arid landscapes, among other services (Stubbington et al., 2020; Vidal-Abarca Gutiérrez et al., 2023). The recent increase in scientific interest for these ecosystems has fueled several prospective efforts and literature reviews to inventory their contributions to people and improve accounting frameworks, yet quantitative research on this topic remains limited (Datry et al., 2021; Kaletova et al., 2021; Nicolás Ruiz et al., 2021; Pastor et al., 2022; Steward et al., 2012; Vidal-Abarca Gutiérrez et al., 2023).

1.1.7. Ceci n'est pas une rivière : (mis)management of non-perennial rivers

Despite their prevalence and unique contributions to people, NPRs tend to be negatively perceived by the general public based on the belief that drying is bad and drying rivers are less valuable than perennially flowing waters (Cottet et al., 2023; Leigh et al., 2019; Rodríguez-Lozano et al., 2020). For example, a survey of landowners in the Chesapeake Bay (Pennsylvania, USA) demonstrated a systematic lack of concern for the water quality of intermittent and ephemeral headwater streams compared to perennial ones (Armstrong et al., 2012). This relative devaluation is interrelated to the historical lack of scientific study and monitoring of NPRs (D. Allen & Datry, 2020; Boulton, 2014), and results in their chronic mismanagement and degradation (**Figure 1.12**; Acuña et al., 2014).



Figure 1.12. Examples of threats on non-perennial rivers and streams.

Rubbish in the dry riverbed of the Hodgsons Creek, Victoria (a) and in Madura gully, West Australia (b). A non-perennial segment of the Chitterne Brook flows through an intensively grazed cow pasture in England, UK (c). Sheep in the non-flowing segments of the Barranc del Carraixet, Spain (d). Sewage effluent turning the non-perennial segment of the Sant Miquel River artificially perennial in Spain (e). Gravel extractions from dry riverbeds in France (Albarine River) (f) and Bolivia (Janq'u Qala) (g). A map showing the non-perennial river segments to be removed from protection by legislation in France (white; one of which is shown in j), on the basis of their non-perenniality (h); the perennial segment (yellow) is the only legally protected part of the river network. Sewage effluent generates a permanent pool in a non-perennial segment of the Albarine River, France (i). Non-perennial river segment that is no longer under protection in eastern France, le Ruisseau des Tendasses (j). Reproduced from Datry, Boulton, et al. (2023). Photos courtesy of T. Sykes (c) and H. Pella (j and h).

Most regulatory and management frameworks either exclude NPRs or cater to the functioning of perennial watercourses (Acuña et al., 2017). In France, a channel legally qualifies as a watercourse under the Water Law only if it exhibits “sufficient flow most of the year”, thereby excluding large swaths of the river network by definition (Instruction Du Gouvernement Du 3 Juin 2015 Relative à La Cartographie et l’identification Des Cours d’eau

et à Leur Entretien, 2015). Similar jurisdictional exclusions based on flow permanence are common elsewhere, including in the USA, Australia, and Europe (Baattrup-Pedersen et al., 2018; Sulliván & Gardner, 2023; Taylor et al., 2011; van Meerveld et al., 2020). When they are included in watercourse management and conservation measures, NPRs are usually treated as if they were perennial or a fully terrestrial ecosystem (Acuña et al., 2017), failing to account for the complex role that flow cessation and shifting aquatic-terrestrial habitat dynamics play for biodiversity and ecosystem processes (Datry, Fritz, et al., 2016). This is the case, for example, in many biological assessments of the ecological condition of river ecosystems (i.e., biomonitoring) and e-flows frameworks (Acuña et al., 2020; Stubbington et al., 2018).

The goal of biomonitoring is to detect and quantify the effect of anthropogenic activities on the ecological conditions of river ecosystems, to evaluate their integrity relative to an uninfluenced state (Kuehne et al., 2017). Biomonitoring is a central tenet of national and international initiatives to improve the ecological quality of rivers and streams, such as the EU Water Framework Directive (WFD) and the US Clean Water Act (Davies & Jackson, 2006; Stubbington et al., 2018). It depends on the establishment of reference conditions that define the species composition of biotic communities that are indicative of minimally disturbed sites (Bonada, Prat, et al., 2006). However, biomonitoring indices have historically been calibrated in perennial sites with higher species diversity than NPRs (Mazor et al., 2014; Reyjol et al., 2014). Therefore, the ecological conditions of reaches undergoing flow cessation have either gone unassessed or been misclassified as degraded because pollution-sensitive species used as indicators are also commonly sensitive to drying. Natural drying and human activities can independently and interactively disturb river ecosystems, so disentangling their respective contribution to observed biodiversity patterns is an arduous task without developing a bespoke system of indices for NPRs (Stubbington et al., 2021). Multiple adjustments have been proposed to better assess the ecological conditions in NPRs. These include defining NPR-specific reference sites (Munné et al., 2021), identifying pollution-sensitive taxa with a range of drying tolerance (Arias-Real et al., 2022), complementing standard indices with dry-phase indicators of ecological quality like terrestrial plants (Stubbington et al., 2019), and accounting for metacommunity processes like dispersal that drive the distribution and abundance of species in hydrologically dynamic river networks (Cid et al., 2020).

Current e-flows frameworks similarly cater to the functioning of perennial watercourses and are unfit to protect or restore spatiotemporal dry-wet dynamics in NPRs (Acuña et al., 2020). Flow cessation is rarely explicitly considered in the design of e-flows, partly due to the difficulty of quantifying and managing the effects of no-flow events on biotic communities and the diversity of aquatic states that ensue (Acuña et al., 2020). Hydrological methods of e-flow design, especially, employ metrics that fail to capture crucial aspects of the flow intermittence regime. For instance, Q_{90} (the low quantity exceeded 90% of the time) may be equal to 0 and would imply that a river could theoretically be kept dry. On the opposite end, setting a minimum flow downstream of a reservoir as a percentage of mean annual flow could suppress no-flow events altogether. Most hydraulic habitat models are unreliable as well in low-flow conditions or once flow stops (Acuña et al., 2020). Holistic methods are more flexible in that they can be adapted to a given ecosystem and incorporate a diversity of data types, including expert knowledge. In response to these shortcomings, several frameworks have been developed over the past few years to improve e-flow design in NPRs, including hydrologic metrics specifically describing the flow intermittence regime (Acuña et al., 2020; Aguilar & Polo, 2016; Conallin et al., 2018; Seaman et al., 2016; Theodoropoulos et al., 2019; Thoms & Sheldon, 2002). Nevertheless, these frameworks also fall short from quantitatively incorporating the important role that metacommunity dynamics play in the ecology of NPRs. They still assume that environmental conditions at individual sites are the only determinant of local community structure, which overlooks the interplay between local (i.e., flow regime in the reach) and regional (i.e., dispersal and connectivity among reaches across the network) processes resulting from the spatiotemporal patterns of drying and rewetting across the river network (Heino, 2013; Poff, 2018).

1.1.8. Data challenges for studying and managing NPRs

Beyond the inadequacy of scientific, regulatory and management frameworks, a major hurdle to the study and management of NPRs is the dearth of reliable data on their ecology, hydrology and distribution (Acuña et al., 2017; Datry, Boulton, et al., 2023; Krabbenhoft et al., 2022). The remoteness of NPRs is part of this challenge. NPRs are most common in remote areas — arid, semi-arid, polar, and alpine regions — where the factors that result in the prevalence of NPRs also tend to hinder human settlement and economic development. Remoteness is thus compounded by limitations in the resources available for monitoring. Even in wetter climates and areas with more scientific resources, NPRs occur in headwaters

and away from urban centers (Kampf et al., 2021). When ecological data are available for NPRs, they usually reflect the flowing phase and do not include lentic species in pools once flow stops, those found active or in aestivation zones (i.e., as a 'seedbank') in the hyporheic, or terrestrial ones temporarily colonizing the channel bed (Stubbington et al., 2019).

In terms of hydrology, non-perennial rivers and streams present particular challenges to the measurement of discharge, which contributes to their under- and misrepresentation in hydrometric networks (van Meerveld et al., 2020; Zimmer et al., 2020). Not only is it difficult to establish and maintain streamflow gauging stations on NPRs (Tilrem, 1986) but discharge measurements on these watercourses are also error prone (Zimmer et al., 2020) and imperfectly capture the spatiotemporal variability and range of hydrological states in NPRs (Eastman et al., 2021; Jaeger et al., 2021; Sefton et al., 2019). The difficulty of establishing and maintaining streamflow gauging stations on IRES has long been recognized, as illustrated by the seminal 1986 WMO publication on "Level and discharge measurements under difficult conditions" (Tilrem, 1986). NPRs are also particularly difficult and onerous to gauge because of the dynamism of their controls and hydrology (Tilrem, 1986). Many lowland NPRs flow through alluvial channels which are susceptible to erosion and accretion and can carry high sediment loads. Rapidly changing braiding and meandering channels, banks, and channel bed structures (i.e., ripples, dunes, standing waves, anti-dunes) render the stage-discharge relationship unstable in those rivers (Tilrem, 1986). At low discharge, streamflow may be constrained within small channels whose position shifts within and between seasons. High sediment loads typical of alluvial channels or glacier-fed watercourses can silt up equipment and prevent point discharge measurements.

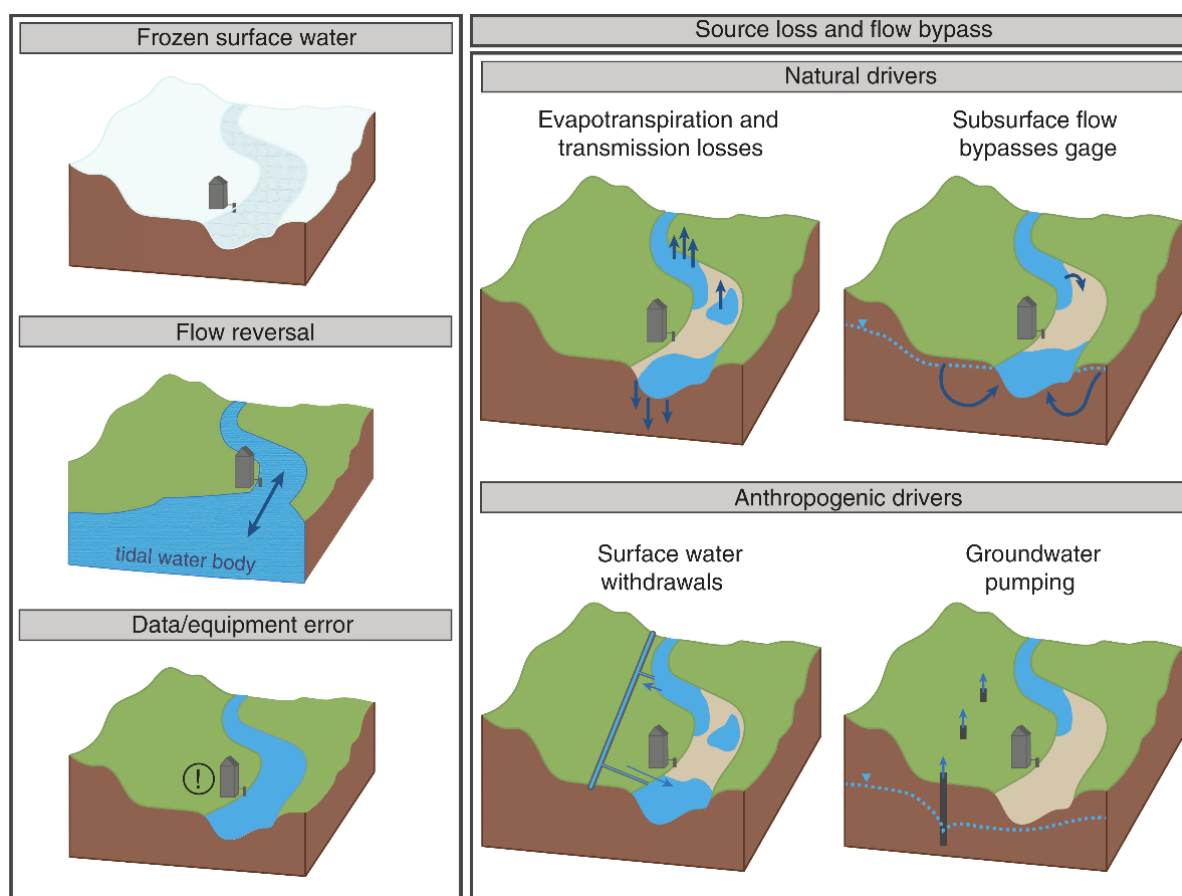


Figure 1.13. Common scenarios of zero-flow readings at gauging stations.

Left pane: situations that can produce a zero-flow reading despite the presence of water; right panel: situations that produce zero-flow readings due to variable drivers. Panel order does not imply prevalence on the landscape. Reproduced from Zimmer et al. (2020)

Even when a gauging station has been installed and a rating curve is regularly maintained for a non-perennial river section, interpreting the resulting discharge measurements can be error prone (**Figure 1.13**; Zimmer et al., 2020). Direct measurements of discharge at low-flow are more difficult, and the lower range of rating curves thus tends to have higher uncertainties because of measurement errors and a lower sensitivity of controls at low flow conditions (Mcmillan et al., 2012; Tilrem, 1986; WMO, 2010a, 2010b). Measurements may not even be taken during the low-flow season, potentially missing short yet crucial rewetting events (Olden et al., 2021). Furthermore, the majority of non-perennial rivers are “losing rivers”, characterized by significant transmission losses through infiltration to groundwater and evapotranspiration (Shanafield et al., 2021). The proportion of streamflow that occurs as hyporheic flow or infiltrates into groundwater, which is not captured by stage measuring gauging stations, can severely affect discharge estimates in NPRs. Yet piezometric stations are seldom linked to surface hydrometric networks. Finally, zero-flow readings at streamflow gauging stations can stem from multiple circumstances. Usually, these readings reflect true

flow cessation due to various natural or anthropogenic processes. However, flow reversal (e.g., due to tidal influence), instrument malfunctioning, and data entry or processing errors are also common events that can result in zero-flow readings in spite of the continued flow of water in the channel (Zimmer et al., 2020). Reported time series data may contain ambiguity between zero-flow and no-data entries, leading to potential underestimation of zero-flow (if masked as no-data). Ideally, each streamflow record would be accompanied by detailed information and flags describing the quality of individual daily values. However, this information is typically unavailable or difficult to access. These limitations have resulted in scant, spatially biased, and qualitatively uneven discharge data for NPRs globally, particularly in arid and semi-arid areas and on small headwater streams (Krabbenhoft et al., 2022; Zimmer et al., 2020).

Even hydrological models struggle to produce robust no-flow predictions despite their importance for management (e.g., to estimate the natural hydrology of NPRs for setting e-flow requirements; Jaeger et al., 2014; Llanos-Paez et al., 2022; Shanafield et al., 2021). Runoff modelling in semi-arid and arid regions remains an outstanding challenge (Pilgrim et al., 1988; Yu et al., 2020). Elsewhere, modelling limitations mainly reside in the difficulty of accurately modeling the diversity of factors leading to intermittency, notably transmission losses and variations in groundwater inputs, as well as the longitudinal succession of wet and dry reaches (Mimeau et al., 2024; Shanafield et al., 2021).

1.1.9. The power and limits of maps for NPR science and management

Scientific and management values of maps

If a picture is worth a thousand words, a map is worth a book (or a thesis). The spatial location and configuration of an ecosystem are inextricable from its functioning and its interrelatedness with other elements of the landscape constitutive (Tobler, 1970; Turner, 1989). This is especially true for river networks, which are uniquely structured and interconnected. Consequently, maps provide indispensable information for scientific analysis, policy development, and ecosystem management. Without access to accurate maps, these endeavors are severely hindered.

Scientifically, maps give us a sense of the scope of a phenomenon, its heterogeneity and connectivity, they seek generality beyond the eye level, unifying ground observations (**Figure 1.14**). At the basin scale, maps underpin fluvial landscape ecology by enabling a continuous

view of river networks and their basin as *riverscapes* (Fausch et al., 2002; Torgersen et al., 2022). This concept of riverscape has been used in academia for decades but only recent advances in remote sensing, modelling, and sampling designs have allowed implementing it quantitatively (Carbonneau et al., 2012). At national to global scales, maps are increasingly helping scientists and the public take stock of the role of river ecosystems in the Earth system and the human pressures threatening their resilience. Only a third of the world's large rivers remain free flowing (Grill et al., 2019). More than one million barriers fragment Europe's rivers (Belletti et al., 2020). Rivers exhale between 112 and 209 Tg of carbon per month (Liu et al., 2022). All three of these statements are based on some form of cartography and have galvanized further research or conservation efforts. In a more technical sense, maps represent geographic gaps in knowledge, support sampling design and statistical analyses that account for the spatial relationships among objects and variables, and enable the upscaling of discrete measurements to the river network scale and beyond.

Maps are a foundational tool for policymakers, environmental agencies, and resource managers. In addition to conveying the extent and characteristics of aquatic ecosystems, they support the development and enforcement of environmental laws and management measures (McDonnell, 2008), for example, by delineating areas subject to water quality standards and habitat protection zones. In the USA, maps of watercourses are needed by land developers for evaluating if a proposed dredging, filling, or discharging activity may affect a "Water of the United States" and requires permitting under the Clean Water Act (Fesenmyer et al., 2021). These maps also aid assessments of environmental risks from flooding and underpin scenario modeling and decision support systems, thus increasing the effectiveness of environmental governance and conservation efforts. The representation of a watercourse on a map influences whether it is managed or not, protected or not, and how.

River classifications

One specific type of map that underlies multiple practices of river science and management are river classifications. River classifications seek to systematically group rivers and streams into types that are most similar in terms of their environmental or hydrological attributes, and most dissimilar to rivers in other groups (Olden et al., 2012). These classifications are used in hydrology for regionalizing hydrologic model parameters and predicting discharge in ungauged catchments (Tasker, 1982; Wagener et al., 2007), to guide the spatial design of monitoring and conservation programmes by providing representative management units among which sites and resources can be strategically allocated (Higgins et al., 2005; Kennard et al., 2010), as well as for biomonitoring and determining the e-flows requirements of rivers. In biomonitoring, river classifications are used to identify groups of ecosystems that have similar natural conditions, usually in terms of biotic community composition; the ecological condition of a site can then be quantified by comparing its species composition to that in anthropogenically uninfluenced sites within the same group (Reynoldson et al., 1997). Such typologies are at the core of ecological condition assessments under the European Water Framework Directive (Lyche Solheim et al., 2019). River classifications constitute pre-requisites for determining and implementing e-flows at regional scales as well (Olden et al., 2012). The Ecological Limits of Hydrologic Alteration (ELOHA) framework (Poff et al., 2010) for example, one of the most widely used regional e-flows assessment approach, calls for a river classification grouping rivers that are similar in terms of flow regime and geomorphology. This classification serves to identify watercourses in which ecosystems respond similarly to anthropogenic changes in hydrology and can thus be managed similarly. The relationships between flow alteration (e.g., change in summer baseflow) and ecological metrics (e.g., salmon juvenile abundance) determined for a limited set of rivers can then be presumptively applied to other rivers of the same type in the region (Arthington et al., 2006; Harris et al., 2000; Poff et al., 2010).

Cartography is scientific, social and political

Natural scientists usually approach maps as objective representations of the structure and arrangement of phenomena on the Earth's surface, yet maps are not neutral or apolitical (Harley, 1989). Every map is the result of an array of subjective choices about what to represent or not, and how. These decisions partly fall on the individual cartographer but also depend on their institutional and societal context, more broadly reflecting their positionality

(Kitchin et al., 2009). Maps are social and political as well because they “codify, legitimate, and promote the world views that are prevalent in different periods and places” (Harley, 1989). By influencing how a space is understood, studied, governed and managed, they are co-constitutive of the spaces they represent (Del Casino & Hanna, 2005). In France, for example, many topographic maps were first drawn for military intelligence (Cinotti & Dufour, 2019). As such, they are thorough representations of hydrographic elements of strategic importance but omit many smaller headwater streams. Nonetheless, these maps are used as the basis to define the jurisdictional scope of environmental laws that protect river ecosystems, which in turn influences the fate of watercourses (ONEMA & IGN, 2015).

Uneven cartography of NPRs: *aqua temporaria incognita*

Compared to their perennial counterparts, NPRs are seldom mapped or inaccurately so, particularly in headwater catchments (**Figure 1.15**) — so much so that intermittent headwater streams have been called *aqua temporaria incognita* (van Meerveld et al., 2020). The primary sources of large-scale information on the distribution of NPRs are national hydrographic datasets, typically extracted from traditional paper topographic maps on which NPRs are represented by dashed lines (Christensen et al., 2022). However, these hydrographic maps exhibit high levels of inconsistency among regions and cartographers in both stream density and the status of individual segments, even for a fixed map scale (e.g., 1:24,000; Colson et al., 2008; Fritz et al., 2013; Stoddard et al., 2005). For example, classifications of streamflow intermittence within the U.S. National Hydrography Datasets (NHDPlus), the reference maps for studying and managing watercourses at both federal and state level, have shown misclassification rates as high as 50% compared to independent field surveys (Fritz et al., 2013; Stoddard et al., 2005). This lack of reliable cartographic data on ephemeral streams was used as a justification by government agencies in the USA not to assess the potential consequences for NPRs of amendments to the jurisdictional scope of the Clean Water Act (Fesenmyer et al., 2021).

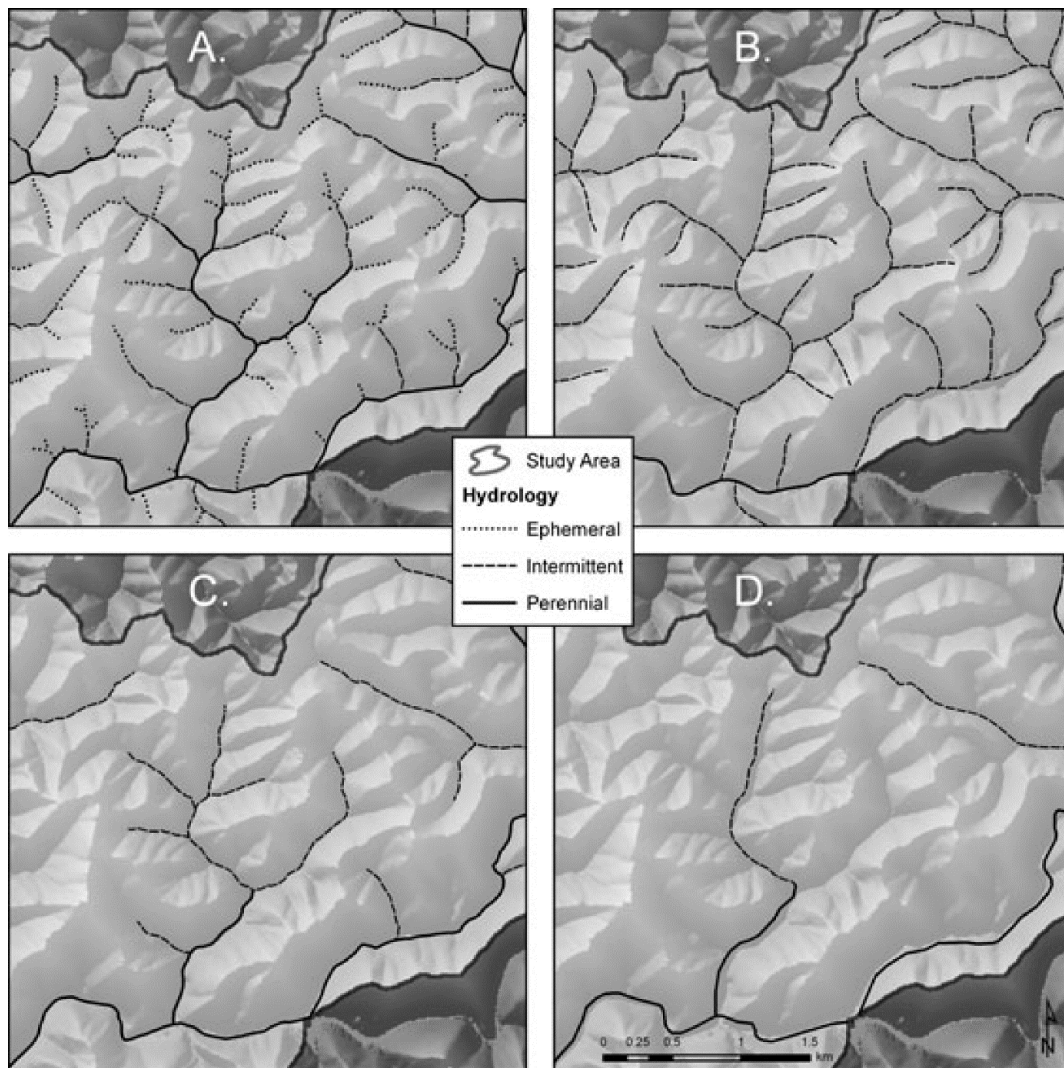


Figure 1.15. Various representations of the stream network of a catchment in Kentucky (USA).

(a) field surveys of channel and flow origins, (b) the digitized national resources conservation service soil map (1:15,840 scale), (c) the US high-resolution National Hydrography Dataset (NHD) flowlines (1:24,000 scale), and (d) the medium-resolution NHD flowlines (1:100,000 scale). Reproduced from Fritz et al. (2013).

This problem is not confined to the USA though. In other countries as well, all studies that have thoroughly mapped temporary streams found greater extents of NPRs in the field than what is represented by standard topographic maps (van Meerveld et al., 2020).

Furthermore, neighboring topographic map sheets often differ in the implementation of criteria used to map flow intermittence, resulting in artificial boundaries between regions in terms of the prevalence of NPRs (Colson et al., 2008; Greenhill et al., 2024). Consequently, national hydrographic datasets can only serve as qualitative benchmarks for assessing the distribution and prevalence of NPRs. Combined with the underrepresentation of NPRs in the global hydrometric network and the inability of hydrological models to reliably simulate flow cessation, this cartographic deficiency perpetuates the historical bias against NPRs in the science and management of river ecosystems.

1.2. Problem statement and objective

Over the past 50 years, the interdisciplinary field of river science has shed light on the unique structure, functioning, and vulnerability of running water ecosystems. We now know that rivers and streams disproportionately contribute to global biodiversity and biogeochemistry as well as to people's well-being and cultures. We also know that, as integral elements of the landscape and of societies, river ecosystems are under inordinate pressure from human activities and climate change, which is rapidly compromising their ecological integrity and associated ecosystem services. Until recently, however, river research and management were singularly focused on perennial watercourses, overlooking non-perennial rivers and streams (NPRs) that recurrently cease to flow. NPRs have been under-valued, under-studied, and under-monitored, leading to their chronic mismanagement, ranging from pollution and habitat destruction of the dry channel to inadequate flow management. In many countries, for example, regulatory definitions of watercourses that establish the scope of environmental protection to freshwater ecosystems exclude most NPRs; and common sustainable management practices like biomonitoring and environmental flows are not adapted to their distinct functioning. Even their prevalence in the landscape remains largely unquantified. Although previous efforts suggested that NPRs may comprise as much as 50% of the global river network length, there has been no dedicated effort to map their distribution and prevalence at the global scale.

The main goal of this thesis is to advance our understanding of the global prevalence and diversity of NPRs, and to improve their integration in river policy and sustainable management. To do so, I endeavored to address three main knowledge, methodological, and management gaps:

- The lack of a global hydrological foundation for the science and management of non-perennial rivers and streams.
- The uneven representation of non-perennial streams in jurisdictional maps of watercourses defining the scope of environmental protection laws.
- The inadequacy of conceptual and operational frameworks for the design and implementation of environmental flows in river networks with high prevalence of non-perennial reaches.

To address these gaps, my thesis is divided into four chapters (Chapters 2 to 5; **Figure 1.16**).

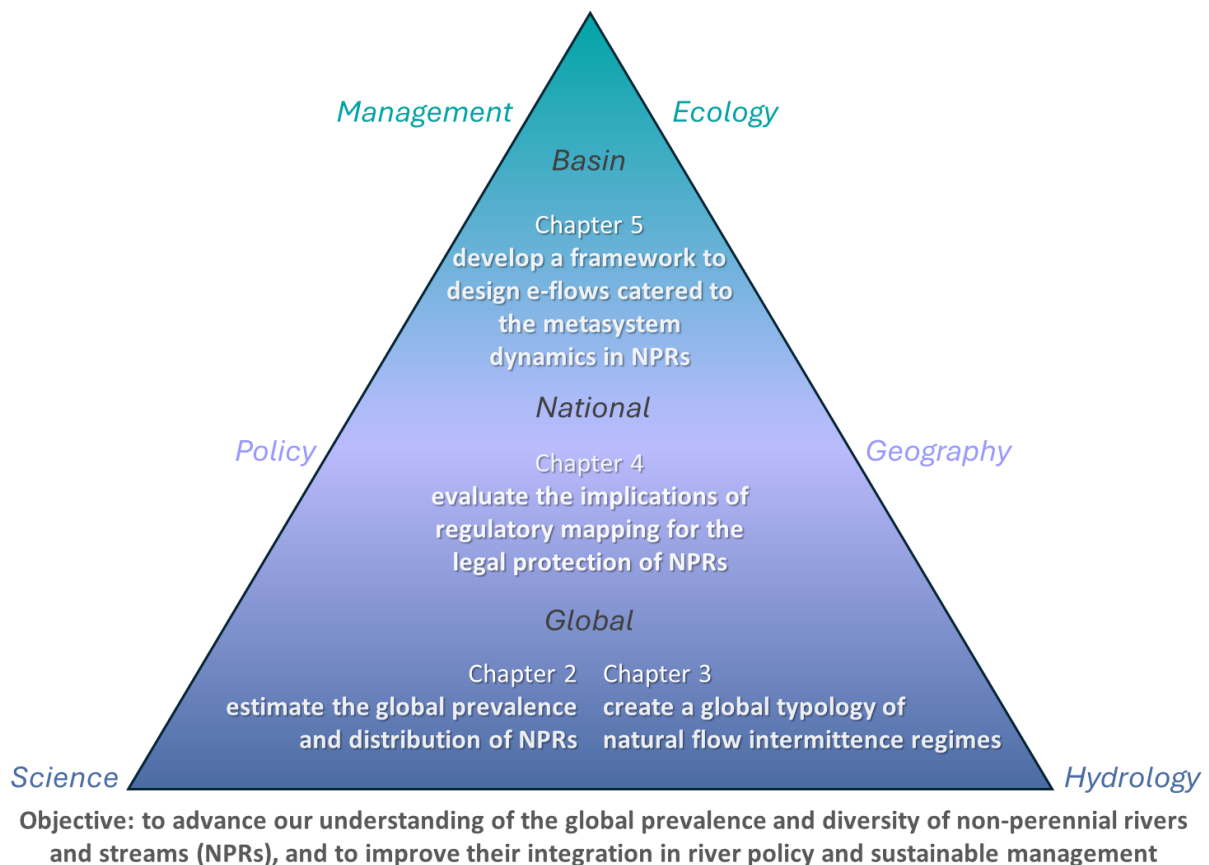


Figure 1.16. Summary diagram of the structure of this thesis.

The four chapters of this thesis span a general gradient across disciplines (hydrology, geography, and ecology), primary applications (science, policy, and management), and scales (global, national, basin), although all four chapters are interdisciplinary, with diverse applications, and rely on the river reach as the primary unit of analysis.

The aim of Chapter 2 is to develop a global model for estimating the natural prevalence and distribution of NPRs across the global river network. The objective of this study is also to produce a spatially explicit dataset of NPRs, which represents a pre-requisite for the global study of their hydrology, ecology, and biogeochemistry.

The aim of Chapter 3 is to evaluate and classify the global diversity of natural flow intermittence regimes. This study performs a hydrological classification to create a typology of global NPRs in terms of long-term intra- and interannual duration, frequency, timing, and climate dependence of no-flow events, and according to the rate of change in discharge magnitude at the seasonal and flow-event scales. This classification provides a hydrological organizing framework that can guide scientific inquiry, modelling, and hypotheses on the processes underlying flow intermittence, and identify management units that can serve for monitoring, water resource planning, and conservation like environmental flow design.

The aim of Chapter 4 is to evaluate the implications of legal definitions of watercourses and their interpretation through jurisdictional mapping on the degree of protection of headwater and non-perennial streams under environmental laws. Taking France as a case study, I compile and analyze the first national map of watercourses protected under the Water Law and quantitatively evaluate whether first-order and non-perennial reaches are disproportionately excluded from this environmental regulatory framework. I compare my findings to analyses conducted in other countries and discuss the broader implications of and possible socio-political factors contributing to the uneven representation of NPRs.

The aim of Chapter 5 is to broaden the set of ecological processes integrated into the design, implementation, and monitoring of e-flow programs with the end goal of better protecting the distinct ecological structure and dynamics of NPRs. Through a conceptual paper, I propose the integration of metacommunity concepts and tools into the science and implementation of e-flows. I first illustrate how metacommunity processes like dispersal and biotic interactions influence ecological responses to hydrological alterations — conceptually, through simulation modeling, and based on empirical examples from the literature. I then present a practical framework for devising e-flow strategies aimed at protecting or reinstating these metacommunity dynamics. I focus particularly on e-flows because this management approach is now well integrated in policies and water resource planning practice worldwide, supported by a large body of scientific literature, and yet particularly maladapted to protect NPRs.

Chapters 2 and 3 exclusively advance our understanding of the geography and hydrology of NPRs whereas Chapters 4 and 5 adopt a broader perspective applicable to all river and stream ecosystems. Each of these latter two chapters includes extensive sections on NPRs, yet they do not limit their focus on the extent of legal protections for watercourses and improving e-flows frameworks specifically for NPRs. I intentionally opt for this inclusive scope — compartmentalizing the study and management of lotic ecosystems between perennial and non-perennial ones would be as unproductive as the historical bias for perennial watercourses and anecdotal treatment of NPRs. The take-home message of this approach is that NPRs are present in and essential to the integrity of nearly all river networks globally, even when confined to the headwaters. As such, improving regulatory and management frameworks to better account for their distinct hydrology and ecology will

improve the effectiveness of protection and restoration measures for river networks in their entirety.

The ultimate aim of this thesis is to put NPRs on the map, both literally and conceptually. Literally by creating a cartographic basis for their study and management, and by quantifying their exclusion from regulatory maps. Conceptually by bringing attention to their prevalence, distribution, and diversity, and by creating an operational framework to more effectively mitigate the deleterious effect of anthropogenic flow alterations on these unique ecosystems.

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Chapter 2

Global prevalence of non-perennial rivers and streams

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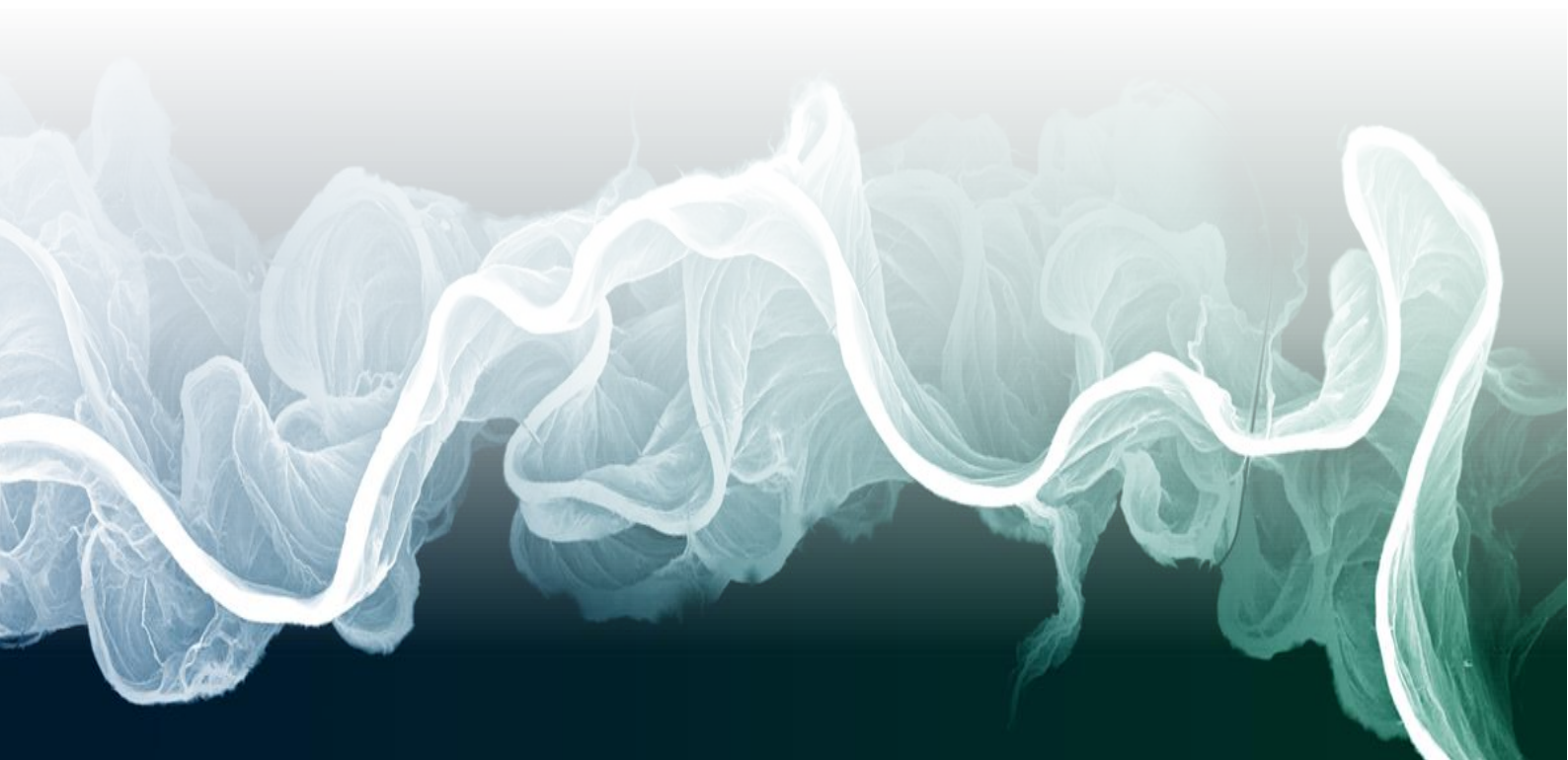
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2.1. Abstract

Flowing waters have a unique role in supporting global biodiversity, biogeochemical cycles and human societies (Datry, Foulquier, et al., 2018; Larned et al., 2010; Leigh & Datry, 2017; Marcé et al., 2019; Steward et al., 2012). Although the importance of permanent watercourses is well recognized, the prevalence, value and fate of non-perennial rivers and streams that periodically cease to flow tend to be overlooked, if not ignored (Acuña et al., 2014; Fritz et al., 2017; Sullivan et al., 2020). This oversight contributes to the degradation of the main source of water and livelihood for millions of people (Steward et al., 2012). Here we predict that water ceases to flow for at least one day per year along 51–60 per cent of the world's rivers by length, demonstrating that non-perennial rivers and streams are the rule rather than the exception on Earth. Leveraging global information on the hydrology, climate, geology and surrounding land cover of the Earth's river network, we show that non-perennial rivers occur within all climates and biomes, and on every continent. Our findings challenge the assumptions underpinning foundational river concepts across scientific disciplines (Allen et al., 2020). To understand and adequately manage the world's flowing waters, their biodiversity and functional integrity, a paradigm shift is needed towards a new conceptual model of rivers that includes flow intermittence. By mapping the distribution of non-perennial rivers and streams, we provide a stepping-stone towards addressing this grand challenge in freshwater science.

2.2. Main text

Almost every river network on Earth includes channels that periodically cease to flow. From Himalayan snow-fed creeks to occasionally water-filled Saharan wadis, river flow cessation is naturally prevalent worldwide. Yet the global extent of intermittent rivers and ephemeral streams (IRES) is largely unknown. IRES vary widely in size and flow duration, encompassing all non-perennial watercourses—from large, rarely intermittent rivers with nearly continuous channel flow to mostly dry streams that only flow after intense rainfall (see **Extended Data Table 2.S1** for additional definitions and IRES terminology). IRES are pivotal components of the landscape, critically contributing to the biodiversity (Larned et al., 2010; Leigh & Datry, 2017), biogeochemical processes and functional integrity of fluvial systems (Datry, Foulquier, et al., 2018; Marcé et al., 2019). Many formerly perennial rivers and streams have become intermittent in the past 50 years owing to water abstractions, climate change and land use transitions, including sections of iconic rivers such as the Nile, Indus, Yellow and Colorado (Datry et al., 2014; Ficklin et al., 2018). Given continued global change, an increasingly large proportion of the global river network is expected to seasonally cease to flow over the coming decades (Jaeger et al., 2014; Pumo et al., 2016).

Despite their prevalence, IRES are frequently mismanaged owing to a lack of recognition (Acuña et al., 2014), or altogether excluded from management actions and conservation laws (Fritz et al., 2017). As a result, non-perennial rivers and streams are being degraded at an alarming rate (Acuña et al., 2014). Recent attempts to further remove IRES from environmental legislation and national water governance systems (for example, in the USA; Sullivan et al., 2020), if implemented, would worsen their already inadequate protection. The long-standing neglect of IRES is partly the result of their continued omission from scientific research. Most freshwater science has focused on the functioning and conservation of perennial water bodies, and only recently has riverine flow cessation become its own subject of study (Allen et al., 2020; Datry et al., 2014; Larned et al., 2010). Consequently, science-based methods for managing these unique ecosystems, such as biomonitoring tools and protocols, are still limited or absent (Steward et al., 2012; Stubbington et al., 2018). Management frameworks also need to be adapted to conserve environmental flows in IRES (Acuña et al., 2020)—that is, the quantity, timing, and quality of freshwater flows necessary to sustain aquatic ecosystems and their associated benefits (Arthington et al., 2018). But

perhaps the most important gap until now has been our inability to quantify and map IRES worldwide. Accurate mapping of non-perennial rivers and streams would provide crucial baseline information to determine and monitor their role in biogeochemical and water cycles and in supporting global biological diversity (Datry, Foulquier, et al., 2018). Streamflow monitoring data for IRES are scant, spatially biased, and of uneven quality (Zimmer et al., 2020). Indeed, most streamflow gauging stations are installed on large, perennial rivers worldwide (Zimmer et al., 2020). The dearth of primary data has triggered the development of alternative methods to map IRES, including citizen science or expert field observations of streamflow state, in situ sensor networks and remote sensing (Beaufort et al., 2018; Jaeger & Olden, 2012; Yu et al., 2020). However, these efforts only provide information at local scales and suffer from several limitations (e.g., remote sensing of smaller rivers can be obstructed by overhanging riparian vegetation and cloud cover; Yu et al., 2020).

Model-based classifications of river types, either IRES-focused (for example, in mainland France; Snelder et al., 2013), the north-western USA (Jaeger et al., 2019), eastern Australia (Yu et al., 2019) or general (for example, Australia; Kennard et al., 2010; California; Lane et al., 2017), have also provided important baseline estimates of the spatial distribution of IRES from the catchment to the national scale. However, a rigorous estimation of the global prevalence and distribution of IRES is still lacking. In this study, we developed a statistical random forest (RF) model (see Methods for details) to produce the first reach-scale estimate of the distribution of IRES for the 23.3 million kilometres of mapped rivers and streams across the globe (except Antarctica) whose long-term average naturalized discharge exceeds $0.1 \text{ m}^3 \text{ s}^{-1}$, and then extrapolated our IRES estimates to the nearly 64 million kilometres of rivers and streams with an average discharge higher than $0.01 \text{ m}^3 \text{ s}^{-1}$. For this purpose, we linked quality-checked observed streamflow data from 5,615 gauging stations (on 4,428 perennial and 1,187 non-perennial reaches) with 113 candidate environmental predictors available globally (**Extended Data Table 2.S2**). Predictors included variables describing climate, physiography, land cover, soil, geology and groundwater, as well as estimates of long-term naturalized (that is, without anthropogenic water use in the form of abstractions or impoundments) mean monthly and mean annual flow (MAF), derived from a global hydrological model (Water-GAP 2.2; Müller Schmied et al., 2014). Following model training and validation, we predicted the probability of flow intermittence for all river reaches in the

RiverATLAS database (Linke et al., 2019), a digital representation of the global river network at high spatial resolution.

2.3. Prevalence and distribution of IRES

We predict that water ceases to flow for at least one day per year, on interannual average, along 41% of the mapped global river network length, that is, all rivers and streams with $MAF \geq 0.1 \text{ m}^3 \text{ s}^{-1}$ (Figure 2.1, Table 2.1).

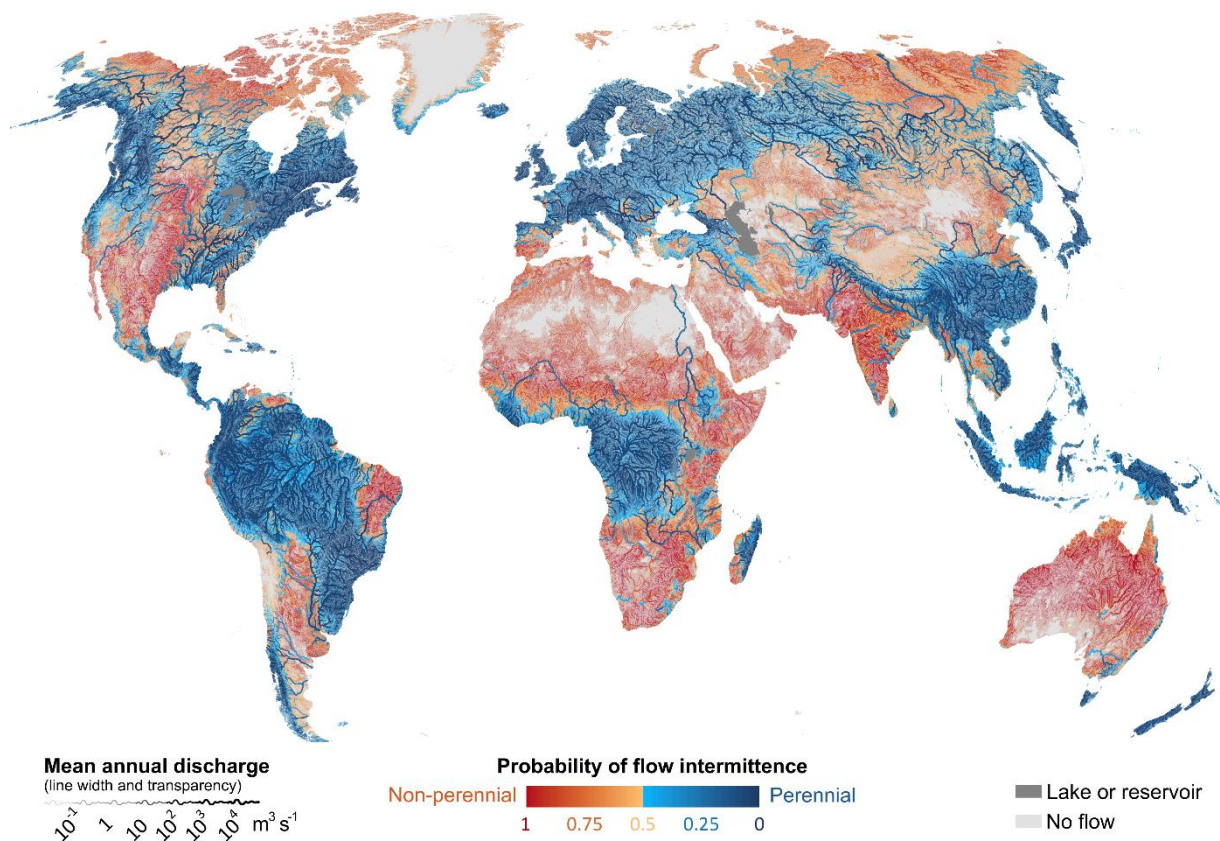


Figure 2.1. Global distribution of non-perennial rivers and streams.

Intermittence is defined as flow cessation for at least one day per year on average. The median probability threshold of 0.5 was used to determine the binary flow intermittence class.

However, any estimate of the percentage of IRES reaches in a river system, whether for a small catchment or for the globe, is inherently dependent on cartographic scale. Although many dryland rivers exhibit downstream decreases in discharge owing to channel evaporation and transmission losses (Tooth, 2000), river flow tends to become more permanent with increasing drainage area and distance from the headwaters in a basin (Costigan et al., 2016), which is well reflected in the predictions of our model. Because of the dendritic nature of river networks, small headwater streams, which are more prone to

intermittence, make up a greater proportion of the total stream length than larger downstream rivers (Benstead & Leigh, 2012). Consequently, the percentage of the river network length that is non-perennial increases with decreasing size of the smallest mapped stream. To account for this distribution, we made a first-order approximation of the prevalence of intermittence in small streams by extrapolating our estimate to streams with $0.01 \text{ m}^3 \text{ s}^{-1} \leq \text{MAF} < 0.1 \text{ m}^3 \text{ s}^{-1}$ (see Methods for details). Including this size class, we estimate that 60% of all rivers and streams globally are IRES; and we found a lower bound of this estimate at 51% after applying an alternative, more conservative extrapolation approach. This demonstrates that IRES represent the world's most widespread type of rivers.

Table 2.1. Global prevalence of IRES across climate zones and streamflow size classes

Climate zone ^a	Prevalence of intermittence (% of network length) by streamflow size class ($\text{m}^3 \text{ s}^{-1}$)							Total intermittence % length	Total stream length ^b ($\times 10^3 \text{ km}$)
	Extrapolated ^c		Mapped					Including (excluding) stream class ^c	
	[10^{-2} , 10^{-1})	[10^{-1} , 1)	[1, 10)	[10, 10^2)	[10^2 , 10^3)	[10^3 , 10^4)	$\geq 10^4$		
Extremely hot and	100	100	100	98	49	0	-	99 (98)	1,032 (249)
Hot and arid	100	100	100	97	46	0	-	99 (98)	990 (238)
Arctic 1	100	92	71	100	-	-	-	96 (92)	11 (6)
Warm temperate	99	96	89	59	11	0	0	96 (89)	1,351 (444)
Extremely cold	100	93	69	34	0	-	-	96 (87)	766 (243)
Extremely hot and	99	90	95	90	45	0	0	95 (89)	4,551 (1,605)
Arctic 2	100	89	18	8	-	-	-	92 (82)	98 (41)
Cool temperate	94	81	70	37	2	0	-	87 (72)	1,709 (552)
Extremely cold	96	70	45	34	26	22	0	83 (61)	8,083 (3,051)
Extremely cold	92	59	10	1	0	-	-	72 (50)	227 (109)
Cold and mesic	90	47	26	6	3	0	0	70 (37)	8,189 (3,084)
Warm temperate	84	45	35	16	1	0	0	63 (39)	3,582 (1,646)
Hot and dry	77	47	36	23	7	0	0	62 (41)	4,054 (1,683)
Cool temperate	65	46	34	11	0	0	0	57 (39)	4,087 (1,325)
Hot and mesic	77	30	24	23	5	0	0	54 (27)	4,452 (2,023)
Extremely hot and	35	18	20	21	4	0	0	30 (18)	19,117 (6,002)
Cool temperate	52	18	10	0	0	0	-	29 (13)	1,164 (691)
Cold and wet	34	1	0	0	0	0	-	14 (1)	493 (299)
World	70	47	35	26	9	1	0	60 (41)	63,956 (23,291)

^a Global Environmental Stratification (GENS; Metzger et al., 2013), see **Extended Data Figure 2.S1a**.

^b Excluding sections of river reaches contained within a lake.

^c Extrapolated statistics based on the main estimate (as opposed to the lower-bound estimate, see Methods for details).

For river flow to occur, water from rainfall, snowmelt, or releases from existing storage (for example, lakes, reservoirs, groundwater) must exceed losses from infiltration and evapotranspiration (Godsey & Kirchner, 2014). Climatic variables, in particular climate-induced aridity, were therefore the leading predictors of river flow cessation and the occurrence of IRES (**Figure 2.2**). Our model indicates that where evaporation rates

considerably exceed precipitation for at least part of the year, as expressed by a low aridity index (that is, the ratio of mean annual precipitation to mean annual potential evapotranspiration), river networks comprise large proportions of IRES. In extremely hot and xeric environments, which cover nearly one-tenth of the global landmass and encompass most of India, northern Australia and the Sahel region of Africa (see **Extended Data Figure 2.S1a** for the global typology of bioclimates; Metzger et al., 2013), 95% of the river and stream network length is prone to flow cessation ($MAF \geq 0.01 \text{ m}^3 \text{ s}^{-1}$; **Table 2.1**). In these environments, we find that even the main stem of major rivers, such as the Niger or Godavari, can dry out. Outside of arid regions, flow in river networks is primarily controlled by catchment processes influenced by interacting climate and basin conditions (Costigan et al., 2016; Larned et al., 2010). In cold climates, for instance, a combination of scarce precipitation, its storage as snow during winter months, and completely freezing streams (Tolonen et al., 2019) can lead to high prevalence of flow intermittence. Although not mapped in our study, even streams in Antarctica are known to flow intermittently owing to seasonal patterns of freezing, thawing and/or drying (Larned et al., 2010). In humid and temperate regions, IRES are concentrated in the upper end of channel networks where small drainage areas and steep slopes lead to rapid delivery of water to and through the river channel, causing a lack of buffering from variations in precipitation (Prancevic & Kirchner, 2019). Therefore, even in the wettest climates (for example, extremely hot and moist; **Extended Data Figure 2.S1a**), up to 35% of headwater streams are non-perennial (**Table 2.1**). In lowland and large basins, temporary storage and subsequent attenuated release from groundwater, lakes and wetlands, as well as the averaging of local hydrologic variability across a larger drainage area lead to more balanced, steady and thus perennial flow (Costigan et al., 2016). Our study presents a novel, empirically grounded effort to specifically quantify the prevalence of flow intermittence of rivers and streams globally, and to show that IRES occur across all climates and biomes, and on every continent (**Figure 2.1**, **Table 2.1**). Previous assessments reported from 29% to 36% of the global length of rivers to be non-perennial (FAO, 2014; Schneider et al., 2017; Tooth, 2000), with inferred and extrapolated estimates exceeding 50% (Datry et al., 2014; Raymond et al., 2013). However, these estimates were either generalized hypotheses (for example, based on the global distribution of drylands; Tooth, 2000), geographically constrained (that is, south of 60° N; FAO, 2014; Raymond et al., 2013; Schneider et al., 2017), or research by-products within

larger projects (for example, using a regional extrapolation to remove IRES from estimates of the global CO₂ emissions of inland waters; Raymond et al., 2013), rather than dedicated global IRES quantification efforts, and are therefore not directly comparable to our predictions. The FAO AQUAMAPS (2014) and GRIN (Schneider et al., 2017) global river networks, for instance, assume that streamflow cessation only occurs in arid and semi-arid areas. See **Supplementary Information section 2.9.1** for a review of how previous estimates relate to our predictions, including maps of AQUAMAPS and GRIN estimates. Our study improves on these previous estimates because it represents diverse hydrometeorological processes beyond aridity at the river reach scale (rather than at the basin scale; Raymond et al., 2013) by leveraging extensive, high-resolution global data on the hydrology, climate, physiography, geology and surrounding land cover of the world's river network. Furthermore, our study uses global empirical streamflow data for training and validation, which enabled our model to make fine-grained predictions of the intermittence class of rivers across all climates.

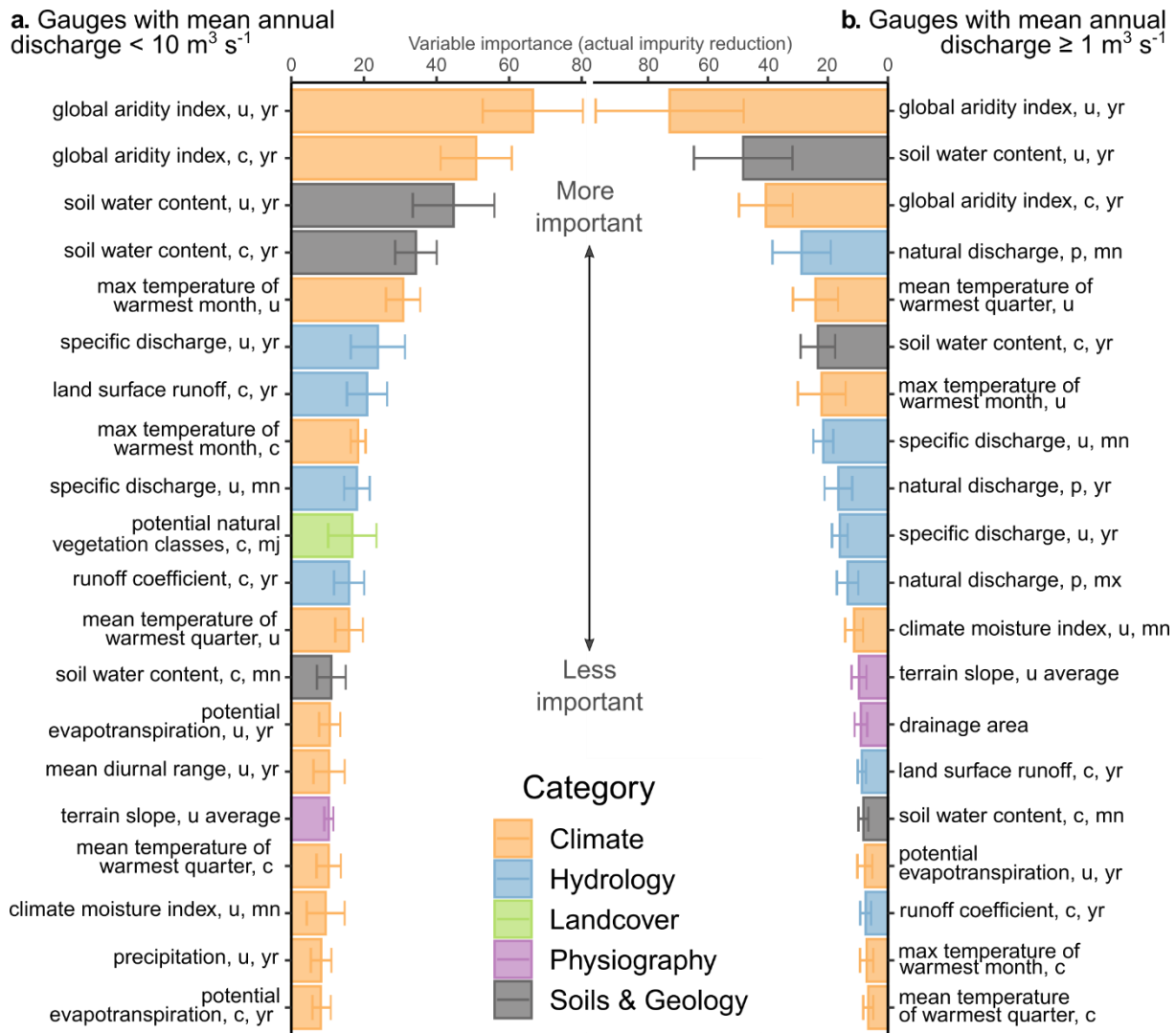


Figure 2.2. Climate-induced aridity and hydrologic variables are the main predictors of global flow intermittence.

a, b, The two sets of ranked predictor variables represent results from a split random forest model trained on gauges with a mean annual naturalized flow $< 10 \text{ m}^3 \text{ s}^{-1}$ (**a**) and gauges with a mean annual naturalized flow $\geq 1 \text{ m}^3 \text{ s}^{-1}$ (**b**). See Methods section ‘Machine learning models’ for details on model structure and implementation. Rectangular bars show the balanced accuracy-weighted average of actual impurity reduction (AIR; Nembrini et al., 2018) across non-spatial cross-validation folds and repetitions. The longer the bar (that is, the higher the AIR), the more important the variable in predicting flow intermittence. Error brackets show $\pm$ one weighted standard deviation of AIR. After the variables’ names, the first abbreviation denotes each variable’s spatial extent: p (derived at the pour point of the river reach), c (derived within the local catchment that drains directly into the reach), or u (derived within the total drainage area upstream of the reach pour point). The second abbreviation denotes each variable’s dimension: yr (annual average), mn (annual minimum), mx (annual maximum), or mj (spatial majority). See Methods and **Extended Data Table 2.S2** for data sources of variables.

2.4. Model performance and uncertainties

Performance analysis showed that our RF model could predict the binary flow intermittence class of streamflow gauging stations with high confidence. Cross-validation yielded an overall classification accuracy (the percentage of correctly classified gauges), ranging from 90% to 92% (depending on cross-validation method), and indicated that model predictions were unbiased globally—that is, adequately reflecting the proportion of IRES gauges in the training dataset. In general, sparsely gauged basins exhibit lower accuracy and higher bias (**Figure 2.3**; for example, in Africa and the Arctic). Boundary areas between climate zones, from mainly non-perennial regions to mainly perennial regions, are also characterized by higher misclassification rates (**Extended Data Figure 2.S2**). See **Figure 2.3** as well as **Extended Data Table 2.S3** for cross-validation results. Our model is based on an inclusive definition of IRES as those rivers and streams that cease to flow at least one day per year on average. To test the sensitivity of our results to the specific threshold of cessation length, we adapted our model and found that 44–53% of the global river network ceases to flow at least one month per year (lower-bound and main estimate, respectively, with $MAF \geq 0.01 \text{ m}^3 \text{ s}^{-1}$; see Methods; **Extended Data Figure 2.S1b, c**). Comparisons with national hydrographic datasets that include information on flow intermittence show that our model predicts a substantially higher prevalence of IRES in the contiguous USA than mapped in the country's atlas (by 31 percentage points), but coincides well with the patterns and extents depicted in the Australian, Argentinian and Brazilian atlases, and with model-generated maps (Snelder et al., 2013) in mainland France (**Extended Data Figures 2.S3–5**). The divergence observed in the USA (and to a limited extent in Australia) largely stems from the thresholds used to define IRES—when applying a minimum of one zero-flow month per year, our predictions more closely concur with the comparison dataset (**Extended Data Figures 2.S3, 2.S5**). At an even more local scale, comparing our model predictions against datasets of ground observation points of flow cessation for the US Pacific Northwest and mainland France reveals particular challenges in predicting flow intermittence for small rivers and streams (median $MAF \approx 0.5 \text{ m}^3 \text{ s}^{-1}$, **Extended Data Figure 2.S6**). Our model only achieved a balanced accuracy of 0.59 for mainland France ($n = 2,297$) and of 0.47 for the US Pacific Northwest ($n = 3,725$), both under- and overestimating reported IRES, respectively. We hypothesize that heavy water abstractions for domestic and agricultural use are the main reason for the greater contemporary prevalence of intermittence observed in France (Tramblay et al.,

2021; from 2012 to 2019) than predicted by our model, which aims to depict the natural distribution of IRES. In the US Pacific Northwest, a lower frequency of observations per site may have led to an underestimation of the prevalence of IRES in the comparison dataset, since the probability of observing a no-flow event increases with the number of observations. In addition, the mountainous landscape of the region is characterized by complex, local hydrological processes associated with snow and groundwater dynamics that our model can only superficially represent (Jaeger et al., 2019). Despite the increasing uncertainties at national and local scales, the global validation findings demonstrate that our overall statistics and large-scale representation of the spatial distribution of IRES are robust. However, we advise caution in using our model outputs to interpret fine-scale variations in intermittence for small spatial units or for small rivers and streams. The quality of our model results is constrained by the resolution of the river network and associated hydro-environmental predictor variables (250–1,000 m grid cells for most predictors; Linke et al., 2019). Accurate, fine-scale data on catchment soil types and lithology (for example, karst areas), riverbed sediments and groundwater dynamics would be needed to capture variation in the processes influencing flow intermittence at the sub-catchment and reach scales (Costigan et al., 2016). Groundwater–surface water interaction in particular is an enduring challenge in global hydrological modelling (Döll et al., 2016) and represents a key process that is only partly represented in our analysis. Also, potential local biases in training data (such as IRES being inconsistently represented in streamflow gauging networks) introduce uncertainties. For instance, model predictions in the south-eastern USA may overestimate the prevalence of IRES, owing to the relative scarcity of gauging stations for model training on small, perennial watercourses in that region. Similarly, the general under- and misrepresentation of small watercourses and arid regions in the global hydrometric network (Zimmer et al., 2020) causes substantial difficulty in consistently predicting the prevalence of IRES across the gamut of river types worldwide. Global hydrological models are known to overestimate flow in arid climates (Tooth, 2000), further complicating IRES mapping in these regions. Finally, our model’s ability to predict the natural prevalence of flow intermittence is affected by the impact of human activities on most gauged basins. Our study aims to depict the natural distribution of non-perennial watercourses by excluding those gauging stations from model training that were affected by flow regulation and/or whose flow intermittence class changed over the discharge record (see Methods). We also used naturalized estimates

of discharge as predictor variables, which exclude anthropogenic water use in the form of abstractions or flow regulation. Nevertheless, disentangling the potential effects of contemporary land use, impoundments and human water abstractions on flow intermittence remains a research frontier (Hammond et al., 2021). We expect that continued improvements in global hydro-environmental datasets and hydrological models, combined with greater access to national hydrometric datasets, will be key to improve future IRES mapping efforts.

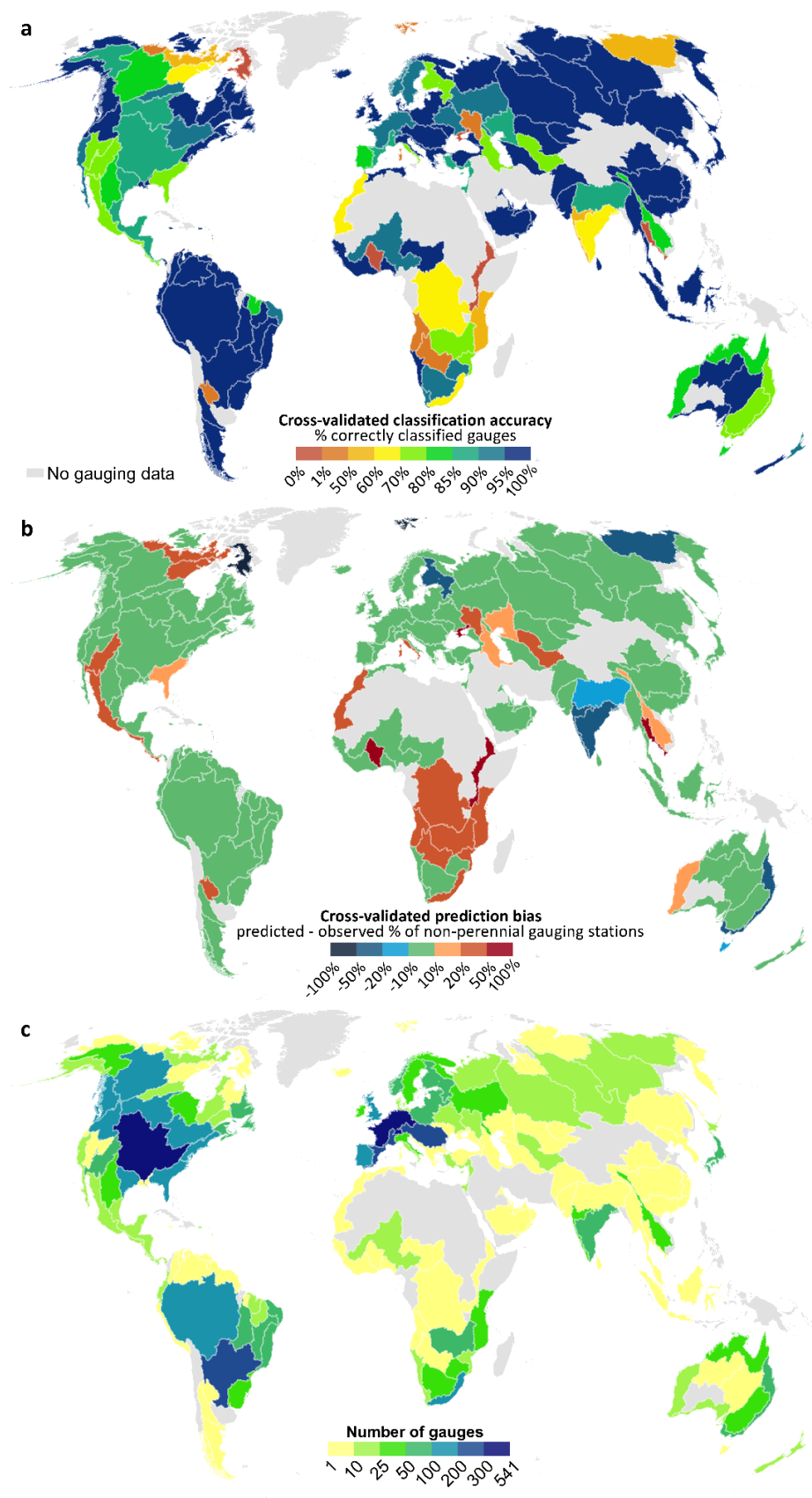


Figure 2.3. Flow intermittence classification accuracy decreases and prediction bias increases in river basins with fewer streamflow gauging stations a–c.

Maps of classification accuracy (a) and prediction bias (b) based on 40-fold spatial cross-validation, and number of streamflow gauging stations per river basin (c). See **Supplementary Figure 2.S11** for the distribution of cross-validation folds. River basins correspond to BasinATLAS27 level 3 subdivisions with an average.

2.5. Understanding and managing IRES dynamics

Our global map of IRES may become a crucial tool for understanding and managing these long-undervalued ecosystems. High-resolution predictions of flow intermittence for all river reaches with $MAF \geq 0.1 \text{ m}^3 \text{ s}^{-1}$ can support spatially explicit studies down to the national scale, and our first-order extrapolation of the total prevalence of non-perennial rivers and streams by region and river basin can offer additional insights into the role of IRES at continental and global scales. Our results also provide an important baseline for the assessment of future changes in flow intermittence in river networks. Quantifying the variability of flow cessation in space and time is required to better understand the impact of climate change, water abstraction and flow regulation. IRES are not only becoming increasingly common but the flow regime of existing IRES can shift; for example, some intermittent rivers are becoming ephemeral, whereas others will turn perennial (Döll & Schmied, 2012). In this study we identified whether and where rivers and streams cease to flow, but further quantification of the spatiotemporal dynamics of flow occurrence across stream networks worldwide is required to determine when and for how long. Knowledge of the natural frequency, duration, and timing of flow cessation—the primary determinants of the functioning of IRES (Datry, Foulquier, et al., 2018; Leigh & Datry, 2017)—forms the basis of flow-alteration analyses that can inform strategies to mitigate the impacts of future changes (Acuña et al., 2020). In particular, tools for assessing environmental flows globally are needed to appraise freshwater planetary boundaries (Gleeson et al., 2020) and to define quantitative targets for the 2030 UN Sustainable Development Goals (Dickens et al., 2019). Yet current tools exclude arid and semi-arid regions (Sood et al., 2017), which are dominated by IRES and where alternative sources of water are scarce (Steward et al., 2012).

2.6. Rethinking the importance of IRES

Our findings call for a paradigm shift in river science and management. The foundational concepts of river hydrology, ecology and biogeochemistry have been developed from and for perennial waterways, and as a result, have all traditionally assumed year-round surface channel flow (Allen et al., 2020). Here we show that this assumption is invalid for most rivers on Earth, which bolsters previous appeals for bringing together aquatic and terrestrial disciplines into river science (Datry et al., 2014; Steward et al., 2012). Multiple conceptual models rely on the assumption that river discharge increases monotonically downstream

from the headwaters to the mouth—for example, the River Continuum Concept (Vannote et al., 1980), a theoretical pillar of river ecology. Moreover, current models define hydrological connectivity within river networks in binary terms, as either free-flowing or perpetually fragmented by barriers such as waterfalls and dams (Grill et al., 2019), but we show that temporary fragmentation by seasonal drying (Stanley et al., 1997) is a widespread phenomenon on Earth. In hydrology, the parameterization and calibration of predictive models of runoff and discharge are usually based on average or peak flows (for example, for flood forecasting) rather than being calibrated to simulate low-flow quantities and timing, including flow cessation events, thus failing to reliably predict intermittence (Yu et al., 2020). Up until now, global estimates of biodiversity have also overlooked IRES, which provide unique habitats for aquatic and terrestrial species (Datry et al., 2014; Steward et al., 2012). Finally, recent research shows that omitting the role of non-perennial inland waters in carbon models may result in underestimating CO₂ emissions from inland waters by approximately 10% (Marcé et al., 2019); similar biases might undermine other global biogeochemical estimates, notably with respect to nitrogen cycling. IRES have always been integral to human societies, whether culturally or as a source of food and water (Steward et al., 2012). We estimate that for 52% of the world's population in 2020, the nearest river or stream is non-perennial (see Methods). The relationship between the seasonal hydrology of IRES and the ecosystem services they provide to society is a pressing area of research, particularly in regions where climate change is disrupting the water pulses to which people's livelihoods are tuned (Datry, Boulton, et al., 2018). In many languages, multiple words exist to designate IRES and their mark on the landscape, highlighting the long history of inter-dependence between humans and seasonal freshwater systems (Steward et al., 2012). However, the spiritual and cultural values that IRES provide, often to Indigenous peoples (for example, in Australia or in sub-Saharan Africa), remain to be acknowledged (Steward et al., 2012).

The past decade has witnessed several efforts to highlight both the values and ongoing degradation of IRES (Acuña et al., 2014; Sullivan et al., 2020), yet current tools and policies still fall short of ensuring their biomonitoring and conservation (Acuña et al., 2020; Stubbington et al., 2018). A recognition of the prevalence and ecological importance of IRES by the scientific community may trigger efforts to adequately manage them and halt current attempts to exclude them from protective legislation (Sullivan et al., 2020). As a stepping-

stone, the dataset we present here intends to provide a baseline for identifying gaps in hydrological and biological monitoring efforts, to inform global biogeochemical upscaling and riverine species distribution models, and to decipher the links between hydrological patterns, culture and language. We hope it can ultimately assist in discerning the role of IRES in the Earth system to safeguard the integrity of river networks and the well-being of those who directly rely on these ecosystems for their livelihood and culture.

2.7. Methods

See **Extended Data Figure 2.S7** for a summary of the data and methods used in this study.

2.7.1. Data

Global underpinning hydrography.

We predicted the distribution of IRES for river reaches in the global RiverATLAS database (Linke et al., 2019). RiverATLAS is a widely used representation of the global river network built on the hydrographic database HydroSHEDS (Lehner et al., 2008; Lehner & Grill, 2013). Rivers are delineated on the basis of drainage direction and flow accumulation maps derived from elevation data at a pixel resolution of 3 arcseconds (~90 m at the equator) and subsequently upscaled to 15 arcseconds (~500 m at the equator). In this study, we only included river reaches with a modelled MAF $\geq 0.1 \text{ m}^3 \text{ s}^{-1}$ and excluded: i) smaller streams (owing to increasing uncertainties in their geospatial location and flow estimates derived from global datasets and models; see also Methods section ‘Hydro-environmental predictor variables’ below); and ii) sections of river reaches within lakes (identified based on HydroLAKES polygons; Messenger et al., 2016). We define a ‘river reach’ as a cartographic—rather than a functional—unit, represented by the smallest spatial element of our global river network, that is, a line segment between two neighbouring confluences. We made predictions for 6,198,485 individual river reaches with an average length of 3.8 km, totalling 23.3 million kilometres of river network.

Reference intermittence data for model training and cross-validation.

Two streamflow gauging station repositories were used as the source of training and cross-validation data for the split random forest (RF) model (**Extended Data Figures 2.S7b, 2.S8**)—the World Meteorological Organization Global Runoff Data Centre (GRDC, 2014) database ($n \approx 10,000$) and a complementary subset of the Global Streamflow Indices and Metadata

archive (GSIM, $n \approx 31,000$), a compilation of twelve free-to-access national and international streamflow gauging station databases (Do et al., 2018). Whereas the GRDC offers daily river discharge values for most stations, GSIM only contains time series summary indices computed at the yearly, seasonal and monthly resolution (calculated from daily records whose open-access release is restricted for some of the compiled data sources; Gudmundsson et al., 2018). Therefore, we used the GRDC database as the core of our training/testing set and complemented it with a subset of streamflow gauging stations from GSIM. A GSIM station was included only if: i) it was not already part of the GRDC database; ii) it included auxiliary information on the drainage area of the monitored reach (for reliably associating it to RiverATLAS); iii) it had a drainage area $<100 \text{ km}^2$ or else (that is, for gauges with a drainage area $\geq 100 \text{ km}^2$) it was located either iv) on an IRES or v) in a river basin that did not already contain a GRDC station (assessed based on level 5 sub-basins of the global BasinATLAS database; Lehner & Grill, 2013; average sub-basin area = $2.9 \times 10^4 \text{ km}^2$). We applied the described GSIM selection criteria to balance the relative amount of non-perennial versus perennial records, and the spatial distribution of stations in the model training dataset. Each station in the combined dataset was geographically associated with a reach in the RiverATLAS stream network and every discharge time series was quality-checked through statistical and manual outlier detection (see **Supplementary Information section 2.9.2** for details on these procedures). Non-perennial gauging stations were only included in the dataset if they were free of anomalous zero-flow values (for example, from instrument malfunction, gauge freezing, tidal flow reversal; Zimmer et al., 2020). We also excluded stations whose streamflow was potentially dominated by reservoir outflow regulation (that is, with a degree of regulation $>50\%$; Lehner et al., 2011; Linke et al., 2019) or whose discharge time series exhibited an alteration (see online research compendium at <https://messamat.github.io/globalIRmap/> for an interactive visualization of processing information for every gauging station) as flow-regulating structures may change the flow class of a river either from perennial to non-perennial or vice-versa depending on their mode and rules of operation (Mackay et al., 2014; Y. Zhang et al., 2015). We further narrowed our selection by adding only gauging stations with a streamflow time series spanning at least 10 years—excluding years with more than 20 days of missing records for the calculation of this criterion and in subsequent analyses. Finally, we classified stations as non-perennial if their recorded discharge dropped to zero at least one day per year on average over the years of

record, and as perennial otherwise. Stations with at least one zero-flow day per year on average (that is, non-perennial) but without a zero-flow day during 20 consecutive valid years of data (those with ≤ 20 missing days), anywhere in their record, were deemed either to have experienced a shift in flow intermittence class (regardless of the direction of the shift) or to have ceased to flow owing to exceptional conditions of drought and were also excluded. On the basis of these selection criteria, the training dataset contained data for 4,428 perennial river reaches and for 1,187 non-perennial reaches, with 41 and 34 years of daily streamflow data on average, respectively, across all continents (except Antarctica; **Extended Data Figure 2.S8**). The threshold used to define flow intermittence varies among studies, ranging from a single zero-flow day across the entire streamflow record (Reynolds et al., 2015; Snelder et al., 2013) to at least five days per year on average (Costigan et al., 2017). Because zero-flow values in streamflow gauging records may be erroneous (Zimmer et al., 2020), other studies have used a flow percentile threshold value (for example, $Q_{99} < 0.0283 \text{ m}^3 \text{ s}^{-1}$ in the US Pacific Northwest; Jaeger et al., 2019). To test the sensitivity of altering our criterion (one zero-flow day per year on average) on the resulting number of non-perennial stations, we changed the threshold to one zero-flow month (30 consecutive or non-consecutive days) per year, which yielded a dataset with 4,735 perennial stations and 880 non-perennial stations, respectively. Given the substantial difference between these thresholds, we also produced model estimates for the latter definition (**Extended Data Figure 2.S1b, c**). Although our training dataset of gauging stations encompasses a wide range of river types found on Earth, it is inherently limited by the global availability of hydrometric data (**Extended Data Figure 2.S8**). Most notably, rivers with $\text{MAF} > 500 \text{ m}^3 \text{ s}^{-1}$ are over-represented whereas those with $\text{MAF} < 50 \text{ m}^3 \text{ s}^{-1}$ are under-represented. In addition, few stations monitor rivers in extreme climates, whether cold or hot, dry or wet (for example, classes 1–4 and 16–18 for extremely cold and extremely hot climates, respectively; **Extended Data Figure 2.S1a** shows the extent of each climate stratum; Metzger et al., 2013). Other under-represented river types include those with annual average snow cover extent $> 75\%$ in their upstream drainage area and rivers with a shallow groundwater table or with $> 90\%$ of karst outcrops across their upstream drainage area.

Hydro-environmental predictor variables.

The primary source of predictor variables was the global RiverATLAS database, version 1.0, which is a subset of the broader HydroATLAS product (Linke et al., 2019). RiverATLAS provides hydro-environmental information for all rivers of the world, both within their contributing local reach catchment and across the entire upstream drainage area of every reach (**Extended Data Table 2.S2**). This information was derived by aggregating and reformatting original data from well established global digital maps, and by accumulating them along the drainage network from headwaters to ocean outlets (Linke et al., 2019). RiverATLAS also includes estimates of long-term (1971–2000) naturalized (that is, without anthropogenic water use in the form of abstractions or impoundments) mean monthly and mean annual flow (MAF). These discharge estimates are derived through a geospatial downscaling procedure (Lehner & Grill, 2013) based on the 0.5-degree resolution runoff and discharge layers provided by the global WaterGAP model (version 2.2 as of 2014; Müller Schmied et al., 2014). A validation of the downscaled discharge estimates against observations at the 2,131 GRDC gauging stations used in this study with ≥ 20 years of streamflow data from 1971 to 2000, representing rivers with MAF between 0.006 and 180,000 m³ s⁻¹, confirmed good overall correlations for MAF (log–log least-square regression, $R^2 = 0.96$, with a symmetric mean absolute percentage error sMAPE of 30%; see **Supplementary Table 2.S1** for all validation results). The sMAPE increased from 5% for rivers with $\text{MAF} \geq 1,000 \text{ m}^3 \text{ s}^{-1}$ to 20% for $10 \text{ m}^3 \text{ s}^{-1} \leq \text{MAF} < 1,000 \text{ m}^3 \text{ s}^{-1}$, and to 52% for $\text{MAF} < 10 \text{ m}^3 \text{ s}^{-1}$.

Minimum monthly discharge was also found to be an effective proxy for Q90 (that is, the daily discharge exceeded 90% of days in the gauging record; $R^2 = 0.84$). We complemented the RiverATLAS v1.0 data with three additional sets of variables. The first set of variables describes the inter-annual open surface water dynamics as determined by remote sensing imagery from 1999 to 2019 (Pickens et al., 2020). In the original dataset, each 30-m-resolution pixel that has been covered by water sometime during this time period was assigned one of seven ‘interannual dynamic classes’ (for example, permanent water, stable seasonal, high-frequency changes) on the basis of a time series analysis of the annual percentage of open water in the pixel. We computed the percent coverage of each of these interannual dynamic classes relative to the total area of surface water within the contributing local catchment and across the entire upstream drainage area of every river

reach. Second, we replaced the soil and climate characteristics in RiverATLAS v1.0 with updated datasets. Specifically, we computed the average texture of the top 100 cm of soil based on version 2 of Soil-Grids250m (Hengl et al., 2017). We also updated the climate variables with version 2 of WorldClim (Fick & Hijmans, 2017; adding all bioclimatic variables to the existing set of variables) as well as the second version of the Global Aridity Index and Global Reference Evapotranspiration (Global-PET) datasets. Finally, we updated the Climate Moisture Index (CMI), computed from the annual precipitation and potential evapotranspiration datasets provided by the WorldClim v2 and Global-PET v2 databases, respectively. We derived a third set of variables by combining multiple variables already included in the model through algebraic operations. These metrics included the runoff coefficient (that is, the ratio of MAF and mean annual precipitation), specific discharge (that is, MAF per unit drainage area), and various temporal (for example, minimum annual/maximum annual discharge) and spatial (for example, mean elevation in local reach catchment/mean elevation in upstream drainage area) ratios.

The application of all described procedures yielded a total of 113 candidate predictor variables to be used in our statistical model development (**Extended Data Table 2.S2**).

2.7.2. Machine learning models

We developed and used a split RF machine learning model to predict the flow intermittence class, as a probability response, of all river reaches globally, with 1 denoting a 100% predicted probability of being an IRES. RF models have already been successfully used to predict the distribution of IRES in Australia and France (Bond & Kennard, 2017; Snelder et al., 2013) and they have been shown to achieve high performance when compared to other approaches, including other machine learning models, logistic regression, and single decision trees (Kotsiantis et al., 2006; Wainer, 2016). Below, we briefly describe the model development and validation procedure conducted for our split RF model; see **Supplementary Information section 2.9.3** for additional information.

Our final predictions are based on the probability RF algorithm developed by (Malley et al., 2012), a derivative of the standard RF algorithm for making probabilistic predictions of class membership, as included in the 'ranger' R package (Wright & Ziegler, 2017). This algorithm was selected following a comparison (Landau, 2018; Lang et al., 2019) of several probability RF variants (namely, conditional inference forest; Hothorn et al., 2006; Hothorn & Zeileis,

2015) and a newly developed regression RF algorithm using maximally selected rank statistics (Wright et al., 2017). To address known biases in RF models from class imbalance in the training data (more perennial than non-perennial gauging stations on large rivers; Jaeger et al., 2019; G. Zhang & Lu, 2012), we implemented random oversampling of non-perennial gauging stations (Japkowicz & Stephen, 2002). For our split model approach, we trained and cross-validated two probability RF sub-models with slightly overlapping ranges in river size, one trained to predict the streamflow intermittence probability of small-to-medium rivers with $MAF < 10 \text{ m}^3 \text{ s}^{-1}$ and the other for medium-to-large rivers with $MAF \geq 1 \text{ m}^3 \text{ s}^{-1}$. Within the overlapping range of $1\text{--}10 \text{ m}^3 \text{ s}^{-1}$ MAF, the average probability was calculated to avoid abrupt transitions at a singular size threshold. This split approach performed better than a single model and was motivated by the distinct class imbalance in training gauging stations between large rivers (4.87:1 perennial to non-perennial ratio) versus small rivers (1.98:1 perennial to non-perennial ratio). With a single model, the use of a common oversampling factor for both size classes underpredicted the prevalence of IRES in large rivers (see **Extended Data Table 2.S3**).

2.7.3. Model development and diagnostics

To optimize the predictive performance of the two sub-models, avoid overfitting, and obtain unbiased estimates of statistical uncertainty, we implemented a nested resampling framework for hyperparameter tuning and cross-validation (Bischl et al., 2012), first for comparison across RF algorithm variants, and then for comparing model performance with and without predictor variable selection (see **Supplementary Information section 2.9.4** for a full description of the tuning and cross-validation procedure; Probst et al., 2019; Probst & Boulesteix, 2018). Tuning was performed for 2–3 hyperparameters (depending on the RF algorithm) through random search with a termination criterion of 100 iterations. The inner (hyperparameter tuning) loop was composed of a fourfold cross-validation and the outer loop (for predictive performance assessment) involved a twice-repeated threefold cross-validation. Cross-validation strategies usually involve 2–10 folds (Probst et al., 2019), with a lower number of folds (as chosen here) yielding a more stringent evaluation of performance (that is, a pessimistic evaluation bias). The outer cross-validation procedure was repeated twice and the results were averaged to reduce the variance caused by randomly splitting the data into few folds (Bischl et al., 2012). A spatial cross-validation procedure based on k -means spatial clustering ($k = 40$, see **Supplementary Figure 2.S11** for the distribution of

clusters) was also used in the outer resampling loop to avoid overoptimistic error estimates that arise in cases of considerable spatial autocorrelation (Brenning, 2012; Meyer et al., 2018, 2019; Schratz et al., 2019). We chose to implement 40 spatial folds to strike a balance between two extremes. Fewer folds would risk evaluating the predictive ability of the model across areas so large that they may represent unique hydro-climatic conditions outside of the model's training set (for a given fold), therefore underestimating the model's performance. More folds would have inflated our estimate of model accuracy by relying on training sets too similar to the testing sets and would have made the computational requirements of cross-validation even greater.

All algorithms were compared using the same inner and outer sets of training and testing partitions. Hyperparameters were tuned to optimize the Balanced class ACCuracy (BACC) metric (Brodersen et al., 2010), which is equivalent to the raw accuracy (or one minus the misclassification rate) but with each sample weighted according to the inverse prevalence of its true class (large river model: 4.87 and 1.00 weights for the non-perennial and perennial classes, respectively; small river model: 1.98 and 1.00 for the non-perennial and perennial classes, respectively). To assess predictor variable importance, weighted averages of Actual Impurity Reduction (AIR, an unbiased version of Gini impurity; Nembrini et al., 2018) and the associated p values (determined via 100 permutations, following Altmann et al., 2010) were computed for each outer resampling cross-validation fold and repetition, using the BACC of each resampling instance as weight. Prior to final model training and evaluation, only predictors with a variable importance p value of <0.05 were retained, so that 92 and 82 variables were retained in the final small-river and large-river models, respectively. Variable selection was implemented to both increase model performance (Amaratunga et al., 2008; Evans et al., 2011) and decrease model training time. In addition to the BACC and the variable importance, several additional diagnostics were examined to determine the performance and characteristics of the RF model as follows: (i) We assessed the classification accuracy (percentage of correctly classified gauges), the sensitivity (percentage of correctly classified IRES reaches, also known as true positive rate or recall), specificity (percentage of correctly classified perennial reaches, also known as true negative rate or selectivity), and precision (percentage of reaches predicted to be IRES that are actually IRES) of the model for each streamflow size class (**Extended Data Table 2.S3**), based on spatial and non-spatial cross-validations. (ii) We examined the geographic, hydrological, and environmental

distributions of the intermittence prediction residuals (IPRs) for each reference stream gauging station (**Extended Data Figure 2.S2**):

$IPR = \text{predicted intermittence probability} - \text{observed intermittence class}$ (1)

with observed intermittence class $IR = \{0: \text{perennial}, 1: \text{non-perennial}\}$.

If $|IPR| \leq 0.5$, the binary intermittence class of the reach associated with the gauging station was accurately predicted, with $|IPR|$ values closer to 0.5 indicating greater uncertainty. If $IPR > 0.5$, the reach was predicted to be non-perennial when it was perennial. If $IPR < -0.5$, the reach was predicted to be perennial when it was non-perennial. We also examined the distribution of classification accuracy and bias (**Figure 2.3**), as well as residual spatial autocorrelation (see **Supplementary Information section 2.9.4**), by river basin. (iii) Partial dependence plots were generated for the 27 most important predictors using the 'edarf' package (Jones & Linder, 2016; see **Supplementary Figure 2.S13**). These plots display estimates of the marginal relationship between each predictor variable and the model's predictions by holding the rest of the predictors at their respective mean values (Friedman, 2001). Assessing the global prevalence of IRES After training the two final probability RF sub-models, the constructed prediction rules were used to estimate the probability of intermittence for each river reach included in the global river network (that is, with $MAF \geq 0.1 \text{ m}^3 \text{ s}^{-1}$). All reaches with a resulting probability ≥ 0.5 were classified to be non-perennial (and perennial otherwise). This threshold was chosen following an analysis of model performance sensitivity to probability thresholds ranging from 0.25 to 0.75 for each RF sub-model which showed a balanced model performance at 0.5 (see **Supplementary Information section 2.9.4**). When adjusting the probability threshold between 0.45 and 0.55, the RF-predicted (that is, non-extrapolated) global prevalence of IRES varied from 36% to 48% (compared to 41% with a 0.5 threshold). We then used the binary intermittence class predictions to compute the global prevalence of IRES by country, continent, climate zone, terrestrial biome, and major freshwater habitat type (**Table 2.1** and **Supplementary Data**; see publication online for the latter). Although gauging stations on reaches with $MAF < 0.1 \text{ m}^3 \text{ s}^{-1}$ were included in the training dataset, we did not produce global RF predictions of the probability of flow intermittence for individual reaches below this discharge threshold for two reasons. First, there existed only 59 gauges with $MAF < 0.1 \text{ m}^3 \text{ s}^{-1}$ and at least 10 valid years of data (including only 13 on perennial reaches), which was insufficient to confidently train a model and assess its uncertainty for this discharge size class. Second, there exists a

discontinuity in RiverATLAS below $0.1 \text{ m}^3 \text{ s}^{-1}$ whereby only those reaches with a drainage area $\geq 10 \text{ km}^2$ are included (Linke et al., 2019), leading to a varying discharge cut-off depending on a region's aridity. Nonetheless, bounding our RF predictions to $0.1 \text{ m}^3 \text{ s}^{-1}$ enabled us to establish a robust estimate of the prevalence of flow intermittence in a range of discharge size classes which we then used for an extrapolation to smaller streams (see Methods section 'Extrapolating the global prevalence of IRES to smaller streams').

2.7.4. Estimating human population near IRES

To estimate the percentage of the global population living near an IRES, we first aggregated 2020 population count data from WorldPop (Bondarenko et al., 2020). We used constrained, rather than unconstrained, top-down WorldPop population estimates to avoid erroneous allocation of population to all land cells (Bondarenko et al., 2020). Population count estimates were aggregated from 3 arcsecond ($\sim 90 \text{ m}$ at the equator) to 15-arcsecond pixels ($\sim 500 \text{ m}$, that is, the resolution of the hydrographic data underpinning the RiverATLAS river network). We associated the population within each larger pixel to the river reach in RiverATLAS (with $\text{MAF} \geq 0.1 \text{ m}^3 \text{ s}^{-1}$) that was nearest to that pixel. Finally, we summed the population across all pixels in the world that were associated with a reach predicted to be non-perennial by our model.

2.7.5. Extrapolating the global prevalence of IRES to smaller streams

To create a first-order approximation of the global prevalence of IRES including even smaller streams, we extrapolated our model estimates to the next smaller streamflow size class range of $[0.01, 0.1) \text{ m}^3 \text{ s}^{-1}$. Although streams of this size class are rarely monitored or mapped globally, they are ecologically and environmentally critical (Colvin et al., 2019). For instance, at least 64% of rivers and streams in the USA (by length) show a $\text{MAF} < 0.1 \text{ m}^3 \text{ s}^{-1}$, and 25% show a $\text{MAF} < 0.01 \text{ m}^3 \text{ s}^{-1}$ (according to the US National Hydrography Dataset, NHDPlus, at medium resolution). We limited our extrapolation to one order of magnitude (that is, we did not include even smaller streams, with $\text{MAF} < 0.01 \text{ m}^3 \text{ s}^{-1}$, that still can form stream channels) as we expect uncertainties to continuously increase when moving further outside the range of our trained and tested RF model. The prevalence of IRES for this stream size class was independently extrapolated for a total of 465 spatial sub-units representing all occurring intersections of 62 river basin regions (BasinATLAS level 2 subdivisions, average surface area $2.2 \times 10^6 \text{ km}^2$; Linke et al., 2019) and 18 climate zones (Global Environmental

Stratification; Metzger et al., 2013). For each basin–climate sub-unit, we first extrapolated the empirical cumulative distribution of total stream length (of all reaches with $\text{MAF} \geq 0.1 \text{ m}^3 \text{ s}^{-1}$) down to $0.01 \text{ m}^3 \text{ s}^{-1}$ MAF using a generalized additive model (GAM; Hastie et al., 2009). We excluded reaches larger than the 95th percentile of MAF (that is, the largest rivers) within the sub-unit from model fitting to avoid common discontinuities at the high end of the empirical distribution that can affect the low end of the power-law-like trendline (see **Supplementary Figure 2.S16a, c**). Second, we extrapolated the prevalence of flow intermittence (in percentage of stream length) down to $0.01 \text{ m}^3 \text{ s}^{-1}$ MAF. In this case, we fitted a GAM for beta-distributed data—that is, with a (0, 1) range—to the prevalence of intermittence in each logarithmic MAF size bin of the sub-unit. MAF logarithmic size bins ($\text{m}^3 \text{ s}^{-1}$) were defined as $[10^i, 10^{i+0.1})$ for every i in $\{-1, -0.9, -0.8, \dots, 5.3\}$ for model fitting, and every i in $\{-2, -1.9, \dots, -1.1\}$ for model extrapolation. See **Supplementary Figure 2.S16b, d** for illustrative examples of this approach. GAMs were used to conduct both extrapolations because this non-parametric, nonlinear approach does not require assumptions to be made regarding what distribution (for example, a power law; Clauset et al., 2009) the empirical cumulative distributions should follow. This is justifiable because the aim of the analysis was to make a pragmatic first-order approximation of IRES prevalence rather than to demonstrate the existence (or not) of a specific distribution. Following the fitting of all GAM models, the length of IRES in each linear MAF size class between $0.01 \text{ m}^3 \text{ s}^{-1}$ and $0.1 \text{ m}^3 \text{ s}^{-1}$ was computed as the product of the extrapolated length of streams and the prevalence of intermittence in that size class. Finally, the total length of IRES in the extrapolated size classes was combined with the predictions from the split RF model to estimate the global prevalence of IRES as a percentage of the total global length of rivers and streams with $\text{MAF} \geq 0.01 \text{ m}^3 \text{ s}^{-1}$. We also produced an additional estimate with the assumption that, for each basin–climate sub-unit, the prevalence of IRES in streams with $0.01 \leq \text{MAF} < 0.1 \text{ m}^3 \text{ s}^{-1}$ was equal to the prevalence of IRES in streams with $0.1 \leq \text{MAF} < 0.2 \text{ m}^3 \text{ s}^{-1}$. Even with this conservative assumption, we estimate that 51% of all global rivers and streams with $\text{MAF} \geq 0.01 \text{ m}^3 \text{ s}^{-1}$ are IRES. In contrast to the RF models, which estimate the probability of flow intermittence at the scale of individual river reaches, the GAM-based extrapolation provides aggregate estimates of IRES prevalence for basin–climate sub-units, which are best suited for global accounting studies.

2.7.8. Model comparisons

Comparisons with reported prevalence of flow intermittence at national scales. The most common source of information on the prevalence of flow intermittence across large regions are national hydrographic datasets, derived mainly from paper topographic maps in which non-perennial watercourses are usually depicted by dashed lines. We compared our model estimates of the percentage of stream length that is non-perennial with this type of hydrographic data for four countries covering a wide range of environmental, geological, and climatic conditions: the contiguous USA, Australia, Brazil, and Argentina (**Extended Data Figures 2.S3, 2.S4**; for data sources see **Extended Data Figure 2.S7b**). In addition, we compared our results in mainland France with predictions of a national model (Snelder et al., 2013). It should be noted that we do not consider these comparisons to be an accuracy assessment of our model outputs, owing to the inherent yet unknown uncertainties in the national hydrographic datasets. Although the national maps represent the most comprehensive records of presumed intermittence, most are characterized by high levels of inconsistency among regions and cartographers, even for a fixed map scale (for example, 1:24,000), in both stream density and flow intermittence assessment (Fritz et al., 2013; Stoddard et al., 2005). For instance, streamflow intermittence classifications contained in the US National Hydrography Dataset (NHDPlus, which was used in this study), based on one-time field surveys typically conducted in the mid-to-late 1900s, have been shown to exhibit misclassification rates as high as 50% compared to independent field surveys (Fritz et al., 2013; Stoddard et al., 2005). Hafen et al. (2020) report only an 80–81% agreement between ground-based streamflow field observations from the US Pacific Northwest and the NHDPlus classifications. Furthermore, in the Brazilian dataset and the NHDPlus, neighbouring topographic map sheets differ in whether flow intermittence was mapped, leading to artefactual hard edges between regions in terms of the prevalence of intermittence (for example, **Extended Data Figure 2.S4**; Colson et al., 2008). Despite these limitations, map-based national hydrographic datasets remain the reference used by most government agencies and institutions in determining the extent and flow intermittence of river networks, and thus provide a useful benchmark for comparing the output of our model.

A custom processing workflow was developed to format each of the four national river network datasets to ensure comparability with our model predictions. This involved filtering each source dataset to keep only river and stream channels (for example, excluding lake

shorelines and marine coastlines), excluding reaches in the source data that do not correspond with the streamflow threshold applied for the mapped rivers in this study ($MAF \geq 0.1 \text{ m}^3 \text{ s}^{-1}$) and excluding artificial channels (for example, canals and ditches). For a full description of the formatting workflow, see **Supplementary Information section 2.9.6**. Following this formatting process, we compared the percentage of river network length that was categorized as IRES in each of the source datasets to our model results for the same region (**Extended Data Figure 2.S5**). We could not perform this quantitative comparison for Brazil and Argentina because there was no measure of river size in these datasets. Lastly, we visually assessed whether spatial patterns of intermittence were similar between the source datasets and our model results. Aside from Argentina, we were unable to compare our predictions to hydrographic maps in countries where sparse hydrometric networks result in higher modelling uncertainties, owing to the unavailability of hydrographic data in these regions.

Comparisons with local on-the-ground visual observations. Datasets of on-the-ground visual observations of flow presence or absence (flow state) by trained individuals provide some of the most reliable records of flow intermittence (Allen et al., 2019; Datry et al., 2016; Jaeger et al., 2019). We compared our predictions of intermittence to datasets of this type for two regions: the US Pacific Northwest and mainland France (**Extended Data Figure 2.S6**; see **Supplementary Information section 2.9.6** for additional details). We did not use these observations directly for the training of the RF sub-models as we could not apply the same criterion to define ‘intermittence’ as for gauging stations (that is, at least one day per year of flow cessation, on average, across the entire record) and their inclusion would have represented a strong regional bias. These datasets instead enabled an independent comparison of the model predictions for smaller rivers and streams (here mostly $<1 \text{ m}^3 \text{ s}^{-1}$), which are poorly represented in the global hydrometric network. For the US Pacific Northwest, we used 5,372 observations across 3,725 reaches (3,547 perennial, 178 non-perennial) from a larger dataset of 24,316 stream observations¹⁰⁰ that occurred from 1 July to 1 October, between 1977 and 2016. The source dataset is a compilation of 11 smaller datasets from independent projects that include aquatic species habitat surveys, wet/dry stream channel mapping, beneficial use reconnaissance surveys, or were collected specifically for the PROSPER intermittent river mapping project (Jaeger et al., 2019; McShane et al., 2017). Streamflow observations included one-time surveys and repeat surveys

extending over several years, as well as discrete locations or continuous sections of a stream channel reach. On the basis of the approach used by (Jaeger et al., 2019), we considered that a river section was perennial only if all observations (1 July–1 October) reported the presence of water. Despite this strict criterion, this dataset may underestimate the prevalence of intermittence since most sites were only observed 1–3 times and the probability that flow cessation was observed at a given reach increased with the number of observations (logistic regression, $n = 9,850$, $p < 0.001$, see **Supplementary Information section 2.9.6** for details). For France, we used 124,112 observations across 2,297 reaches (878 perennial, 1,419 non-perennial) from a larger set of approximately 3,300 sites uniformly distributed across France from the national river drying observatory (ONDE) network (Nowak & Durozoi, 2014). The ONDE network provides a stable set of sites on river and stream reaches of Strahler orders under five which, since 2012, have been inspected by agency employees from the French Office for Biodiversity (OFB) at least monthly between May and September. We considered an observation to reflect flow intermittence if it was classified as either ‘with no visible flow’ or ‘dried out’ (as opposed to ‘with visible flow’). In case of multiple observations on one reach, we considered the reach to be non-perennial if a single observation of flow cessation existed. All flow state observations were linked to the RiverATLAS stream network through custom semi-automated procedures designed for each dataset, using the proximity between the point observations and the reach locations in RiverATLAS, as well as associated information from local river network datasets and ancillary attribute data provided for each location (for example, drainage area, site name; see **Supplementary Information section 2.9.6** for details). Following data formatting and harmonization, we assessed the degree of agreement at the river reach level between the binary intermittence class predicted by our model and that reported by the two datasets of visual observations.

2.8. Extended Data

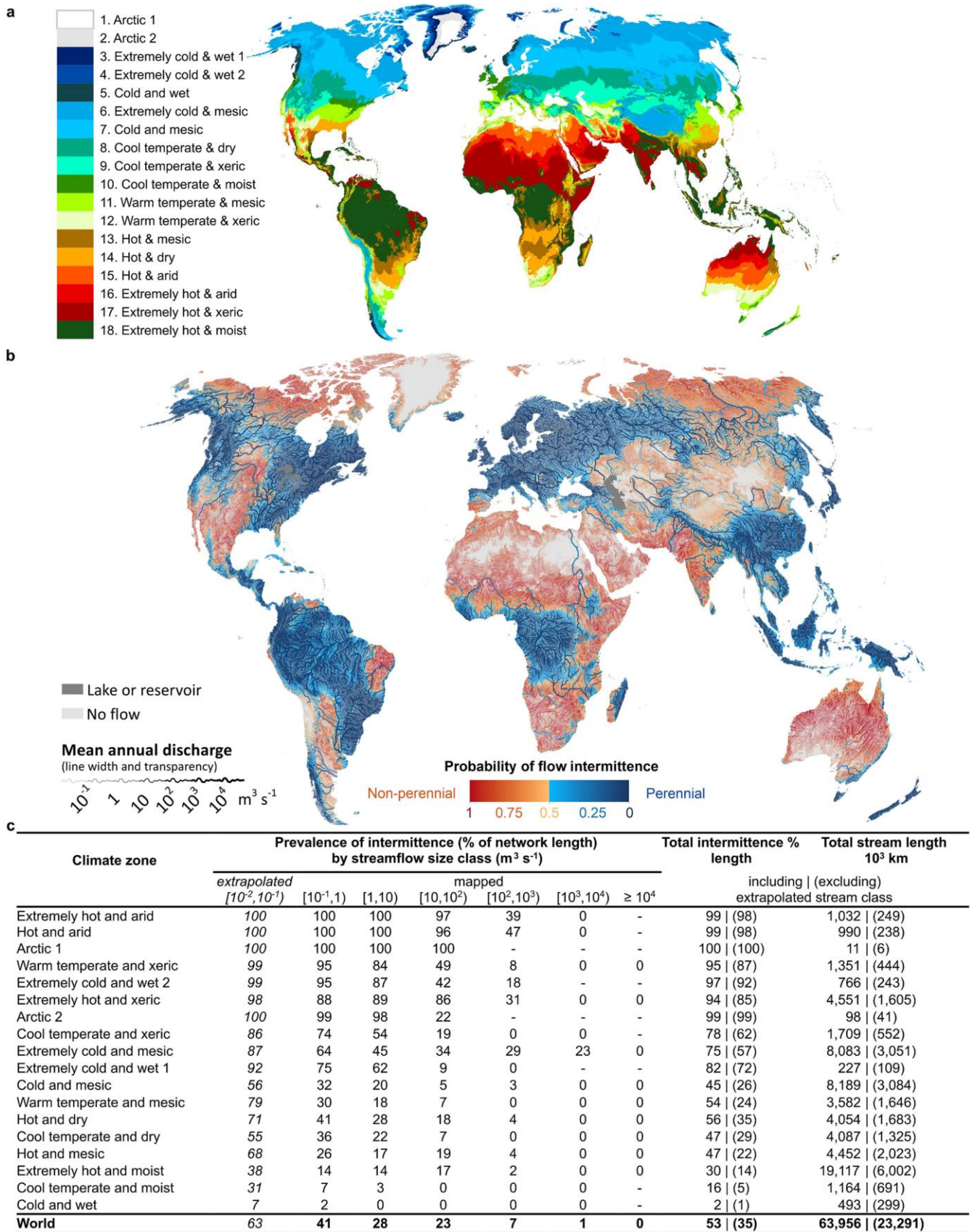


Figure 2.S1. Global prevalence of IRES with at least one zero-flow month per year on average. See caption details on the following page.

a, Distribution of global climate zones used in this study. Data provided by Global Environmental Stratification (GEnS; Metzger et al., 2013). **b**, Predicted probability of river flow intermittence, defined as at least one zero-flow month (30 days) per year on average, across the global river and stream network (Linke et al., 2019). The median probability threshold of 0.5 was used to determine the binary flow intermittence class for each reach. **c**, Global prevalence of IRES with at least one zero-flow month (30 days) per year on average, across climate zones and streamflow size classes (based on long-term average naturalized discharge). Note that in regions with sparse training data, the model results can differ substantially from the results shown in **Table 2.1**, as the underlying random forest and extrapolation models were developed independently. No stations were available in climate zones Arctic 1 and Arctic 2, and few stations were available in 'Extremely cold and wet' (1 and 2) and in 'Extremely hot and arid' climates (together representing 3% of global river and stream length). Rows are sorted in the same order as in **Table 2.1**, and the same footnotes as in **Table 2.1** apply. Mapping software: ArcMap (ESRI).

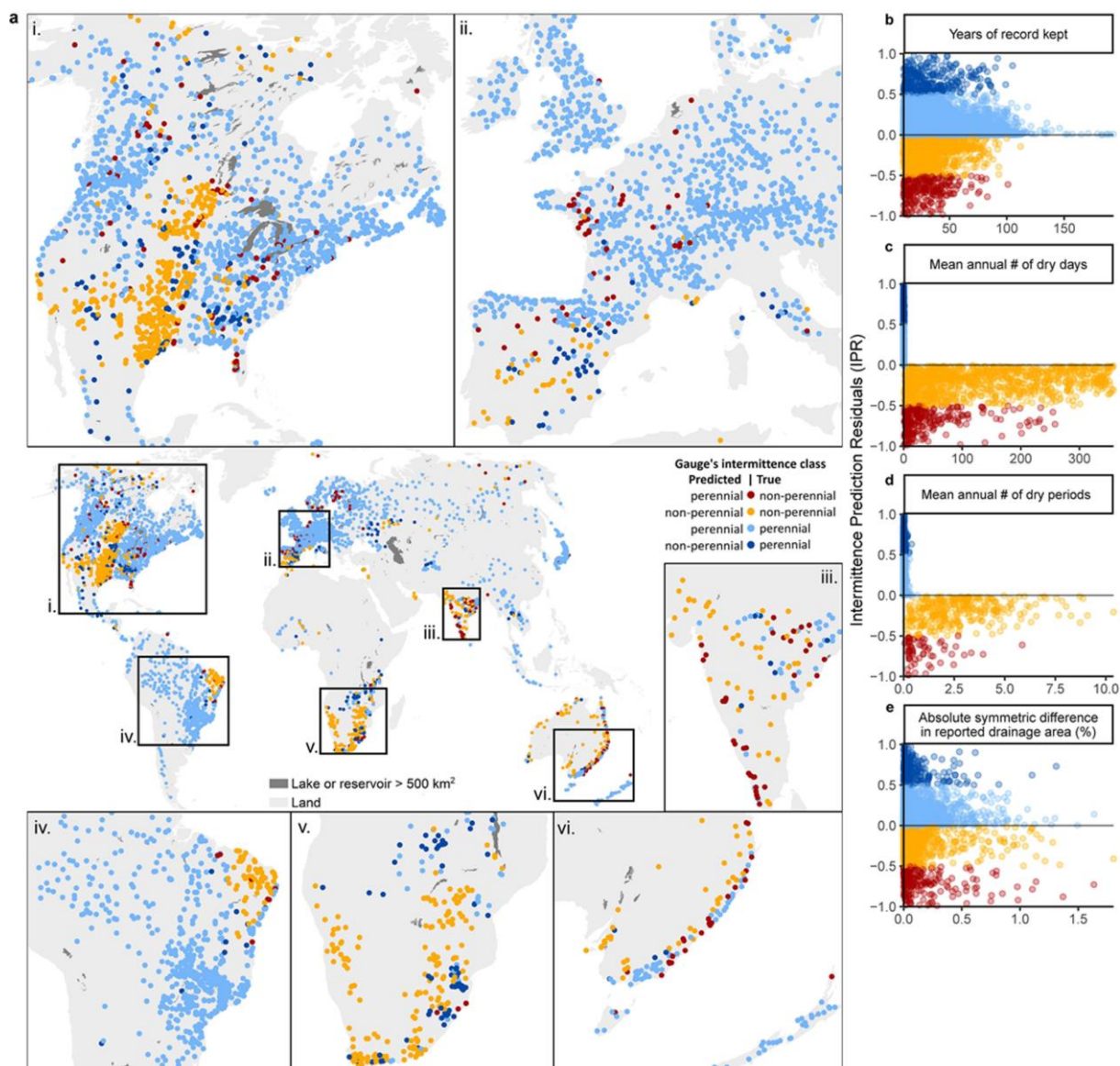


Figure 2.S2. Distribution of cross-validation results.

a, Maps of spatially cross-validated predictive accuracy of flow intermittence for streamflow gauging stations. See **Supplementary Figure 2.S11** for the distribution of spatial cross-validation folds and details on the cross-validation procedure. The classification errors shown here are not necessarily present in the final predictions but illustrate the ability of the model to predict the flow intermittence class for each region if that region was excluded from the training set. For instance, it shows that the model would be unable to predict the presence of IRES in western France and northern Spain (inset ii, dark red dots), or in western India (inset iii) without training stations in these regions. **b–e**, Intermittence prediction residuals versus gauging station characteristics and environmental variables. The mean intermittence prediction residual (IPR) is the difference between the average predicted probability of flow intermittence (across three cross-validation folds and two repetitions) and the observed flow intermittence of the gauging station (1 = non-perennial, 0 = perennial). Overall, prediction errors and uncertainties decrease with an increase in the number of recorded years by gauging stations as well as the drainage area and the degree of flow intermittence (average annual number of zero-flow days and flow cessation events) of the corresponding reaches. Mapping software: ArcMap (ESRI).

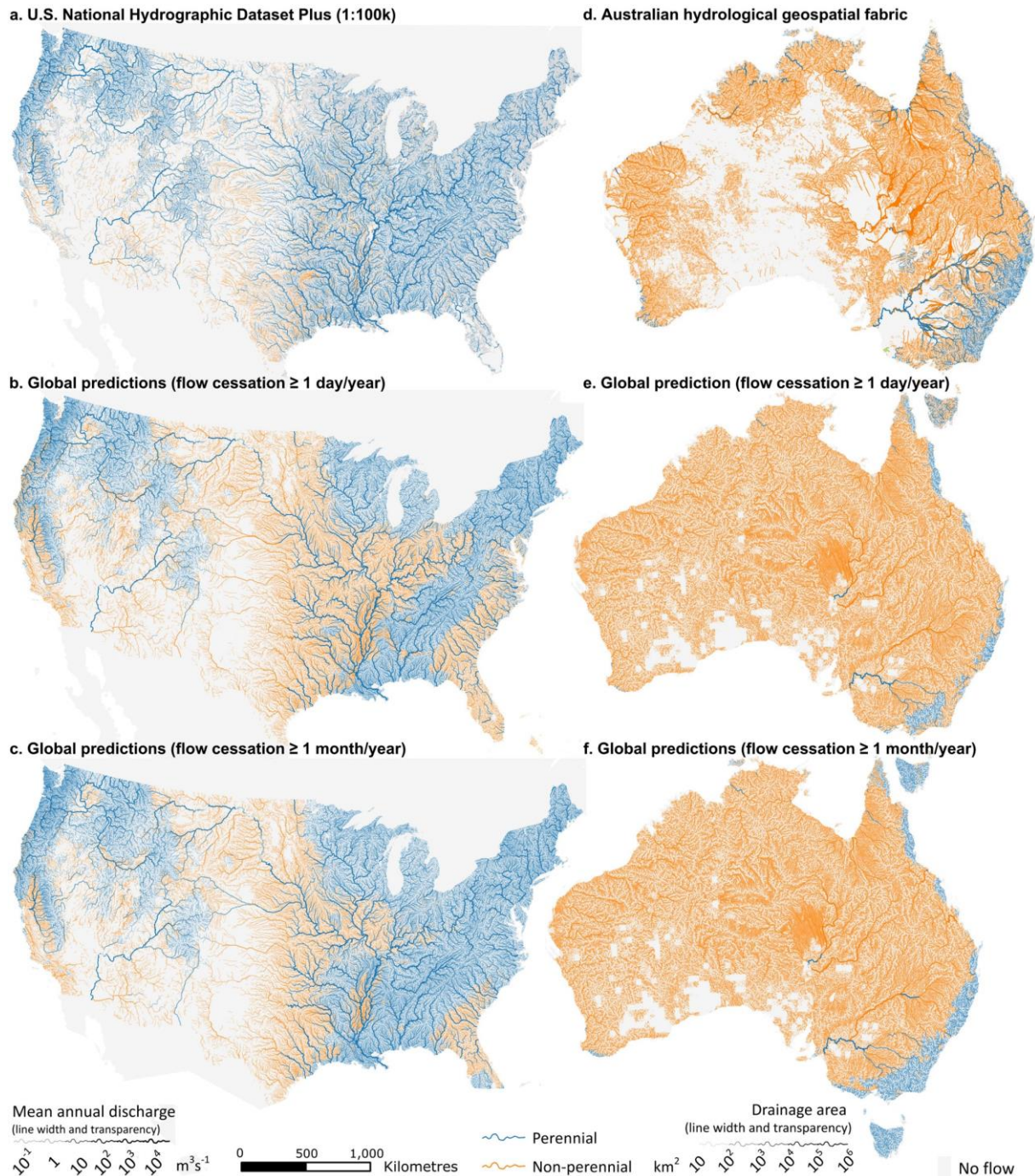


Figure 2.S3. Comparing global predictions to national maps of IRES in the USA and Australia.

Comparison of **a**, the US National Hydrography Dataset (NHDPlus, medium resolution) and **d**, the Australian hydrological geospatial fabric, with our model predictions based on two thresholds of flow intermittence, either ≥ 1 zero-flow day per year (**b**, **e**), or ≥ 1 zero-flow month (30 days) per year (**c**, **f**), on average. Only rivers and streams with $\text{MAF} \geq 0.1 \text{ m}^3 \text{s}^{-1}$ are shown for the USA (**a–c**) and with drainage area $\geq 10 \text{ km}^2$ for Australia (**d–f**). The US reference dataset portrays 19–22% of the length of rivers and streams as non-perennial, depending on whether reaches without flow intermittence status are assumed to be perennial or removed; our estimates range from 51% (≥ 1 zero-flow day per year) to 36% (≥ 1 zero-flow month per year). We hypothesize that the remaining gap in IRES prevalence is attributable to a tendency of our model to overpredict intermittence across the eastern USA and an under-accounting of intermittence in medium to large rivers by the national dataset. The Australian reference dataset portrays 91% of the length of rivers and streams as non-perennial; our estimates range from 95% (≥ 1 zero-flow day per year) to 92% (≥ 1 zero-flow month per year). See **Extended Data Figure 2.S7b** for data sources. Mapping software: ArcMap (ESRI).

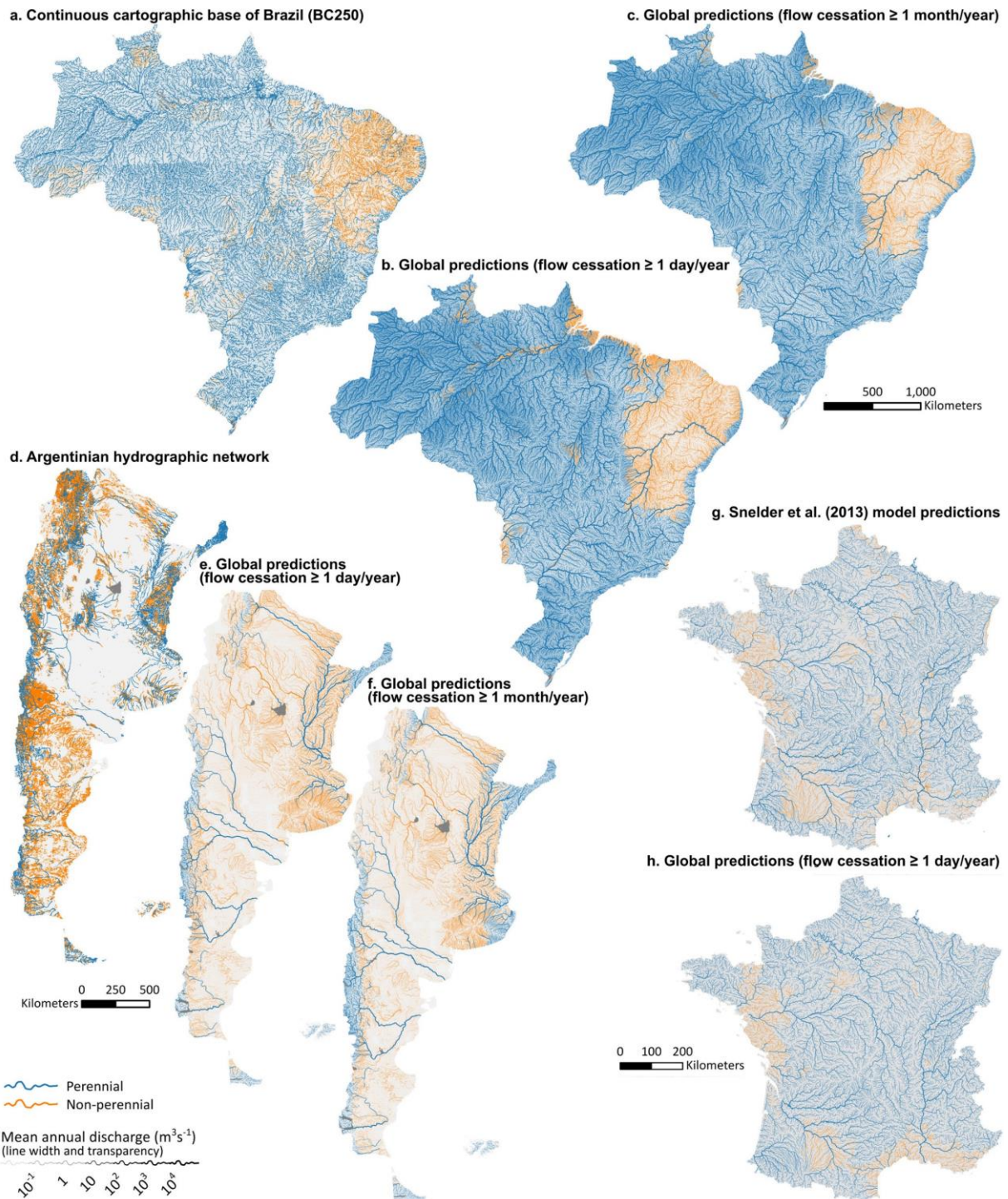


Figure 2.S4. Comparing global predictions to national maps of IRES in Brazil, Argentina, and France.

Comparison of **a**, the continuous cartographic base of Brazil (BC250), **d**, the Argentinian hydrographic network, and **g**, model predictions for France from (Snelder et al., 2013), with our model predictions based on two thresholds of flow intermittence, either ≥ 1 zero-flow day per year (**b**, **e**, **h**) or ≥ 1 zero-flow month (30 days) per year (**c**, **f**), on average. In **a** and **d**, only first-order streams (determined through network analysis) are visually differentiated (finer, semi-transparent lines), owing to the lack of a watercourse-size attribute in the Brazilian and Argentinian datasets. In **b**, **c**, **e**–**h**, only rivers and streams with $\text{MAF} \geq 0.1 \text{ m}^3 \text{ s}^{-1}$ are shown. Snelder et al. (2013) predict that 17% of the length of rivers and streams in France are nonperennial. We predict that 14% are non-perennial. This slight divergence may be partly driven by the difference in definition of flow intermittence: Snelder et al. (2013) classified stations with ≥ 1 zero-flow day in the streamflow record as IRES whereas we used a threshold of 1 zero-flow day per year across the streamflow record. See **Extended Data Figure 2.S7b** for data sources. Mapping software: ArcMap (ESRI).

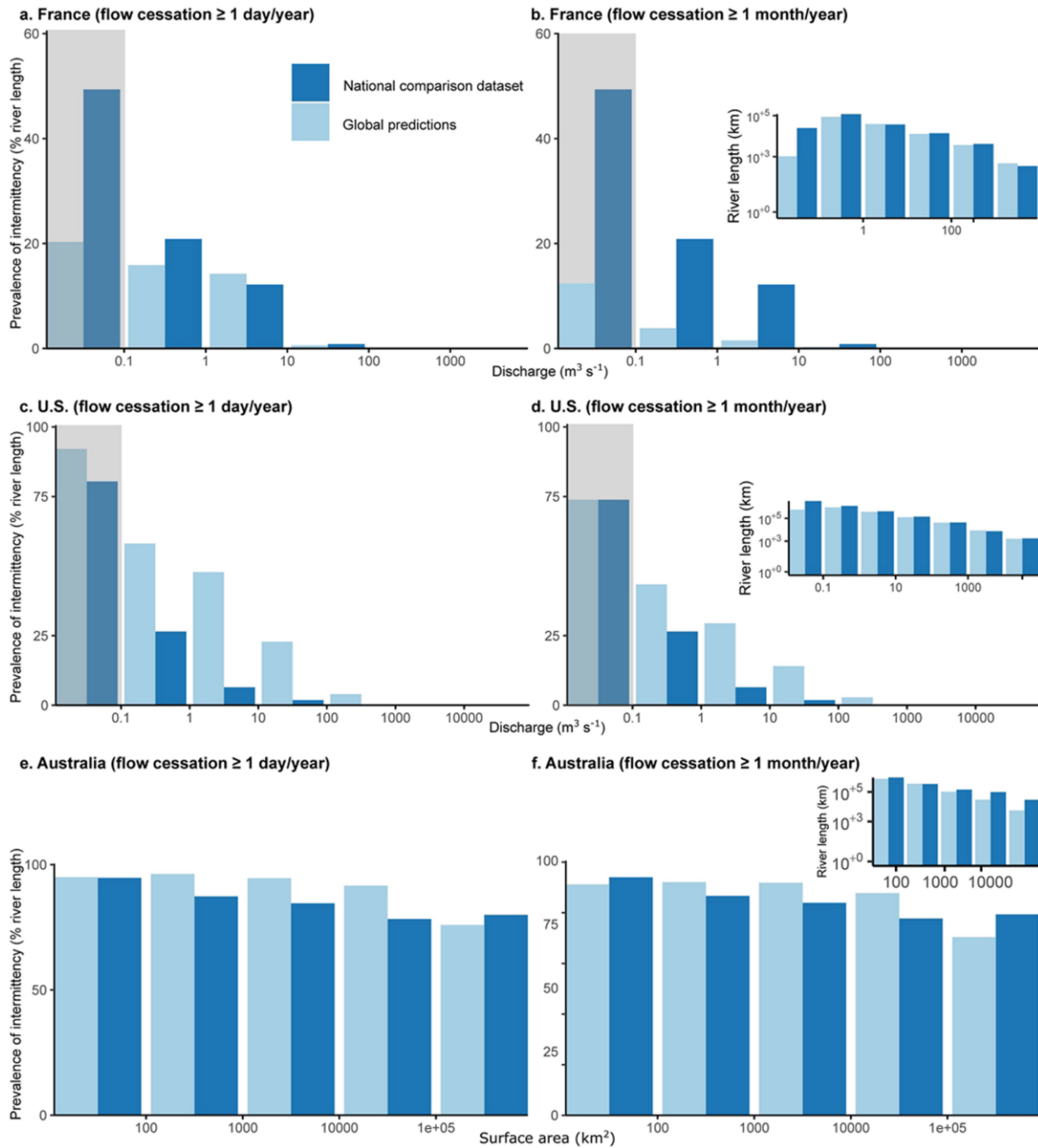


Figure 2.S5. Quantitative comparison between the predicted prevalence of flow intermittence and national estimates.

a–f, Comparisons were conducted for France (**a, b**), the USA (**c, d**), and Australia (**e, f**), on the basis of two thresholds of flow intermittence, either ≥ 1 zero-flow day per year (**a, c, e**) or ≥ 1 zero-flow month (30 days) per year (**b, d, f**), on average. Bars for mapped rivers and streams with $\text{MAF} < 0.1 \text{ m}^3 \text{ s}^{-1}$ (for France and the USA) are greyed out as they were not included in the calculation of summary statistics. Inset graphs in **b, d, f** show comparisons of total river network length (log-transformed y axis), which in case of discrepancies can explain some of the differences in the predicted prevalence of intermittence.

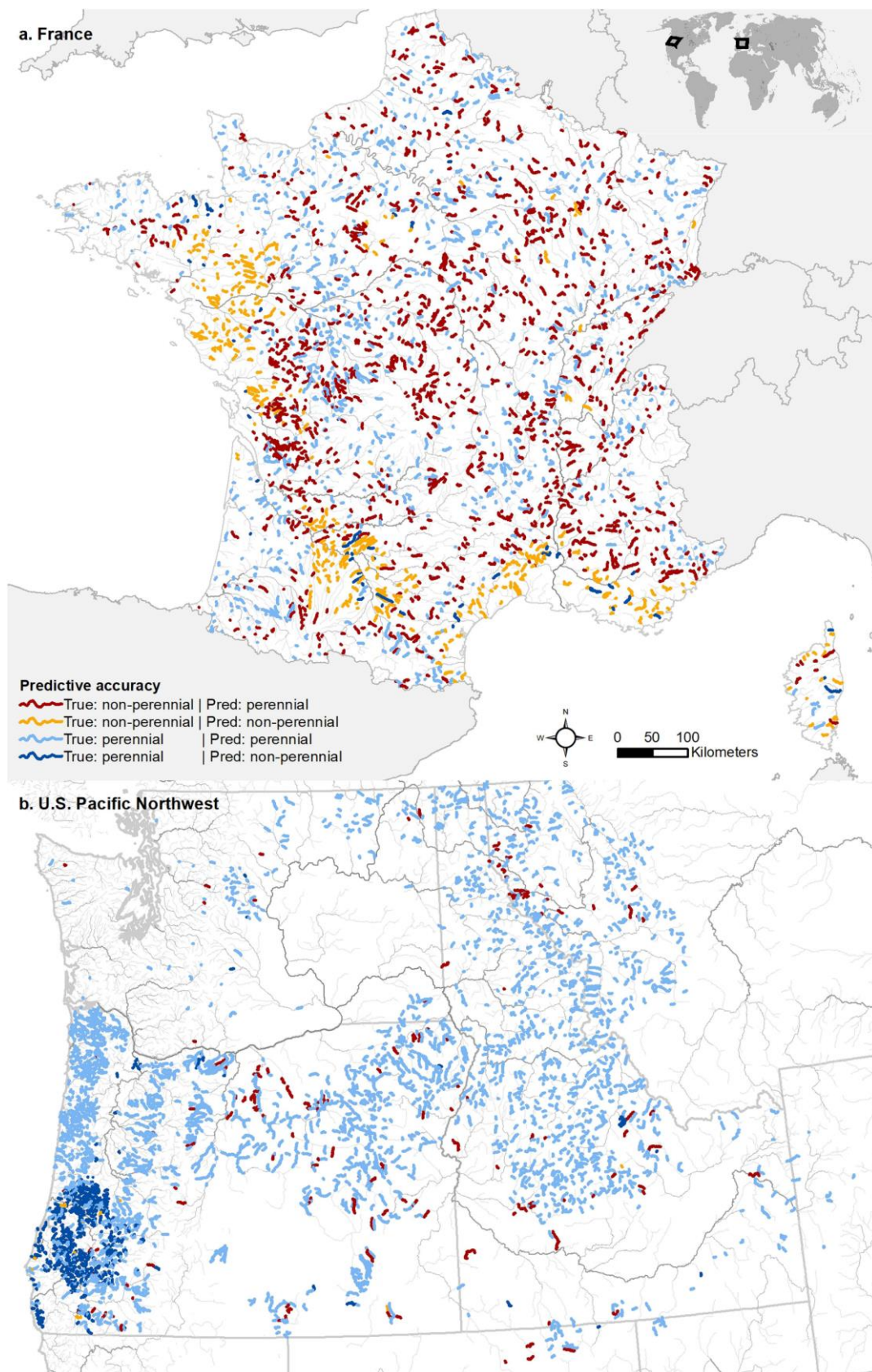


Figure 2.S6. Comparing global predictions to on-the-ground observations of flow cessation. **a, b,** Maps show individual RiverATLAS reaches and their predictive accuracy for France (**a**), and the US Pacific Northwest (**b**). Maps are drawn at identical cartographic scales. France ($n = 2,297$): balanced accuracy = 0.59, classification accuracy = 51%, sensitivity = 24%, specificity = 94%. US Pacific Northwest ($n = 3,725$): balanced accuracy = 0.47, classification accuracy = 80%, sensitivity = 10%, specificity = 83%. See **Extended Data Figure 2.S7b** for data sources. Mapping software: ArcMap (ESRI).

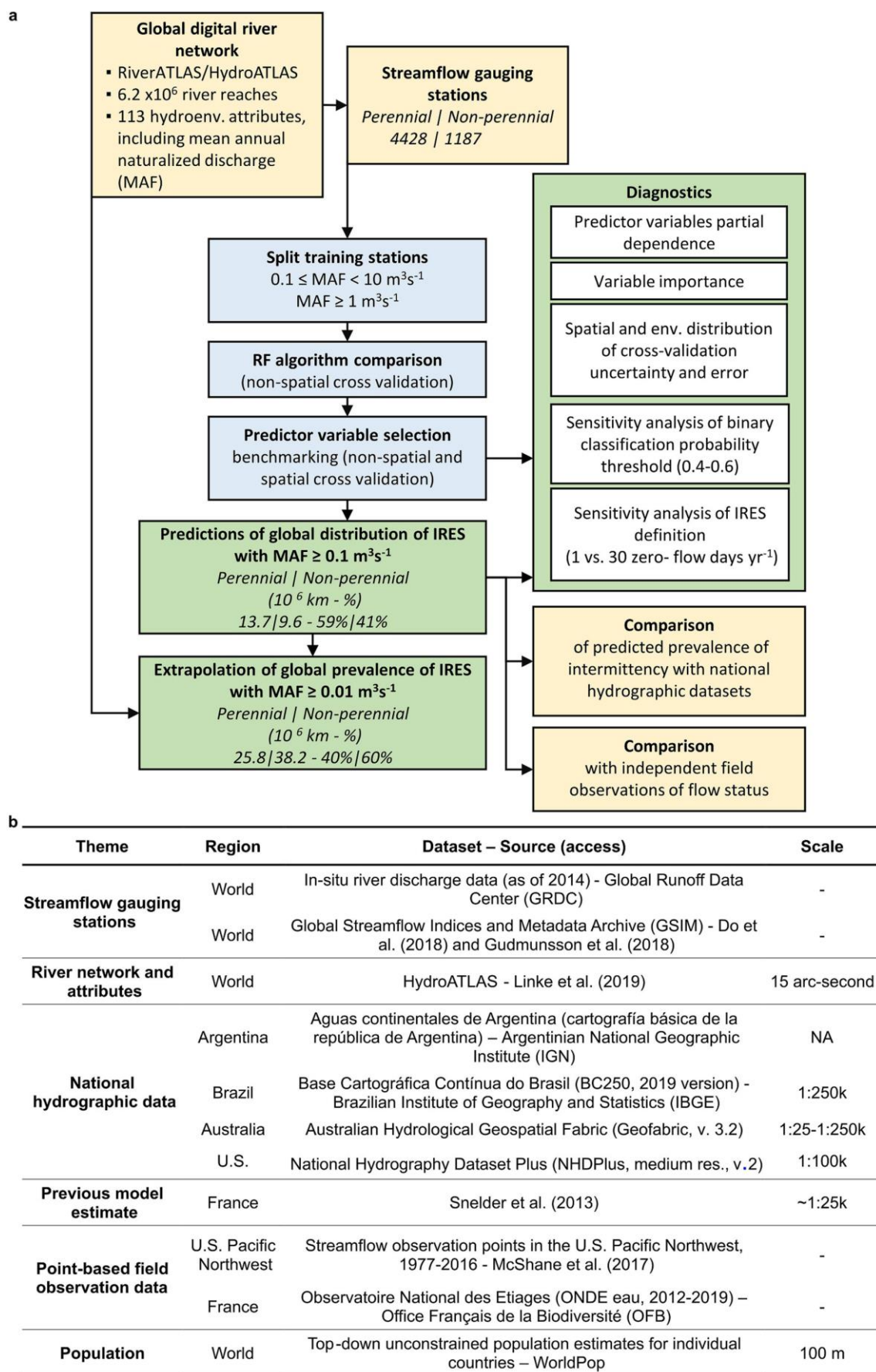


Figure 2.S7. Overview of study design and main data sources.

a, Diagram of modelling workflow. **b**, Main data sources used in model development, predictions, diagnostics and comparisons.

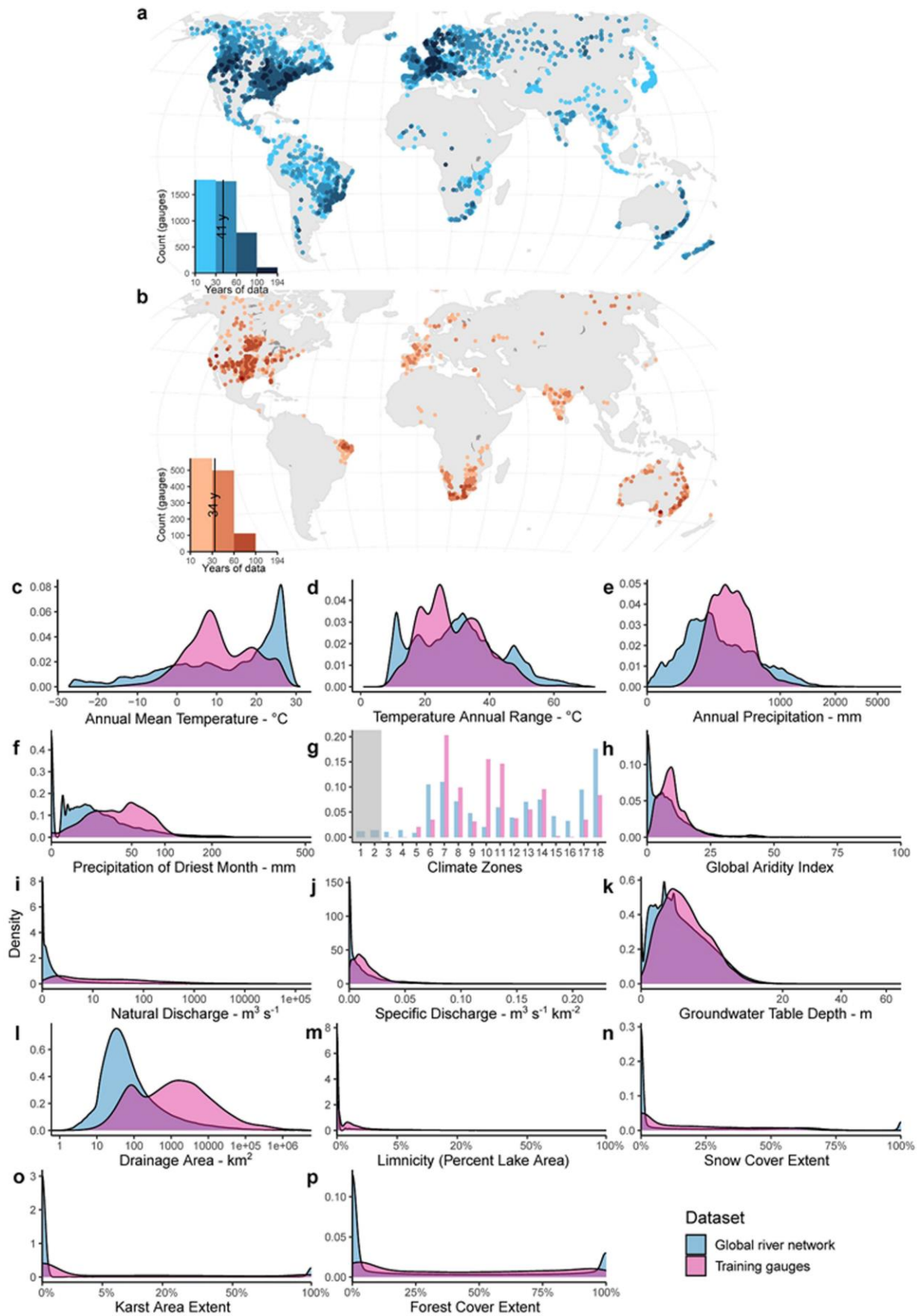


Figure 2.S8. Spatial and environmental distribution of streamflow gauging stations used in model training and cross-validation. See caption on the following page.

a, b, Gauging stations ($n = 5,615$) were deemed perennial (**a**) if their streamflow record included less than one zero-flow day per year, on average, across their record, or non-perennial (**b**) if they included at least one zero-flow day per year, on average, and at least one zero-flow day in every 20-year moving window across their record. Stations fulfilling neither condition **a** nor **b** were excluded. Darker points symbolize longer streamflow records. Only gauging stations with streamflow time series spanning at least 10 years were included in this analysis, excluding years with more than 20 missing days. **c–p**, Distribution of values for 14 hydro-environmental variables across the streamflow gauging stations used for model training/testing (purple, $n = 5,615$) and across all reaches of the global river network (blue, $n = 6.2 \times 10^6$). The distribution plots show empirical probability density functions (that is, the area under each density function is equal to one) for all variables, aside from climate zones (**g**) for which the relative frequency distribution is shown. All variables were averaged across the total drainage area upstream of the reach pour point associated with each gauging station or river reach, respectively. See **Extended Data Table 2.S2** for a description of the variables and **Extended Data Figure 2.S1a** for a description of the climate zones. No stations were available for climate zones Arctic 1 and Arctic 2. Mapping software: R statistical software (R Core Team).

Table 2.S1. Definitions of commonly used terms for non-perennial rivers and streams

Term	Definition	Source
Non-perennial	Any lotic, freshwater system that periodically ceases to flow and/or is dry at some point in time and/or space.	Busch et al. (2020)
Intermittent	A non-perennial river or stream with a considerable connection to the groundwater table, having variable cycles of wetting and flow cessation, and with flow that is sustained longer than a single storm event. These waterways are hydrologically gaining [surface water from groundwater] the majority of the time when considering long-term flow patterns.	Busch et al. (2020)
Ephemeral	A non-perennial river or stream without a considerable groundwater connection that flows for a short period of time, typically only after precipitation events. These waterways are hydrologically losing [surface water to groundwater] the majority of the time when considering long-term flow patterns.	Busch et al. (2020)
Intermittent rivers and ephemeral streams (IRES)	Flowing waters confined within a channel are called rivers or streams. Rivers are considered to be larger and deeper than streams, although the distinction is a loose one of common usage rather than based on fixed size and depth thresholds. The same common usage applies to describing differences in patterns of flow duration: the term ‘ephemeral’ implies a shorter duration and lower predictability than ‘intermittent’ — but again, there are no fixed boundaries. Therefore, given the broad association of channel size with flow duration, a stream is more likely to be ephemeral and a river intermittent, prompting the generalization.	Adapted from Datry et al. (2017)
Temporary	Rivers that cease to flow for a period of time during cycles of drying and rewetting.	Busch et al. (2020)

Table 2.S2. Hydro-environmental characteristics used as candidate predictor variables in the split random forest model.

Spatial representations refer to: p (derived at the pour point of the river reach), c (derived within the local catchment that drains directly into the reach), or u (derived within the total drainage area upstream of the reach pour point). See Linke et al. (2019) for a full description of the methodology to calculate the variables.

Category	Attribute	Spatial	Aggregation	Source	Citation
Climate	Annual mean temperature (BIO1)	c, u	average	WorldClim v2	Fick & Hijmans (2017)
Climate	Mean diurnal range (BIO2)	c, u	average	WorldClim v2	Fick & Hijmans (2017)
Climate	Isothermality — (BIO2/BIO7) ×100 (BIO3)	c, u	average	WorldClim v2	Fick & Hijmans (2017)
Climate	Temperature seasonality (SD ×100) (BIO4)	c, u	average	WorldClim v2	Fick & Hijmans (2017)
Climate	Max. Temperature of warmest month (BIO5)	c, u	average	WorldClim v2	Fick & Hijmans (2017)
Climate	Min. Temperature of coldest month (BIO6)	c, u	average	WorldClim v2	Fick & Hijmans (2017)
Climate	Temperature annual range (BIO7)	c, u	average	WorldClim v2	Fick & Hijmans (2017)
Climate	Mean temperature wettest quarter (BIO8)	c, u	average	WorldClim v2	Fick & Hijmans (2017)
Climate	Mean temperature driest quarter (BIO9)	c, u	average	WorldClim v2	Fick & Hijmans (2017)
Climate	Mean temperature warmest quarter (BIO10)	c, u	average	WorldClim v2	Fick & Hijmans (2017)
Climate	Mean temperature coldest quarter (BIO11)	c, u	average	WorldClim v2	Fick & Hijmans (2017)
Climate	Annual precipitation (BIO12)	c, u	average	WorldClim v2	Fick & Hijmans (2017)
Climate	Precipitation of wettest month (BIO13)	c, u	average	WorldClim v2	Fick & Hijmans (2017)
Climate	Precipitation driest month (BIO14)	c, u	average	WorldClim v2	Fick & Hijmans (2017)
Climate	Precipitation seasonality (BIO15)	c, u	average	WorldClim v2	Fick & Hijmans (2017)
Climate	Precipitation of wettest quarter (BIO16)	c, u	average	WorldClim v2	Fick & Hijmans (2017)
Climate	Precipitation driest quarter (BIO17)	c, u	average	WorldClim v2	Fick & Hijmans (2017)
Climate	Precipitation of warmest quarter (BIO18)	c, u	average	WorldClim v2	Fick & Hijmans (2017)
Climate	Precipitation of coldest quarter (BIO19)	c, u	average	WorldClim v2	Fick & Hijmans (2017)
Climate	Climate moisture index	c, u	annual min.	WorldClim v2 & Global-PET v2	Fick & Hijmans (2017)
Climate	Climate zones	c	spatial majority	GENS	Metzger et al. (2013)
Climate	Global aridity index	c, u	average	Global Aridity Index v2	Trabucco & Zomer (2019)
Climate	Actual evapotranspiration	c, u	annual average	Global Soil-Water Balance	Trabucco & Zomer (2010)
Climate	Potential evapotranspiration	c, u	annual average	Global-PET v2	Trabucco & Zomer (2019)
Climate	Snow cover extent	c, u	annual average	MODIS/Aqua	Hall & Riggs (2016)
Climate	Snow cover extent	c	annual max.	MODIS/Aqua	Hall & Riggs (2016)
Hydrology	Groundwater table depth	c	average	Global Groundwater Map	Fan et al. (2013)
Hydrology	Inundation extent	c, u	annual min.	GIEMS-D15	Fluet-Chouinard et al. (2015)
Hydrology	Inundation extent	c, u	annual max.	GIEMS-D15	Fluet-Chouinard et al. (2015)
Hydrology	Land surface runoff	c	annual average	WaterGAP v2.2	Müller Schmied et al. (2014)
Hydrology	Limnity (percent lake area)	c, u	% extent	HydroLAKES	Message et al. (2016)
Hydrology	Naturalized discharge	p	annual average	WaterGAP v2.2	Müller Schmied et al. (2014)
Hydrology	Naturalized discharge	p	annual min.	WaterGAP v2.2	Müller Schmied et al. (2014)
Hydrology	Naturalized discharge	p	annual max.	WaterGAP v2.2	Müller Schmied et al. (2014)
Hydrology	Naturalized discharge	p	min/max	WaterGAP v2.2	Müller Schmied et al. (2014)
Hydrology	Naturalized discharge	p	min/average	WaterGAP v2.2	Müller Schmied et al. (2014)
Hydrology	Runoff coefficient (runoff/precipitation)	c	average	WaterGAP v2.2, WorldClim v2	Müller Schmied et al. (2014)
Hydrology	Specific discharge (discharge/upst. area)	u	annual average	WaterGAP v2.2	Müller Schmied et al. (2014)
Hydrology	Specific discharge	u	annual min.	WaterGAP v2.2	Müller Schmied et al. (2014)
Hydrology	Surface water dry period	c, u	average	GLAD	Pickens et al. (2020)
Hydrology	Surface water high frequency	c, u	average	GLAD	Pickens et al. (2020)
Hydrology	Surface water loss	c, u	average	GLAD	Pickens et al. (2020)
Hydrology	Surface water maximum extent	c, u	average	GLAD	Pickens et al. (2020)
Hydrology	Surface water permanent	c, u	average	GLAD	Pickens et al. (2020)
Hydrology	Surface water seasonal	c, u	average	GLAD	Pickens et al. (2020)
Hydrology	Surface water wet period	c, u	average	GLAD	Pickens et al. (2020)
Landcover	Forest cover extent	c, u	% extent	GLC2000	Bartholomé & Belward (2005)
Landcover	Glacier extent	c, u	% extent	GLIMS	GLIMS; NSIDCenter (2012)
Landcover	Land cover classes	c	spatial majority	GLC2000	Bartholomé & Belward (2005)
Landcover	Agricultural extent	c, u	% class 16	GLC2000	Bartholomé & Belward (2005)
Landcover	Permafrost extent	c, u	% extent	PZI	Gruber (2012)
Landcover	Potential natural vegetation classes	c	spatial majority	EarthStat	Ramankutty & Foley (1999)
Landcover	Pan, brackish/saline wetland extent	c, u	% class 7	GLWD	Lehner & Döll (2004)
Landcover	Intermittent wetland/lake extent	c, u	% class 9	GLWD	Lehner & Döll (2004)
Landcover	Wetland extent (incl. lakes, reservoirs, rivers)	c, u	% class group 1	GLWD	Lehner & Döll (2004)
Landcover	Wetland extent (excl. lakes, reservoirs, rivers)	c, u	% class group 2	GLWD	Lehner & Döll (2004)
Physiography	Drainage area	u	-	HydroSHEDS	Lehner & Grill (2013)
Physiography	Relative elevation	(c-u)/u	average	EarthEnv-DEM90	Robinson et al. (2014)
Physiography	Terrain slope	c, u	average	EarthEnv-DEM90	Robinson et al. (2014)
Soils+Geology	Karst area extent	c, u	% extent	Rock Outcrops v3.0	Williams & Ford (2006)
Soils+Geology	Lithological classes	c	spatial majority	GLiM	Hartmann & Moosdorf (2012)
Soils+Geology	Clay fraction in soil 0-100 cm	c, u	average	SoilGrids250m v2	Hengl et al. (2017)
Soils+Geology	Sand fraction in soil 0-100 cm	c, u	average	SoilGrids250m v2	Hengl et al. (2017)
Soils+Geology	Silt fraction in soil 0-100 cm	c, u	average	SoilGrids250m v2	Hengl et al. (2017)
Soils+Geology	Soil water content	c, u	annual average	Global Soil-Water Balance	Trabucco & Zomer (2010)
Soils+Geology	Soil water content	c, u	annual min.	Global Soil-Water Balance	Trabucco & Zomer (2010)

Table 2.S3. Performance summary of binary flow intermittence class predictions

a–c, Tables show summary results for the split model approach based on a twice-repeated threefold non-spatial cross-validation (CV; **a**) and a once-repeated 40-fold spatial CV (**b**), as well as, for comparison, a single (non-split) model approach based on a twice-repeated threefold non-spatial CV (**c**). The colour coding mirrors **Extended Data Figure 2.S2** with light colours slightly darkened for readability. The split model approach involves training two random forest sub-models with slightly overlapping MAF ranges, one trained to predict the streamflow intermittence probability of small-to-medium rivers with $\text{MAF} < 10 \text{ m}^3 \text{ s}^{-1}$ and the other for medium-to-large rivers with $\text{MAF} \geq 1 \text{ m}^3 \text{ s}^{-1}$. Within the overlapping range of $1\text{--}10 \text{ m}^3 \text{ s}^{-1}$ MAF, the average probability was calculated to avoid abrupt transitions at a singular size threshold. Gauging stations monitoring streams with a mean annual naturalized discharge $< 0.1 \text{ m}^3 \text{ s}^{-1}$ were included in model training and testing (shown in grey font); however, no global model predictions were made below this discharge threshold. Sensitivity is the proportion of non-perennial reaches correctly classified as non-perennial. Specificity is the proportion of perennial reaches correctly classified as perennial. Precision is the proportion of reaches classified as non-perennial that are truly non-perennial. See **Supplementary Figure 2.S11** and **Supplementary Information section 2.9.4** for the distribution of spatial cross-validation folds and details on the cross-validation procedure.

a. Split model approach: twice-repeated 3-fold non-spatial cross-validation

Streamflow size class ($\text{m}^3 \text{ s}^{-1}$)	Prediction (number of gauging stations) Non-perennial Perennial		Total (N)	Prevalence of IRES (%) Pred. True	Accuracy (%)	Sensitivity (%)	Specificity (%)	Precision (%)
	True: Non-perennial	True: Perennial						
(0, 0.1)	42 4	7 6	59	83 78	91	91	46	86
[0.1, 1)	292 55	44 504	895	38 39	89	84	92	87
[1, 10)	490 70	111 1217	1888	32 30	90	88	92	82
[10, 10^2)	175 24	82 1459	1740	15 11	94	88	95	68
[10^2 , 10^3)	33 1	24 757	815	7 4	97	97	97	58
[10^3 , 10^4)	1 0	2 187	190	2 1	99	100	99	33
$\geq 10^4$	0 0	0 28	28	0 0	100	-	100	-
All	1033 154	270 4158	5615	23 21	92	87	94	79

b. Split model approach: 40-fold spatial cross-validation

Streamflow size class ($\text{m}^3 \text{ s}^{-1}$)	Prediction (number of gauging stations) Non-perennial Perennial		Total (N)	Prevalence of IRES (%) Pred. True	Accuracy (%)	Sensitivity (%)	Specificity (%)	Precision (%)
	True: Non-perennial	True: Perennial						
(0, 0.1)	43 3	9 4	59	88 78	80	93	31	83
[0.1, 1)	280 67	54 494	895	37 39	86	81	90	84
[1, 10)	459 101	151 1177	1888	32 30	87	82	89	75
[10, 10^2)	146 56	87 1454	1740	13 11	92	72	94	62
[10^2 , 10^3)	14 20	16 765	815	4 4	96	41	98	47
[10^3 , 10^4)	0 1	0 189	190	0 1	99	100	100	-
$\geq 10^4$	0 0	0 28	28	0 0	100	-	100	-
All	939 248	317 4111	5615	22 21	90	80	93	75

c. Single (non-split) model approach: twice-repeated 3-fold non-spatial cross-validation

Streamflow size class ($\text{m}^3 \text{ s}^{-1}$)	Prediction (number of gauging stations) Non-perennial Perennial		Total (N)	Prevalence of IRES (%) Pred. True	Accuracy (%)	Sensitivity (%)	Specificity (%)	Precision (%)
	True: Non-perennial	True: Perennial						
(0, 0.1)	42 4	9 4	59	86 78	78	91	31	82
[0.1, 1)	303 44	64 484	895	41 39	88	87	88	83
[1, 10)	498 62	123 1205	1888	33 30	90	89	91	80
[10, 10^2)	166 33	62 1479	1740	13 11	95	83	96	73
[10^2 , 10^3)	30 4	20 761	815	6 4	97	88	97	60
[10^3 , 10^4)	1 0	1 188	190	1 1	99	100	99	50
$\geq 10^4$	0 0	0 28	28	0 0	100	-	100	-
All	1040 147	279 4149	5615	23 21	92	88	94	79

2.9. Supplementary Information

2.9.1. *Comparison between model predictions and previous estimates*

Several studies have made first-order approximations of the prevalence of IRES globally (Datry et al., 2014; FAO, 2014; Raymond et al., 2013; Schneider et al., 2017; Tooth, 2000).

Below, we describe the sources, objectives, and approaches of these main estimates currently cited in the literature (Acuña et al., 2020; Marcé et al., 2019; Sadid et al., 2017; Theodoropoulos et al., 2019).

Tooth (2000):

- Objective: to provide a general overview of fluvial research in drylands.
- Estimated that drylands comprise 50% of the world's landmass (based on the UNEP World Atlas of Desertification, 1992).
- Although this study did not provide a quantitative estimate or explicitly state that all rivers within drylands are IRES, it is commonly cited to state that IRES comprise most of the world's rivers.

Raymond et al. (2013):

- Objective: to provide spatial maps of global inland water CO₂ evasion, excluding IRES.
- Extrapolated the prevalence of flow intermittence from the U.S. hydrographic dataset (NHDPlus) to the rest of the world with multiple linear regression models of precipitation and temperature.
- Predicted that 69%, 56%, 49%, 42%, and 34% of stream orders 1-5 are "ephemeral", respectively.
- Based on the same hydrographic framework as the one used in our study (HydroSHEDS at 15 arc-second resolution), but only accounting for areas south of 60°N, and all predictions are made at the basin scale, rather than at the reach scale.
- Not assessed or validated outside of the U.S.

Datry et al. (2014):

- Objective: to review benefits and challenges of incorporating IRES into modern concepts, knowledge, and methods in freshwater and terrestrial ecology.

- Hypothesised, based on Tooth (2000) and regional studies, that the global prevalence of IRES is at least $\geq 30\%$ of the global length of rivers, and probably $\geq 50\%$.
- Commonly cited as a source of estimate.

Food and Agriculture Organization AQUAMAPS (FAO, 2014):

- Objective: to create a global digital river network with hydrological attributes on flow regime.
- Determined a constant Aridity Index threshold (ratio of mean annual precipitation to mean annual potential evapotranspiration), for each Strahler order, below which a stream was classified as non-perennial, using the FAO African Water Resources Database (<http://www.fao.org:80/geonetwork?uuid=cb123b20-f3c8-11db-adea-000d939bc5d8>, published in 2007) as reference.
- Estimated the global prevalence of IRES as 34% of the global length of rivers (statistics from Table 1 in Schneider et al. 2017).
- Based on the same hydrographic framework as the one used in our study (HydroSHEDS at 15 arc-second resolution), but only accounting for areas south of 60°N and rivers with a drainage area $\geq 100 \text{ km}^2$.

Schneider et al. (2017):

- Objective: to develop simple models for global river network extraction and make first-order flow intermittence assessment.
- Classified all watercourses in areas with precipitation below a given threshold as non-perennial using the Australian national geofabric dataset as reference.
- Estimated that 29% to 36% of the world's rivers are IRES, by length (based on precipitation thresholds of 600 mm yr^{-1} and 500 mm yr^{-1} , respectively).
- Based on the same hydrographic framework as the one used in our study (HydroSHEDS at 15 arc-second resolution), but only accounting for areas south of 60°N and used a variable threshold to delineate rivers (i.e., minimum drainage area thresholds from 0.3 to 193 km^2 , depending mostly on climate).

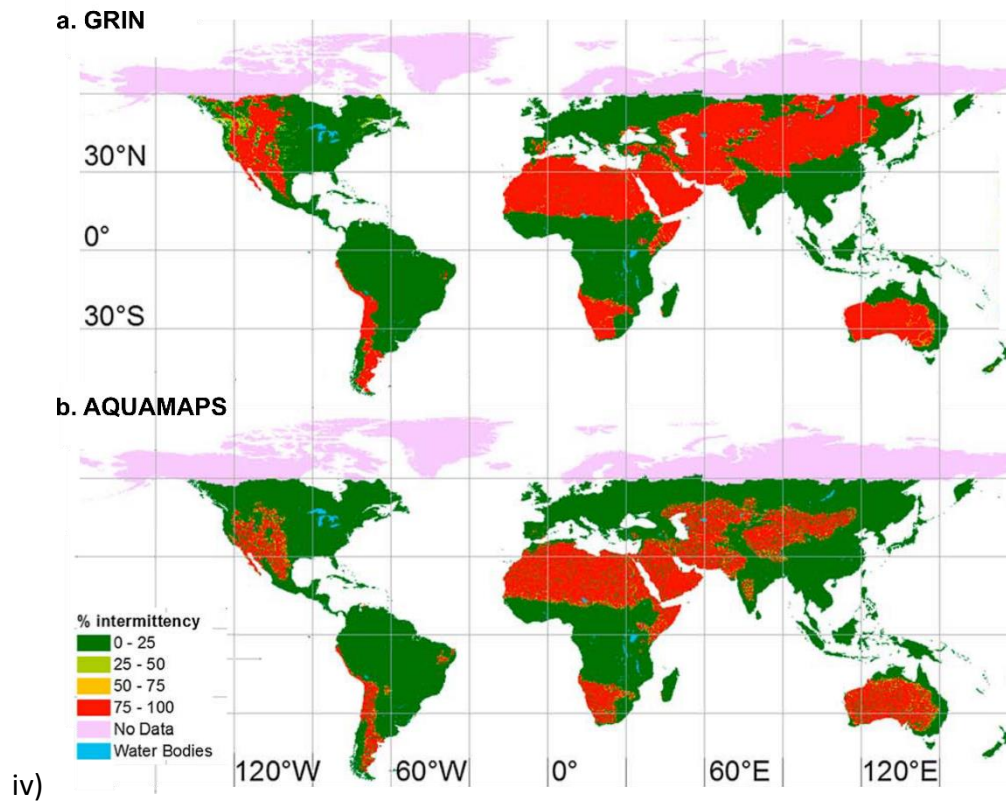


Figure 2.S9. Distribution of IRES according to previous spatially-explicit estimates. Panels show the prevalence of flow intermittence as modelled by (a) GRIN (Schneider et al., 2017) and (b) AQUAMAPS (FAO, 2014).

All areas above 60°N are excluded as they were not contained in the original version of the HydroSHEDS database (Lehner et al., 2008) which provided the underpinning river network for GRIN and AQUAMAPS. Adapted from Figure 3 in Schneider et al. (2017).

2.9.2. Selection and pre-processing of gauging station and discharge data

Streamflow gauging stations: assignment of river network location

To assemble training and cross-validation datasets of streamflow gauging stations, we first linked the Global Runoff Data Center (GRDC) hydrometric dataset to the RiverATLAS global river network. We then complemented the GRDC dataset with a subset of gauging stations from the Global Streamflow Indices and Metadata Archive (GSIM; Do et al., 2018; Gudmundsson et al., 2018).

The linkage of GRDC stations to RiverATLAS followed a three-step process:

- i) The stations were associated with the HydroSHEDS flow accumulation grids (Lehner et al., 2008) based on the procedure documented in GRDC Report number 41 (Lehner, 2012): each station was automatically linked to the location within five kilometres around the original location reported in the GRDC database that optimized the agreement between the reported drainage area in the GRDC database and the modelled drainage area derived from HydroSHEDS, while limiting the distance from its original location.
- ii) Following this placement, only stations whose HydroSHEDS drainage area diverged by less than 5% from the reported GRDC areas were retained for subsequent steps. Each station was then associated with a river reach in the RiverATLAS river network (vector-based):
 - Each station was first associated with the nearest river reach (from the location determined in the previous step).
 - If the drainage area at the pour point of the reach differed by more than 10% from the reported drainage area in the GRDC database, we manually inspected, and corrected if appropriate, the location of the station (see step iii).
- iii) Manual inspection involved verifying that the reach a station had been associated with in the RiverATLAS digital river network corresponded to the actual waterway the station was located on, based on topographic and high-resolution satellite imagery (ESRI ArcGIS basemaps). If we could not ascertain the position of the gauging station, the GRDC-reported river and station names were verified in close vicinity (~10 km), exploiting the fact that station names often originate from nearby settlements, roads, or other geographic features. If a station could not be verified within this vicinity, the search was

extended to within 50-100 km. If still no location was found that matched the river and/or station name, the station name was queried in search engines and online maps to see whether a location with this name existed. In all cases, the final decision on whether a station was moved to a new and “reliable” location depended on whether at least two out of the following four indicators could be matched reasonably well: a) location on corresponding waterway based on satellite imagery or topographic map; b) river name; c) station name and d) drainage area (match between reported GRDC value and modeled RiverATLAS value). Some final decisions were subjective as difficult combinations could arise (e.g., multiple agreements yet also disagreement(s) in the different indices).

Of the 6,543 GRDC stations with point coordinates that had daily streamflow data post-1961 (as of July 2014), 2,001 were removed in step (ii) and 25 were removed in step (iii), yielding a set of 4,517 stations (including 225 stations whose position was manually adjusted) that could be reliably matched with a river reach in RiverATLAS for subsequent analysis.

Following this spatial pre-processing/filtering, we removed GRDC stations with less than 10 years of daily discharge data (excluding years with more than 20 missing days), yielding a final dataset of 3,748 stations.

We applied a similar process of spatial pre-processing to an initial subset of 4,076 GSIM stations (out of 30,959) which:

- were not already part of the GRDC database, and
- included auxiliary information on the size of the drainage area associated with the station, and
- had at least 10 years of daily discharge data (excluding years with more than 20 missing days), and
- had a reported drainage area $\geq 5 \text{ km}^2$ or a reported mean annual discharge $\geq 0.01 \text{ m}^3 \text{ s}^{-1}$ (as RiverATLAS only includes rivers with a drainage area $\geq 10 \text{ km}^2$ or mean annual discharge $\geq 0.1 \text{ m}^3 \text{ s}^{-1}$ to which we added a margin of error), and
- either:
 - o had a drainage area $< 100 \text{ km}^2$, or
 - o were located on an IRES, or
 - o were located in a river basin which did not already contain a selected GRDC station (based on HydroBASINS level 5 sub-basins, average area globally = $2.9 \times 10^4 \text{ km}^2$).

All GSIM stations had already been associated with the HydroSHEDS flow accumulation grids by Do et al. (2018) following the same procedure documented in Lehner (2012) and outlined above for GRDC stations (step i). Therefore, we directly associated all GSIM stations with a river reach in the RiverATLAS river network following the same approach as described for GRDC stations above (step ii). Given the diversity of original data sources compiled in the GSIM database, an additional level of caution was applied in linking GSIM stations to the network so that every station was manually inspected following the procedure described above for GRDC stations (step iii). We manually modified the position of 1,736 GSIM stations and removed 791, keeping 3,284 stations for subsequent analysis.

Following this spatial pre-processing, we also removed 160 stations located on the same RiverATLAS river reach as another station (keeping the station with the smallest difference in reported drainage area compared to that computed in RiverATLAS for the reach's pour point). There was no instance of stations with different flow intermittence classes being associated with the same RiverATLAS reach. We also removed 632 stations whose degree of flow regulation (DOR) by upstream reservoirs (Lehner et al., 2011) exceeded 50%. The resulting dataset at this point contained 6,240 stations.

Streamflow gauging stations: quality-checking of discharge information

A custom procedure was developed to ensure the quality of the streamflow time series (rather than the spatial location) associated with the gauging stations. The focus of this quality-checking procedure was to ensure the validity of zero-flow readings and the flow intermittence class assigned to each gauge (i.e., perennial or non-perennial). Zero-flow readings at streamflow gauging stations can stem from multiple circumstances. Usually, these readings reflect true river drying due to various natural or anthropogenic processes. However, river freezing, flow reversal (e.g., due to tidal influence), instrument malfunctioning, and data entry or processing errors are also common events that can result in zero-flow readings in spite of the continued flow of water in the channel (Zimmer et al., 2020). Reported time series data may contain ambiguity between zero-flow and no-data entries, leading to potential underestimation of zero-flow (if masked as no-data). In addition, river diversions and reservoirs associated with dams can modify the flow intermittence of a monitored river reach from perennial to non-perennial (e.g., interrupting water flow as a single event during the initial filling of the reservoir; periodic to permanent dewatering of

the downstream channel due to water diversion) and vice versa (e.g., keeping a constant flow of water for hydroelectricity production). Ideally, each streamflow record would be accompanied by detailed information and flags describing the quality of individual daily values. However, this information is typically unavailable or difficult to access. Notably, the GRDC has stopped providing data quality flags in recent updates, and both the GRDC and the European Water Association (EWA) recommend users not to rely on existing quality flags (Gudmundsson et al., 2018).

For GSIM stations, a statistical quality-checking procedure was already performed by Gudmundsson et al. (2018) to flag suspect daily values and remove them prior to computing hydrological indices. For databases that provided reliable quality (QA/QC) flags, all flagging typologies were translated to a common framework (see Table 1 in Gudmundsson et al., 2018) and suspect values were removed.

For station records originating from databases that did not provide quality flags (or that recommended not to use them, i.e., EWA and GRDC), a statistical procedure was applied by Gudmundsson et al. (2018) to flag and remove suspect values with the following characteristics:

- i) Days with negative recorded discharge.
- ii) Daily values with more than 10 consecutive equal discharge values larger than zero. This rule is motivated by the fact that many days with consecutive streamflow values often occur due to instrument failure (e.g., damaged sensors, ice jams) or flow regulations.
- iii) Daily streamflow values (Q) if $\log(Q+0.01)$ was larger or smaller than the mean value of $\log(Q+0.01)$ plus or minus 6 times the standard deviation of $\log(Q+0.01)$ computed for that calendar day for the entire length of the series. The mean and standard deviation are computed for a 5-day window centred on the calendar day to ensure that enough data are considered. See Gudmundsson et al. (2018), Gudmundsson & Seneviratne (2016), and Klein Tank et al. (2009) for the rationale behind these criteria.

We used the same criteria to automatically flag individual daily streamflow values in the streamflow records of the GRDC gauging stations. However, rather than directly removing flagged daily streamflow values, as was done for GSIM by Gudmundsson et al. (2018), the values that we flagged as being suspect were further investigated through a visual inspection

of the gauges' streamflow records. Prior to visual inspection, we removed all stations for which only integer streamflow values were available, as any daily discharge value $< 0.5 \text{ m}^3 \text{ s}^{-1}$ is reported as zero by the data provider at these stations.

We visually inspected plots of the discharge time series for both GSIM and GRDC stations. For GRDC stations, we inspected time series of daily streamflow values with flagged suspect values. For GSIM stations, we inspected plots depicting the mean (± 2 standard deviations), minimum and maximum monthly discharge, as daily streamflow records from GSIM stations are unavailable. In addition, as we did not have access to the daily streamflow records used in producing GSIM, none of the values flagged and removed by Gudmundsson et al. 2018 were available for our visual inspection. If unable to determine the validity of the record with reasonable confidence (often a subjective decision given the lack of auxiliary information), we erred on the side of caution, i.e., we deemed the gauging station as unreliable and excluded it from subsequent analysis.

When a station exhibited a flow regime that we suspected was caused by a flow regulating structure (e.g., a dam or reservoir), we inspected satellite and topographic imagery for the presence of a regulating structure upstream of the station and excluded the station if one was present. Indicators of flow regulation included abrupt changes in seasonality or decreases in the magnitude of peak- or low-flows, signs of hydropeaking (i.e., short duration, high flow events at regular intervals), sometimes following a temporary dip in discharge (due to reservoir filling). See our online research compendium (<https://messamat.github.io/globalRmap/>) for an interactive visualization of processing information for every gauging station that was removed, including the reason for its removal and associated time-series plots.

Due to a pre-processing artefact in the production of GSIM by Gudmundsson et al. (2018), daily streamflow values for stations located in the U.S. had been rounded to two decimals, leading to very low discharge values ($< 0.005 \text{ m}^3 \text{ s}^{-1}$) being rounded to 0. Therefore, we made sure of the validity of zero-flow values for all U.S. stations which, according to GSIM records, had at least one zero-flow day per year on average (i.e., would be considered non-perennial in the subsequent analysis): we downloaded and computed flow intermittence statistics directly from the original daily discharge data provided by the United States Geological

Survey (USGS). All stations with ≥ 1 zero-flow day per year according to GSIM but < 1 zero-flow day per year according to USGS data were excluded from further analysis.

An additional level of caution was used for stations on river reaches undergoing flow cessation exclusively in winter and for stations in the vicinity of a marine coastline, as instrument freeze-up and tidal flow reversal are both documented sources of anomalous zero-flow values (Zimmer et al., 2020). “Winter-only” non-perennial gauging stations were defined as those whose stream record contained less than one zero-flow day per year on average during months with long-term mean air temperature over 10°C (averaged across the local catchment immediately draining to the river reach, according to WorldClim 2; Fick & Hijmans, 2017). In other words, “winter-only” non-perennial gauging stations were those which would not have qualified as non-perennial according to our criterion if only non-winter months were taken into account. “Marine” stations were defined as those within 3 km of a coastline. For GSIM stations with visually suspect anomalous records (e.g., abrupt shift down to $0 \text{ m}^3 \text{ s}^{-1}$ that may be driven by station freezing), we attempted to obtain original daily streamflow records from the original agencies whose data was used to produce GSIM if they were freely available online (e.g., from HYDAT in Canada or USGS in the United States).

Following this statistical outlier detection and manual time series inspection, we excluded 625 suspicious gauging stations and conducted the rest of the analysis with 5,615 gauging stations for model training and cross-validation, which represented a wide range of river types found on Earth (**Extended Data Figure 2.S8**).

Quality-checking of discharge estimates provided in RiverATLAS

Table 2.S4. Summary performance statistics of RiverATLAS discharge estimates.

Naturalised discharge estimates from RiverATLAS (downscaled from the global WaterGAP hydrological model, version 2.2) were compared to recorded discharge at 2,131 streamflow gauging stations with at least 20 years of daily records (excluding years with more than 20 missing days) for the 1971-2000 climate normal. The chosen time period matches that of the WaterGAP discharge estimates (Linke et al., 2019).

Performance statistics were computed for:

- top half of table: observed (obs.) against (~) estimated (est.) Mean Annual Flow (MAF)
- bottom half of table: observed Q90 (10th percentile of streamflow) against estimated annual minimum monthly flow (monthly min.).

R^2 values are based on ordinary least-square regressions either including or excluding extreme outliers (based on absolute studentized residuals > 3). MAE is the mean absolute error while SMAPE is the symmetrical mean average percentage error.

Streamflow size class (m ³ s ⁻¹)		R^2	R^2 (no outliers)	MAE (m ³ s ⁻¹)	SMAPE (%)	<i>N</i> (total)	Number of outliers
obs. MAF ~ est. MAF	< 1	0.14	0.14	0.61	75	192	0
	1-9	0.24	0.26	2.27	44	540	1
	10-99	0.72	0.75	8.87	24	848	3
	100-999	0.92	0.95	33.52	12	424	3
	1000-9999	0.99	0.99	141.80	5	109	2
	>=10000	1.00	1.00	1511.61	5	18	1
	All (log-log)	0.96	0.96	30.85	30	2131	3
obs. Q90 ~ est. monthly min.	< 1	0.03	0.03	0.24	-	192	0
	1-9	0.12	0.12	1.32	-	540	3
	10-99	0.25	0.25	9.52	83	848	3
	100-999	0.43	0.48	63.76	60	424	2
	1000-9999	0.84	0.81	419.88	44	109	1
	>=10000	0.99	0.99	3131.90	25	18	2
	All (log-log)	0.84	0.84	64.76	-	2131	1

2.9.3. Random forest implementation

Background

Originally developed by Breiman (2001), Random Forest (RF) is applicable to a wide range of problems because it can cope with high-dimensional data, strongly correlated predictors and non-linear relationships between predictors and response variables. RF is also easy to implement as it does not require the user to specify a model underlying the data, only has a few tunable hyperparameters, performs well with default settings, and is parallelizable (sub-components of the model can be computed simultaneously, in contrast to e.g., boosted regression trees). Here we refer to hyperparameters as the tunable settings that determine how exactly the RF algorithm works rather than parameters (often also called coefficients) as defined for parametric models, which in that case are estimated at the time of fitting the model to the data (Kuhn & Johnson, 2013). Owing to its high predictive ability and ease of use, RF has become widely adopted across disciplines, including in the water resource sciences (Beck et al., 2016; Hengl et al., 2018; Tyrallis et al., 2019), and a host of publications have reviewed its functioning, biases and implementation (Biau & Scornet, 2016; Boulesteix et al., 2012; Hastie et al., 2008). Accordingly, only a brief explanation of the algorithm will be provided here.

RF is based on the aggregation of many decision trees, each constructed from a subset of the full training dataset and internally validated, so that the resulting ensemble yields unbiased predictions (i.e., overfitting is minimized). RF can accommodate both classification and regression problems.

In its classic form, the random forest algorithm independently grows a user-defined number of different, randomized, classification and regression trees (CART) as follows. For each tree, a fraction of observations is selected at random from the original dataset and becomes the only subset of observations used in the training of that tree. The root node of the tree contains all selected observations. Starting at this 'parent' node, a unidimensional split in the predictor variable space partitions the observations into two distinct subsets, forming two 'child' nodes (i.e., observations are separated based on a value split for a single variable). Child nodes in turn become parent nodes. All nodes are recursively split this way until the last terminal nodes contain a user-defined minimum number of observations. At each node, the algorithm determines the split point that maximizes the CART-criterion. For regression

problems, the CART-criterion is the sum of squared deviations of the values within the resulting partitioned subsets of observations. For classification problems, the decrease in Gini impurity within the partitions is used which, in a binary classification, decreases as the proportions of the two classes in the nodes become more imbalanced — as the resulting nodes become “purer”. For instance, Gini impurity is lower for 70/30 than for 50/50 proportions. An individual tree in RF differs from classical CART in that it subsamples the training data, it only evaluates a random subset of predictor variable values at each node split (rather than the whole range of variables and their values), and in that the tree is not pruned. Once constructed, a single regression (or classification) tree predicts the value (or class) for a new observation by following the decision rule at all nodes iteratively, until the predicted value (or class) for the new observation is determined by the average value (or majority class) in the terminal node. In a regression RF, the ensemble predicted response for the new observation is the average of the predictions of all trees. In a classification RF, the class of a new observation is determined by majority voting across all trees.

There exist several algorithms derived from this original form developed by Breiman (2001). Derivative algorithms vary in the way the subset of data used for constructing each individual tree is selected, the way each tree is constructed, and the way predictions are aggregated across trees to produce a single ensemble prediction.

Comparison of RF algorithms

Our final predictions are based on the probability RF algorithm developed by Malley et al. (2012), a derivative of the standard RF algorithm for making probabilistic predictions of class membership, as included in the *ranger* R package (Wright & Ziegler, 2017). This algorithm, hereafter referred to as the ‘default RF’, was selected following a comparison of several probability RF variants (described in this section). We performed this comparison with the *mlr3* R package (version 0.6.0), a scalable, model-agnostic, machine learning model development interface (Lang et al., 2019).

In the chosen default RF algorithm, individual classification trees are first grown based on the original RF algorithm described in the previous section. Second, to estimate the probability that a new observation not used in the training dataset is non-perennial for a single tree, the predictor variables for that observation are run through the tree’s recursive splitting rules until the observation is assigned to a terminal node. Third, the proportion of

non-perennial rivers in that terminal node is determined and the final probability estimate from the full RF is, as a last step, calculated as the average of the proportions determined this way across all trees (Malley et al., 2012).

We compared this algorithm to two other RF algorithm variants, namely:

- i) the Conditional Inference Forest (CIF; Hothorn et al., 2006) with probability predictions as implemented in the partykit R package (Hothorn & Zeileis, 2015), and
- ii) a custom implementation in the ranger package of the regression RF using MAXimally selected rank STATistics (MAXSTAT) developed by Wright et al. (2017).

The CIF and MAXSTAT algorithms were both tested to address a common pitfall in the original RF algorithm. The original RF tends to favor predictors with many possible values or categories during the split selection process (Hothorn et al., 2006; Strobl et al., 2007). This can lead to suboptimal predictions and biased measures of variable importance in which the predictive importance of predictors with few values/categories is underestimated. To cope with this limitation, we first implemented a CIF, which relies on permutation-based hypothesis testing at every tree split to address issues of variable selection bias and overfitting (Hothorn et al., 2006). However, CIF can be orders of magnitude more computationally expensive than conventional RF and relies on linear rank statistics to select the optimal splitting variable, which cannot detect non-linear effects in the predictor variables. We therefore tested a recent RF regression algorithm which uses maximally selected rank statistics ('MAXSTAT') for the split point selection (Wright et al., 2017), using flow intermittence as a dummy continuous response variable (despite its binary nature). This approach makes unbiased split variable selection possible while being as computationally efficient as more conventional algorithms. In both CIF and MAXSTAT, hypothesis testing complements the user-defined minimum terminal node size, such that tree construction stops once the association between possible predictors for splitting and the response is too weak (above a given p -value).

We parameterized all algorithms to perform the initial sampling of training data without replacement, since sampling with replacement has also been shown to accentuate biases in variable importance measures towards predictors with many categories (Strobl et al., 2007).

Addressing class imbalance

Another bias afflicts RF predictions when the training dataset is characterized by an imbalanced proportion of classes. Our training data comprised nearly four times more gauging stations on perennial than non-perennial rivers. As reported elsewhere (Jaeger et al., 2019; G. Zhang & Lu, 2012), we therefore observed that, at a probability threshold of 0.5, the three tested RF algorithms tended to focus more on the prediction accuracy of the majority class (perennial rivers and streams) and underestimated the prevalence of the minority class in predictions (IRES). To cope with this apparent bias, we tested two commonly used techniques: random oversampling of the minority class for all three algorithms, and unequal weighting of the classes (also known as cost-sensitive learning) for the default RF and CIF. Both techniques have been shown to reduce class imbalance problems in RF models that are parameterized without replacement (Japkowicz & Stephen, 2002). Unequal weighting of the classes was not implemented for MAXSTAT because class weighting cannot be implemented for regression RF.

2.9.4. Model development and diagnostics: technical documentation

Hyperparameter tuning

RF has only a few tunable hyperparameters and is known to be relatively insensitive to hyperparameter tuning (Probst et al., 2019). Nonetheless, the effectiveness of tuning is dependent on the problem at hand so that it must be done to ensure optimal predictive performance. Consequently, we implemented a tuning routine for three hyperparameters: (1) the fraction of the original training data that is randomly sampled without replacement to construct each tree (α), (2) the number of predictors that are sampled from the full set of predictors and used for splitting each tree node (m_{try}), and (3) the minimum number of observations that a terminal node can contain which, when segmented, causes tree construction to stop (min_node_size). For the MAXSTAT algorithm, another hyperparameter, the maximum p -value used to determine when tree construction should stop, was also tuned. Hyperparameter tuning was not implemented for CIF as this algorithm was too computationally intensive — instead, default hyperparameter settings were used. The search space boundaries to define the minimum and maximum tested values for each hyperparameter for the default RF and MAXSTAT are detailed in **Table 2.S5**. The role of tuning for the different hyperparameters is detailed in Probst et al. (2019) and will not be expanded upon here. We did not tune the number of trees in the forest because it is not *per*

se considered to be a hyperparameter. Indeed, the performance of RF has been demonstrated to monotonically and asymptotically increase with the number of trees, such that it should be set as high as computationally feasible (Probst & Boulesteix, 2018). We set the number of trees at 800 (the default is usually 500).

Hyperparameter tuning was performed through 100 iterations of a random search across unique combinations of hyperparameters. A four-fold cross-validation (CV) procedure was used to select the best set of hyperparameters, as CV provides an unbiased evaluation of performance by preventing overfitting. Through k -fold CV, the dataset is first split into k partitions. Then, the model is trained on $k-1$ partitions and validated on the remaining partition, the test set, for predictive accuracy. This is performed k times for all combinations of $k-1$ training partitions, each time with a different testing partition. CV provides an assessment of how the model would perform on new data that were not used in its training, and therefore avoids overoptimistic estimates of the model's predictive ability. In this case, the RF model was fitted with the 100 randomly drawn hyperparameter settings separately on the four partitions, and the hyperparameter settings that yielded the highest performance on average across the four testing sets were selected. We used the weighted Balanced class ACCuracy (BACC) metric (Brodersen et al., 2010) as the performance indicator (i.e., the metric to optimize through tuning) for all algorithms, aside from the MAXSTAT regression RF algorithm, for which the Mean Absolute Error (MAE) metric was used. We chose BACC over the standard Out-Of-Bag (OOB) error used in conventional RF validation to further minimize biases stemming from the disproportionate number of perennial rivers in the reference data. BACC is equivalent to raw accuracy (or one minus the misclassification rate) but each sample is weighted according to the inverse prevalence of its true class:

$$BACC = \frac{1}{\sum_i w_i} \sum_i 1(\hat{y}_i = y_i) w_i \quad (\text{Equation S1})$$

where $\hat{y}_i$ and y_i are the predicted and observed flow classes for gauge i , and w_i is the class weight (large rivers: 4.87 and 1.00; small rivers: 1.98 and 1.00, for the non-perennial and perennial classes, respectively).

To evaluate the model using BACC during tuning, the probabilistic predictions were first converted into a binary response with a threshold of 0.5 — i.e., a test observation was classified as non-perennial if the RF-predicted probability that it is non-perennial was ≥ 0.5 ,

and otherwise classified as perennial. We also assessed differences in computational duration for training and prediction among RF algorithms to evaluate trade-offs with predictive performance. The default RF and MAXSTATS algorithms were faster than CIF by an order of magnitude. Therefore, default RF and MAXSTATS were by default preferred even if equally accurate to CIF, as they enabled greater scaling capability and a more robust assessment of performance with additional cross-validation.

Table 2.S5. Hyperparameter tuning and cross-validation settings for comparison of Random Forest (RF) algorithms and predictor variable selection.

Modeling stage refers to either comparing RF algorithms (*Algorithm*, see **Section III.b - Comparison of RF algorithms**) or comparing the selected RF algorithm with and without excluded predictor variables (*Predictors*, see **Section IV.c - Variable importance measure and predictor variable selection**). For each stage, greyed rows show which model option was selected (the same model type, i.e., the default RF with oversampling, was selected for both sub-models).

Algorithm denotes which RF algorithm (default, Conditional Inference Forest, or MAXSTATS) and class imbalance coping technique (none, oversampled, or weighted classes) were used and whether predictors were subset.

RF type refers to whether the algorithm consisted of a classification or a regression RF.

inner CV folds denotes the number of cross-validation (CV) folds used in inner resampling for tuning (see **Sections IV.a - Hyperparameter tuning and IV.b - Nested spatial resampling and benchmarking**). No tuning was performed for Conditional Inference Trees (*algorithm*: CIF) as this RF algorithm is computationally intensive.

tuning evals refers to the number of hyperparameter combinations tested within each inner resampling loop.

alpha is the significance threshold (or range thereof) used to determine whether to create an additional split in the trees grown in hypothesis test-based RF algorithms (CIF and MAXSTAT).

m_{try} is the number of predictors sampled from the full set of predictors at each tree node and used for splitting at that node.

min.node.size is the minimum number of observations that a terminal node can contain which when segmented causes tree construction to stop (only applies to default RF as hypothesis-based algorithms stop tree growing based on *alpha*).

fraction is the proportion of the original training data that is randomly sampled without replacement to construct each tree.

minor weight / ratio is the relative class weight or oversampling ratio used to cope with class imbalance in the training dataset of gauging stations (e.g., non-perennial gauges with $MAF < 10 \text{ m}^3 \text{ s}^{-1}$ were oversampled by a factor of 1.98).

N pred. is the number of predictor variables used in the RF model.

Modeling stage	Algorithm	RF type	inner CV folds	tuning evals	alpha	m_{try}	min. node size	fraction	minor weight ratio	N pred.	
Small-to-medium stream gauges ($< 10 \text{ m}^3 \text{ s}^{-1}$)	Algorithm	default	Classif.	4	100	-	11-56	1-10	0.2-0.8	-	113
		CIF	Classif.	-	1	0.05	11	-	0.632	-	113
		default - oversampled	Classif.	4	100	-	11-56	1-10	0.2-0.8	1.98	113
		CIF - oversampled	Classif.	-	1	0.05	11	-	0.632	1.98	113
		default - weighted classes	Classif.	4	100	-	11-56	1-10	0.2-0.8	-	113
		CIF - weighted classes	Classif.	-	1	0.05	11	-	0.632	-	113
		MAXSTAT	Regr.	4	100	0.01-0.1	11-56	-	-	-	113
		MAXSTAT-oversampled	Regr.	4	100	0.01-0.1	11-56	-	-	1.98	113
	Predictors	default - oversampled	Classif.	4	100	-	11-56	1-10	0.2-0.8	-	113
		default - oversampled selected variables	Classif.	4	100	-	9-46	1-10	0.2-0.8	1.98	92
Medium-to-large stream gauges ($\geq 1 \text{ m}^3 \text{ s}^{-1}$)	Algorithm	default	Classif.	4	100	-	11-56	1-10	0.2-0.8	-	113
		CIF	Classif.	-	1	0.05	11	-	0.632	-	113
		default - oversampled	Classif.	4	100	-	11-56	1-10	0.2-0.8	4.87	113
		CIF - oversampled	Classif.	-	1	0.05	11	-	0.632	4.87	113
		default - weighted classes	Classif.	4	100	-	11-56	1-10	0.2-0.8	-	113
		CIF - weighted classes	Classif.	-	1	0.05	11	-	0.632	-	113
		MAXSTAT	Regr.	4	100	0.01-0.1	11-56	-	-	-	113
		MAXSTAT-oversampled	Regr.	4	100	0.01-0.1	11-56	-	-	4.87	113
	Predictors	default - oversampled	Classif.	4	100	-	11-56	1-10	0.2-0.8	-	113
		default - oversampled selected variables	Classif.	4	100	-	8-41	1-10	0.2-0.8	4.87	82

Nested spatial resampling and benchmarking

Since the selection of optimal hyperparameters is data-dependent, the hyperparameter selection step and the associated cross-validation procedure cannot be used for evaluating the model itself, as it can lead to biased performance estimates (Bischl et al., 2012). Instead, all parts of the model building should be included in the resampling and repeated for every pair of training/test data. Therefore, we implemented a nested resampling strategy (Bischl et al., 2012). **Figure 2.S10** below illustrates the procedure for parameter tuning with 3-fold cross-validation in the outer and 4-fold cross-validation in the inner loop.

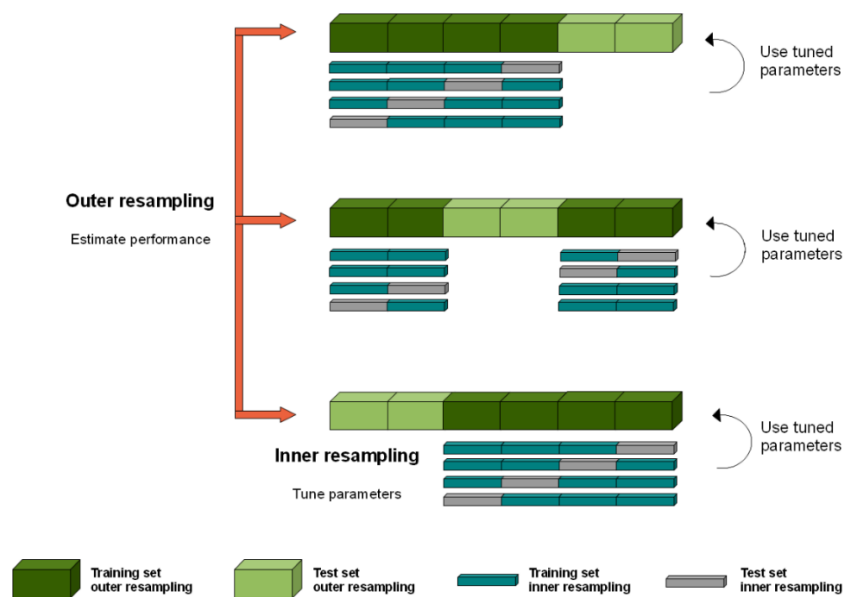


Figure 2.S10. Schematic representation of a cross-validation nested resampling procedure with 3-fold cross-validation in the outer and 4-fold cross-validation in the inner loop.

There are three pairs of training (dark green) and test (light green) sets in the outer resampling loop. The inner resampling loop for parameter tuning is performed on each of these outer training sets, partitioning each outer training set into four pairs of inner training (blue) and test (grey) sets. Tuning is thus performed 12 times in total. One set of hyperparameters is selected for each outer training set. Then, the RF is fitted on each outer training set using the corresponding selected hyperparameters and evaluated for performance on the outer test sets. The overall performance metric is calculated as an average across all outer test sets. Adapted from Becker et al. (2021): <https://mlr3book.mlr-org.com/nested-resampling.html>.

In the comparison across RF algorithm variants, the inner (hyperparameter tuning) loop was composed of a 4-fold CV for hyperparameter tuning and the outer loop involved twice-repeated 3-fold CVs for each algorithm. A twice-repeated CV limits noise from random sampling with a small number of folds. All algorithms were compared using the same inner and outer sets of training and testing partitions. This model evaluation allowed us to choose an algorithm for subsequent steps. A spatial CV procedure was also used in the outer resampling loop for evaluating the final selected model. We used spatial CV to avoid

overoptimistic error estimates that arise in cases of significant spatial autocorrelation (Brenning, 2012; Meyer et al., 2018; Schratz et al., 2019) — a model can exhibit strong performance with random subsets but may fail to make predictions beyond the spatial extent of the training samples or in specific regions (Meyer et al., 2019). The spatial CV was implemented following Brenning (2012) such that spatial partitions (folds) were derived by *k*-means clustering of the gauging stations' spatial coordinates, with *k*=40 folds (see **Figure 2.S11** below for a map of the spatial distribution of the folds/gauge clusters).

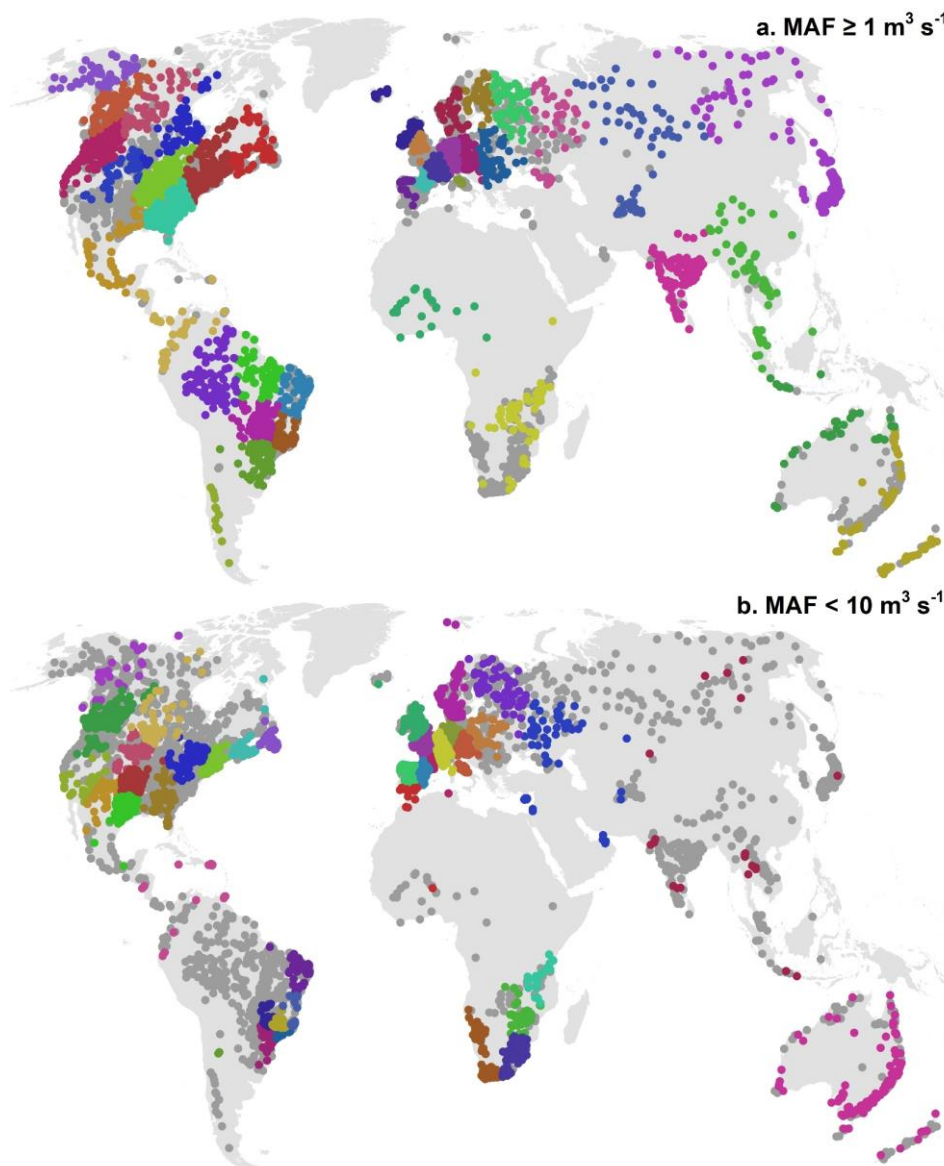


Figure 2.S11. Spatial cross-validation fold membership of gauging stations.

Panels show 40 spatial cross-validation folds for each RF sub-model: (a) gauges with $\text{MAF} \geq 1 \text{ m}^3 \text{ s}^{-1}$ and (b) gauges with $\text{MAF} < 10 \text{ m}^3 \text{ s}^{-1}$. Each cluster of coloured points represents the gauging stations in one CV fold. Grey points show gauging stations that were used in the other sub-model e.g., in (b), grey points show gauging stations with $\text{MAF} \geq 10 \text{ m}^3 \text{ s}^{-1}$. Mapping software: ArcMap™ (ESRI).

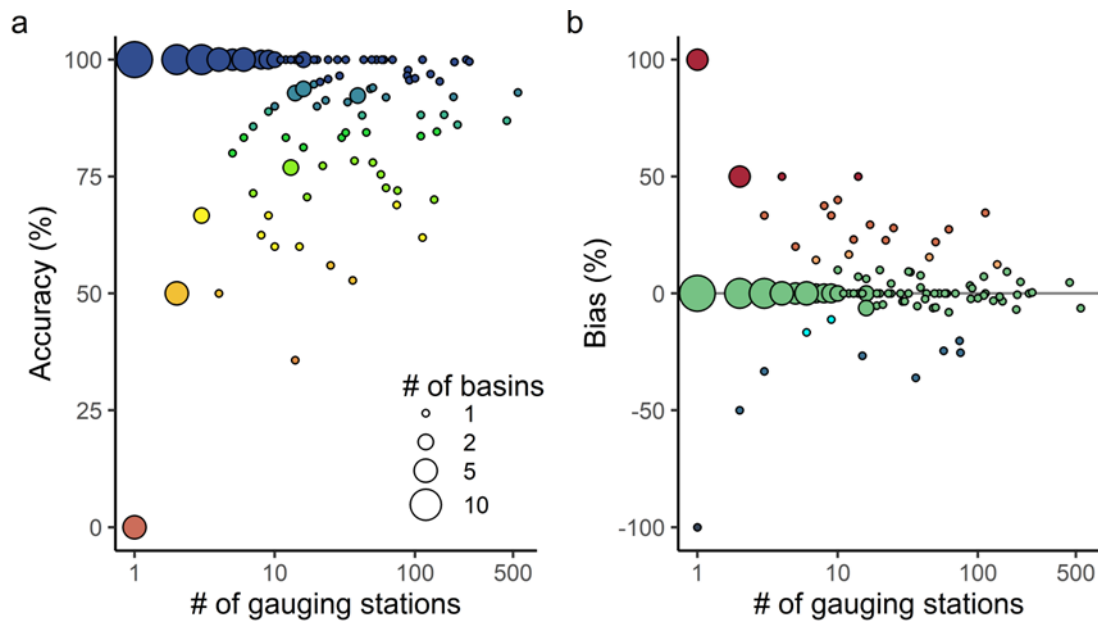


Figure 2.S12. Flow intermittence classification accuracy decreases and prediction bias increases in river basins with fewer streamflow gauging stations.

Assessment based on 40-fold spatial cross-validation. (a) Accuracy is the percentage of correctly classified gauging stations. (b) Bias is equal to the predicted percentage of gauging stations that are IRES minus the observed percentage of IRES stations. Point colours correspond to **Figure 2.3** in main text. River basins correspond to BasinATLAS level 3 subdivisions with an average surface area of $4.6 \times 10^5 \text{ km}^2$.

Variable importance measure and predictor variable selection

RF presents the advantage over several other machine learning techniques that variable importance measures can be computed to understand the relative contribution of predictors to the predictive ability of the model. Here we computed a variable importance measure based on a corrected version of Gini impurity, the Actual Impurity Reduction (AIR), developed by Nembrini et al. (2018). AIR is unbiased regarding the number of categories/values in the predictors, regardless of the original RF algorithm. Weighted averages of AIR and the associated p -values (determined via 100 permutations, following Altmann et al., 2010) were computed for each outer resampling CV fold and repetition using the BACC of each resampling instance as weight.

Prior to the final model training and evaluation, only predictors with a variable importance p -value < 0.05 were retained for training the final model (p -values were computed based on the initial model that was built for comparing algorithms, i.e., at the *Algorithm* modeling stage in **Table 2.S6**). This variable selection was implemented to both increase model performance (Amaratunga et al., 2008; Evans et al., 2011) and decrease model training time. Forward Feature Selection (FFS) based on spatial CV, as outlined in Meyer et al. (2018) and Meyer et al. (2019) was not implemented because it was not yet included in the *mlr3*

framework at the time of this study and would have increased computation time by at least an order of magnitude.

Table 2.S6. Benchmark comparison of Random Forest (RF) algorithms and predictor variable selection.

Modeling stage refers to either comparing RF algorithms (*Algorithm*, see **Section III.b** - Comparison of RF algorithms) or comparing the selected RF algorithm with and without excluded predictor variables (*Predictors*, see **Section IV.c** - Variable importance measure and predictor variable selection). For each stage, greyed rows show which model option was selected (the same model type, i.e., the default RF with oversampling, was selected for both sub-models).

Algorithm denotes which RF algorithm (default, CIF, or MAXSTATS) and class imbalance coping technique (none, oversampled, or weighted classes) were used and whether predictors were subset.

RF type refers to whether the algorithm consisted of a classification or a regression random forest.

Resampling type denotes whether non-spatial or spatial cross-validation (CV) was used.

Outer repeats and *Outer folds* are the number of CV repetitions and folds, respectively, in the outer resampling loop (see **Section IV.b** - Nested spatial resampling and benchmarking and **Section IV.c** - Variable importance measure and predictor variable selection). Performance metrics were computed and averaged across all outer resampling CV folds and repetitions.

BACC is the Balanced class ACCuracy (Brodersen et al., 2010).

SPE is specificity (proportion of correctly classified perennial gauging stations).

SEN is sensitivity (proportion of correctly classified non-perennial stations).

PRE is precision (proportion of stations classified as non-perennial that are truly non-perennial).

BBRIER is the Binary BRIER score (Brier, 1950).

AUC is the area under the receiver operating characteristic curve (Hanley & McNeil, 1982).

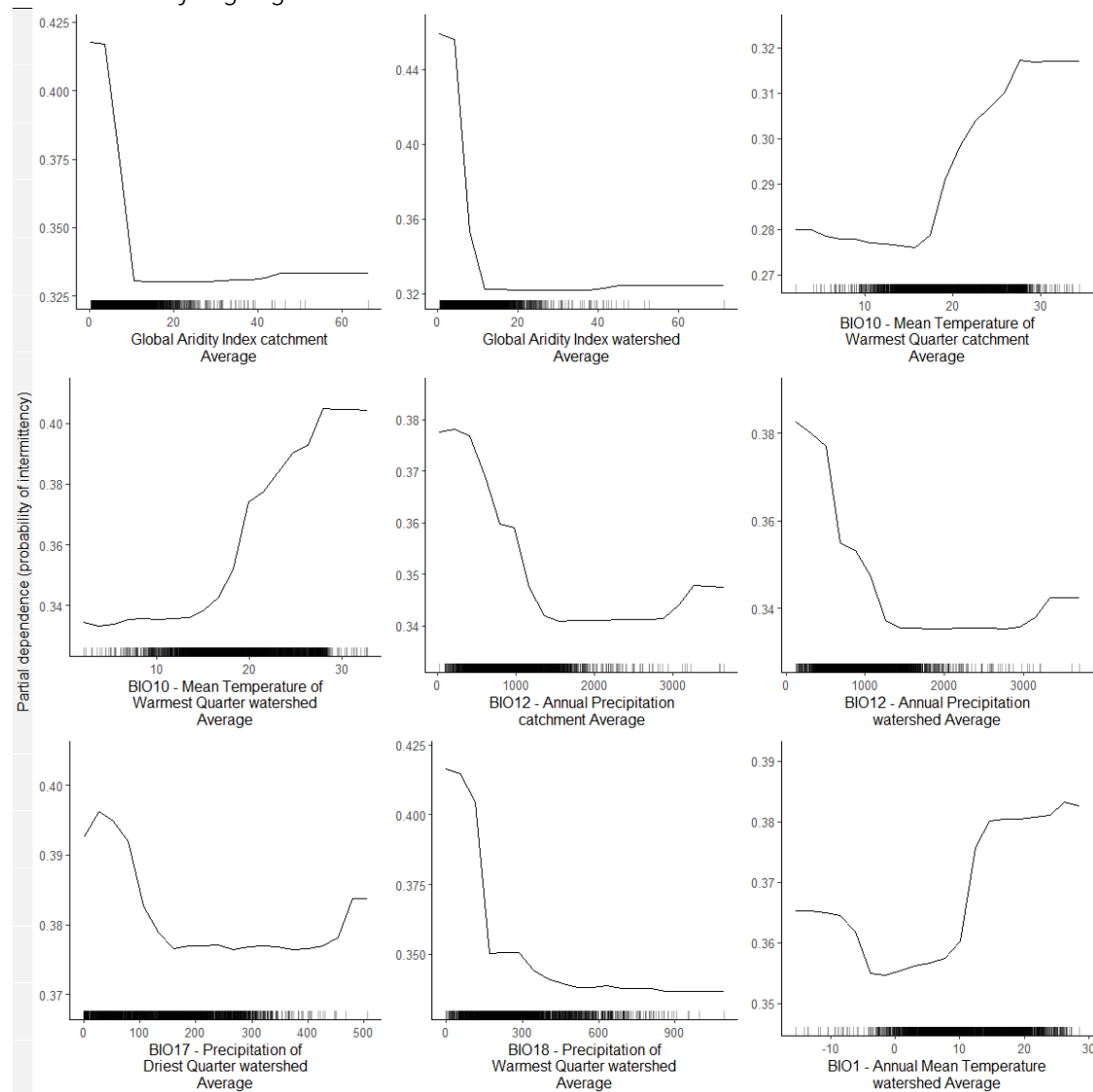
Modeling stage	Algorithm	RF type	Resampling type	Outer repeats	Outer folds	BACC	SPE	SEN	PRE	BBRIER	AUC
Small-to-medium stream gauges ($< 10 \text{ m}^3 \text{ s}^{-1}$)	default	Classif.	non-spatial CV	2	3	0.88	0.94	0.81	0.88	0.08	0.88
	CIF	Classif.	non-spatial CV	2	3	0.87	0.94	0.79	0.88	0.08	0.87
	default - oversampled	Classif.	non-spatial CV	2	3	0.88	0.93	0.84	0.85	0.08	0.88
	CIF - oversampled	Classif.	non-spatial CV	2	3	0.88	0.91	0.85	0.83	0.08	0.88
	default - weighted classes	Classif.	non-spatial CV	2	3	0.88	0.92	0.84	0.84	0.08	0.88
	CIF - weighted classes	Classif.	non-spatial CV	2	3	0.88	0.92	0.83	0.84	0.08	0.88
	MAXSTATS	Regr.	non-spatial CV	2	3	0.86	0.94	0.78	0.87	0.08	0.95
	MAXSTATS - oversampled	Regr.	non-spatial CV	2	3	0.86	0.94	0.78	0.87	0.08	0.95
	default - oversampled	Classif.	non-spatial CV	2	3	0.88	0.91	0.85	0.83	0.08	0.88
	default - oversampled selected variables	Classif.	non-spatial CV	2	3	0.88	0.92	0.85	0.84	0.08	0.88
	default - oversampled selected variables	Classif.	spatial CV	1	40	0.84	0.88	0.81	0.78	0.10	0.85
Medium-to-large stream gauges ($\geq 1 \text{ m}^3 \text{ s}^{-1}$)	default	Classif.	non-spatial CV	2	3	0.87	0.98	0.76	0.88	0.05	0.87
	CIF	Classif.	non-spatial CV	2	3	0.84	0.98	0.69	0.89	0.05	0.84
	default - oversampled	Classif.	non-spatial CV	2	3	0.91	0.94	0.88	0.75	0.06	0.91
	CIF-oversampled	Classif.	non-spatial CV	2	3	0.90	0.95	0.85	0.79	0.05	0.90
	default - weighted classes	Classif.	non-spatial CV	2	3	0.91	0.94	0.88	0.74	0.06	0.91
	CIF - weighted classes	Classif.	non-spatial CV	2	3	0.88	0.97	0.78	0.83	0.05	0.88
	MAXSTATS	Regr.	non-spatial CV	2	3	0.83	0.98	0.69	0.88	0.05	0.96
	MAXSTATS - oversampled	Regr.	non-spatial CV	2	3	0.84	0.98	0.70	0.88	0.05	0.96
	default - oversampled	Classif.	non-spatial CV	2	3	0.91	0.94	0.88	0.75	0.06	0.91
	default - oversampled selected variables	Classif.	non-spatial CV	2	3	0.91	0.94	0.89	0.74	0.06	0.91
	default - oversampled selected variables	Classif.	spatial CV	1	40	0.84	0.93	0.79	0.70	0.07	0.86

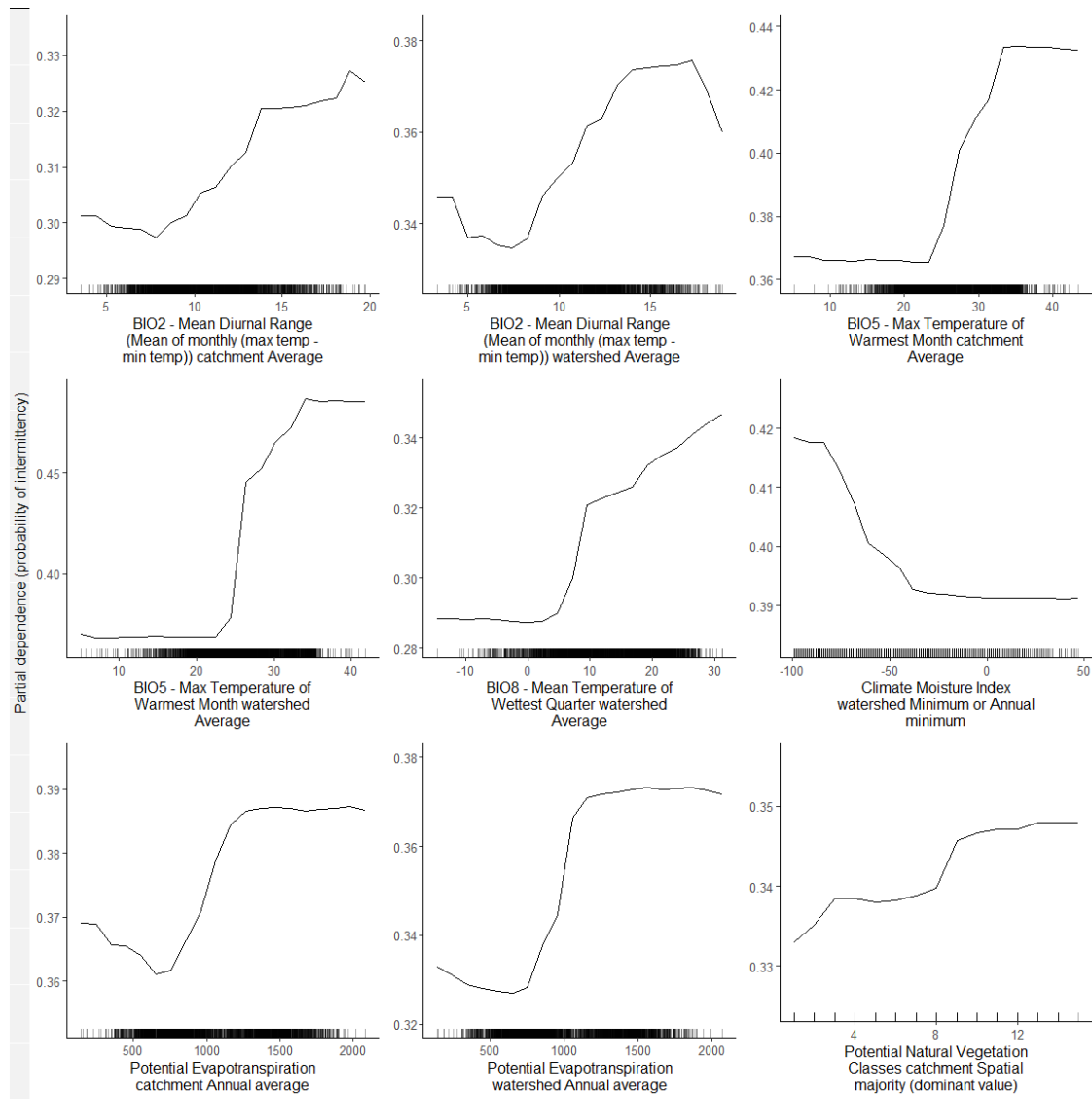
The final model ('default RF') was re-evaluated with and without the excluded predictor variables using the same inner sampling tuning procedure (4-fold CV) as was used to compare RF algorithms (**Table 2.S6**). Partial dependence plots were also generated for the 27 most important predictors using the *edarf* package (Jones & Linder, 2016)). These plots display estimates of the marginal relationship between each predictor variable and the model's predictions by holding the rest of the predictors at their respective mean values (Friedman, 2001).

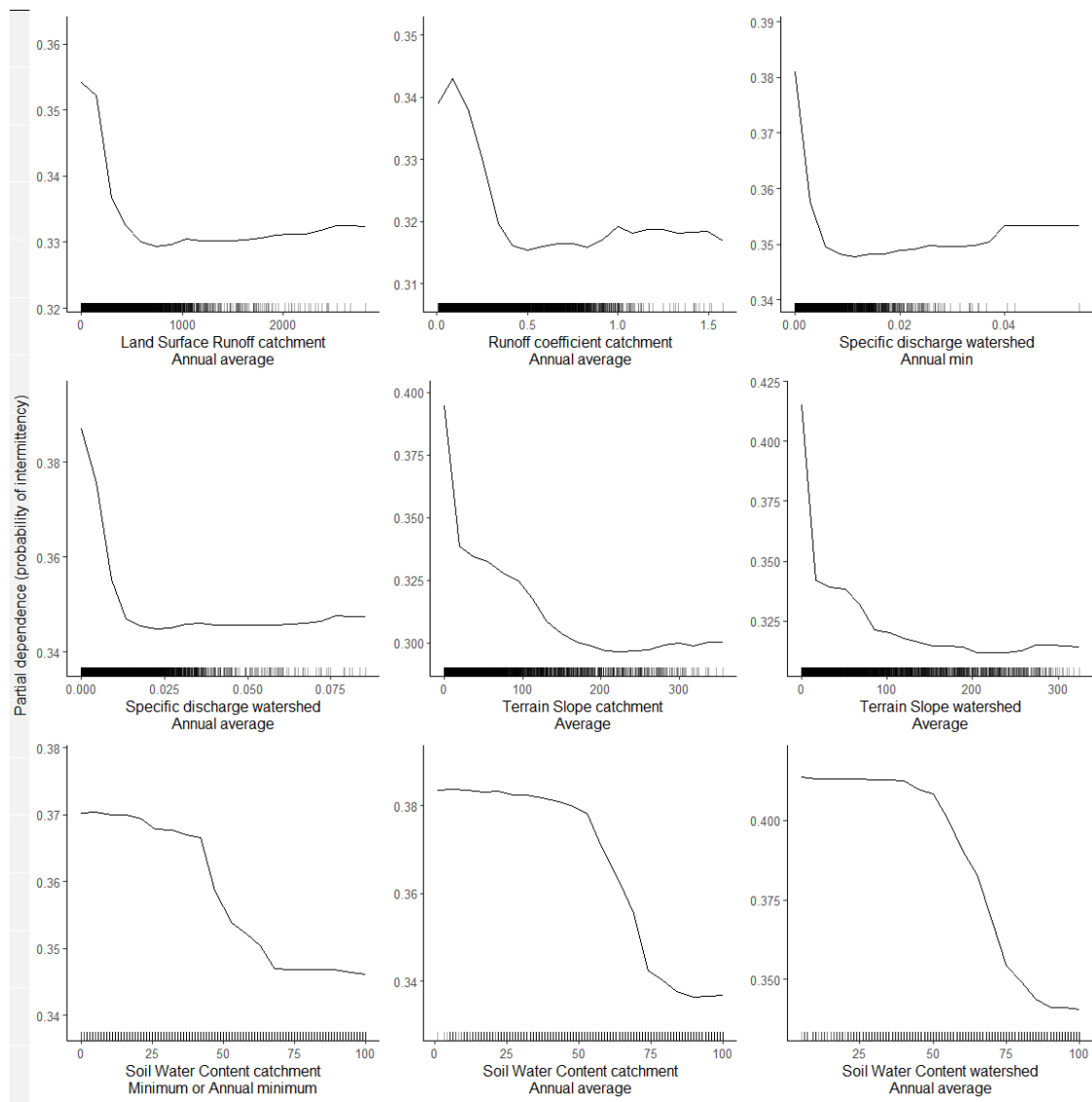
Figure 2.S13. Partial dependence plots.

Plots show the marginal relationship between each predictor variable and the model's predictions (probability of being an IRES) by holding the rest of the predictors at their respective mean values (a) for gauges with $MAF < 10 \text{ m}^3 \text{ s}^{-1}$ and (b) for gauges with $MAF \geq 1 \text{ m}^3 \text{ s}^{-1}$. The rug plots on the horizontal axes show the distribution of training/testing gauging stations for each variable. The 27 most important predictor variables are displayed in alphabetical order (see **Figure 2.2** in main text for variable importance).

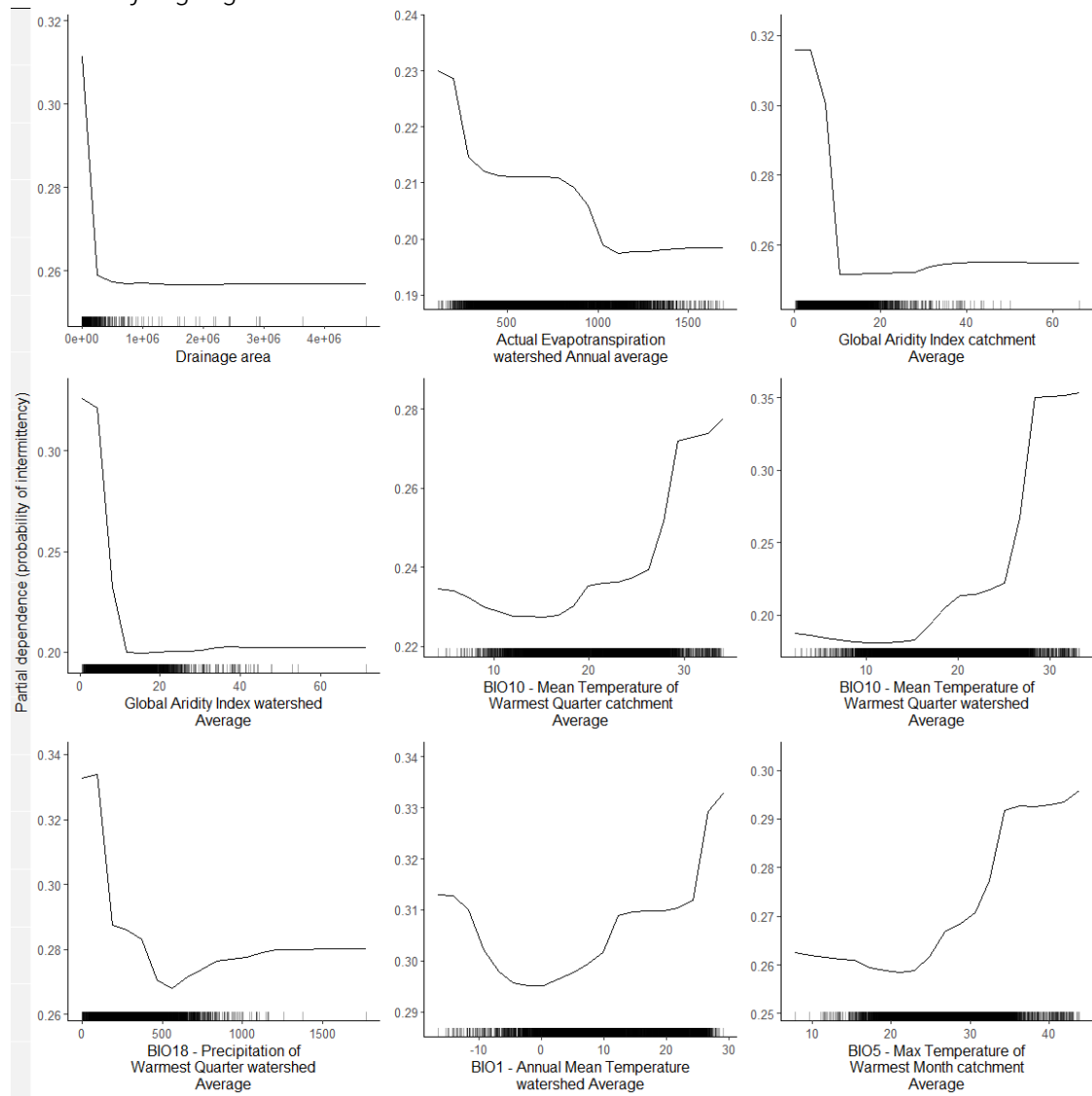
a. Sub-model for gauges with $MAF < 10 \text{ m}^3 \text{ s}^{-1}$

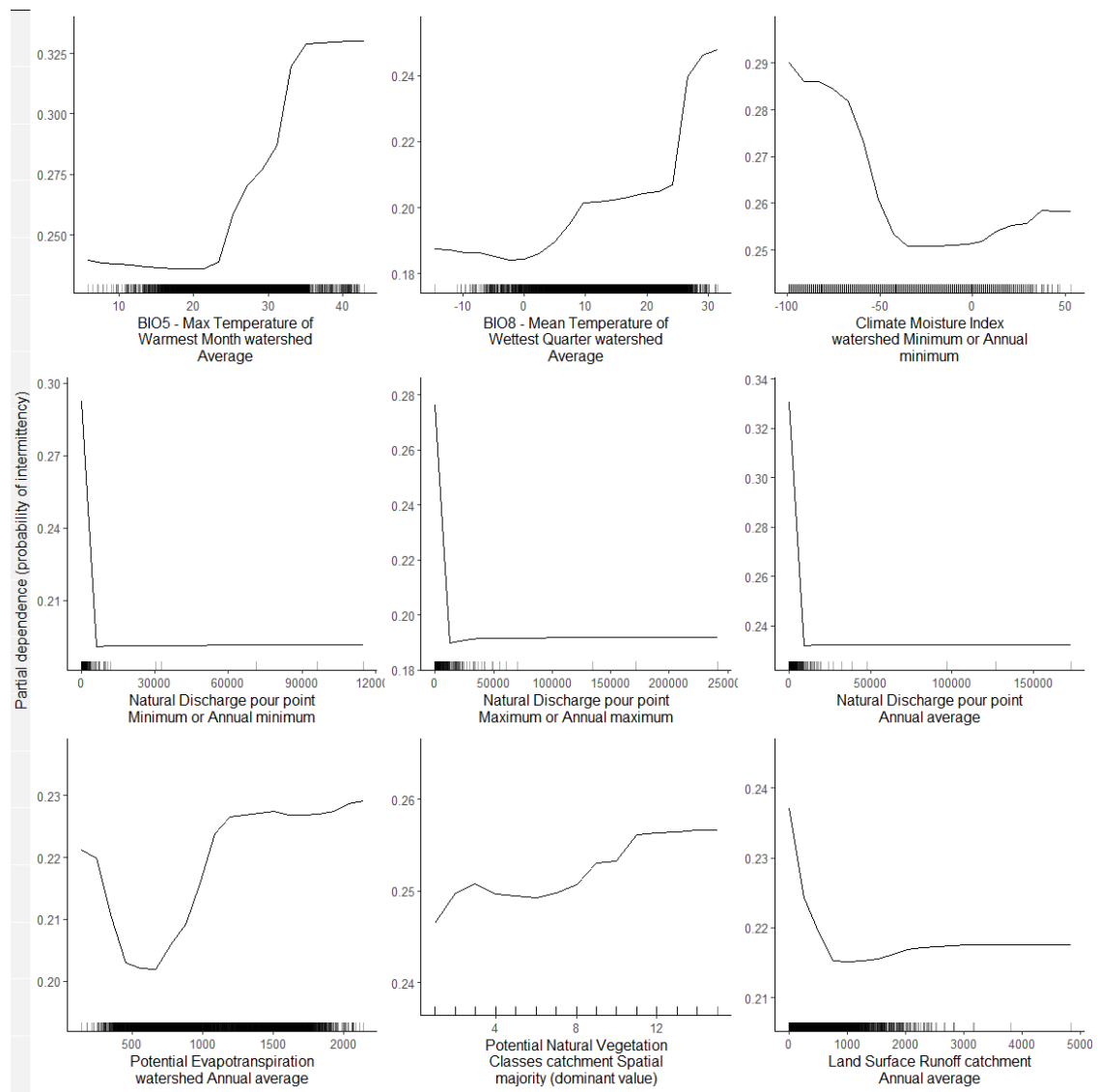


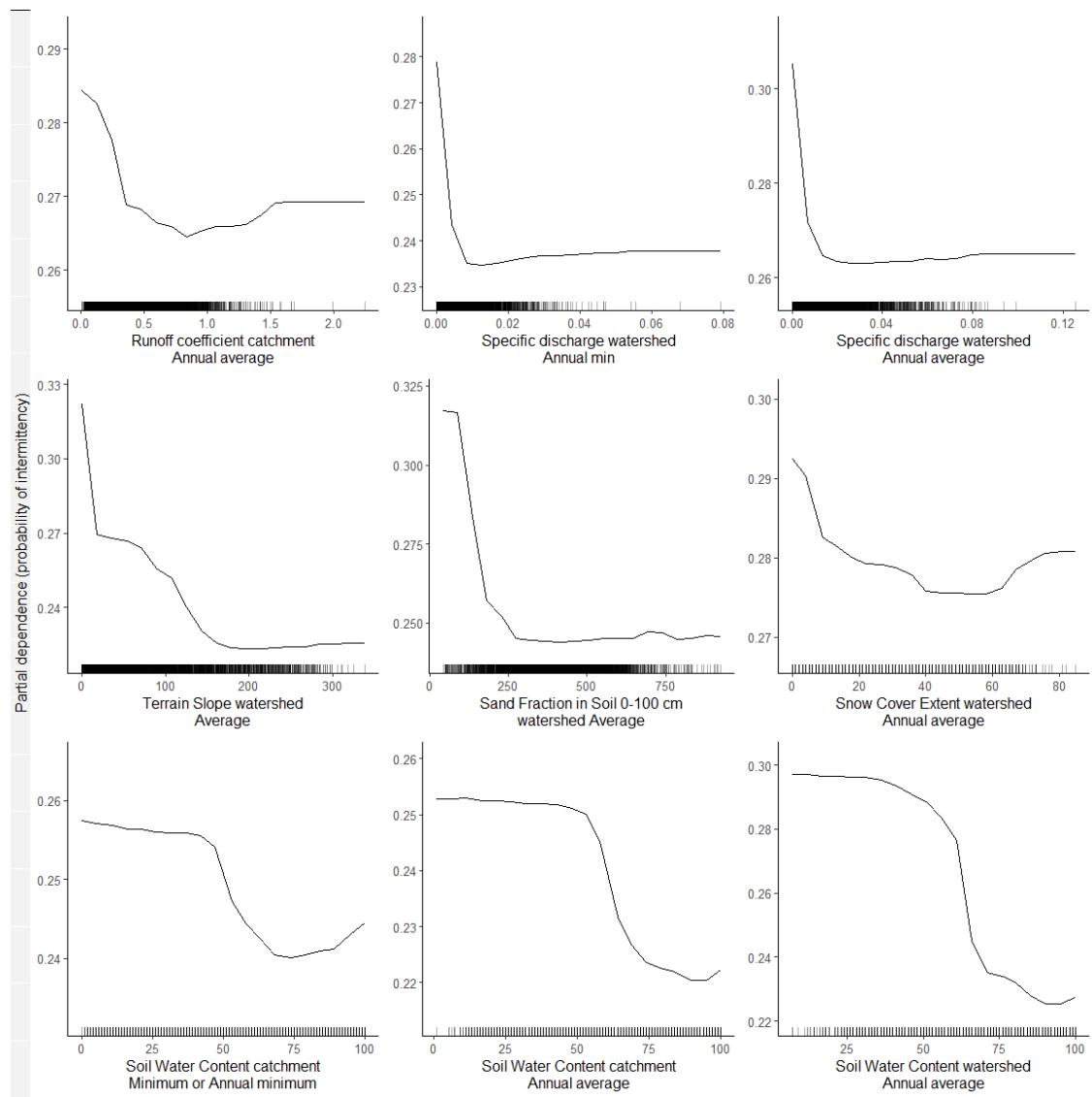




b. Sub-model for gauges with $MAF \geq 1 \text{ m}^3 \text{ s}^{-1}$







Assessment of spatial autocorrelation in predictions

Although we minimized prediction bias stemming from the disproportionate number of streamflow gauging stations on perennial sites in the training/testing dataset (see **Section III.c - Addressing class imbalance**), regional biases in training data may still influence results at finer hydroclimatic scales, which is unavoidable. The geographic extent of individual CV folds was too large to adequately portray spatial autocorrelation in model errors at fine scales. The presence of spatially autocorrelated errors among neighboring stations would indicate that our model only partly represents observed heterogeneity in flow intermittence at finer hydroclimatic scales. Therefore, we mapped a measure of residual spatial autocorrelation among stations within each river basin (BasinATLAS level 3 subdivisions with an average surface area of $4.6 \times 10^5 \text{ km}^2$) to better quantify this unresolved source of uncertainty. We assessed whether the predicted flow intermittence class of gauging stations was more clustered than their observed distribution. In simple terms, does the model result in clumps of IRES and perennial stations while reference data indicate more fine-scaled patterns? A greater degree of clustering in predicted versus observed flow intermittence classes would indicate the presence of residual spatial autocorrelation in the predictions, suggesting that the model could not fully account for fine-scale hydroclimatic variations.

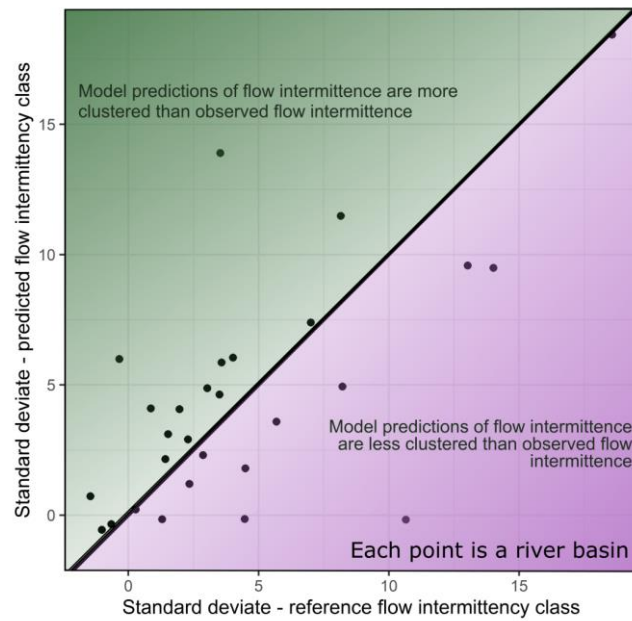
For each river basin that included both IRES and perennial stations and contained at least 20 gauging stations, we tested whether spatial predictions of intermittence differed further from a random spatial distribution than the observed patterns. We did so as follows:

- i) We measured the degree of clustering separately for the observed and predicted flow intermittence class of gauging stations — by computing the join-count statistics (Cliff & Ord, 1981) based on four nearest neighbors (see Salima & de Bellefon, 2018).
- ii) We assessed whether the predicted spatial distribution of intermittence differed more from what would be expected by chance (i.e., a random distribution) than the observed distribution. This assessment was based on the standard score between the estimated join-count statistics and the statistics that would be obtained based on a random spatial distribution of flow intermittence classes among stations, using 1000 permutations.

The join-count statistics and permutations were computed with the spatial-cross validation predictions, using the *joincount.mc* function from the *spdep* package (Bivand et al., 2009).

This approach did not reveal a systematic tendency for basin-wide over-clustering in predictions, as shown in **Figure 2.S14** below.

a



b

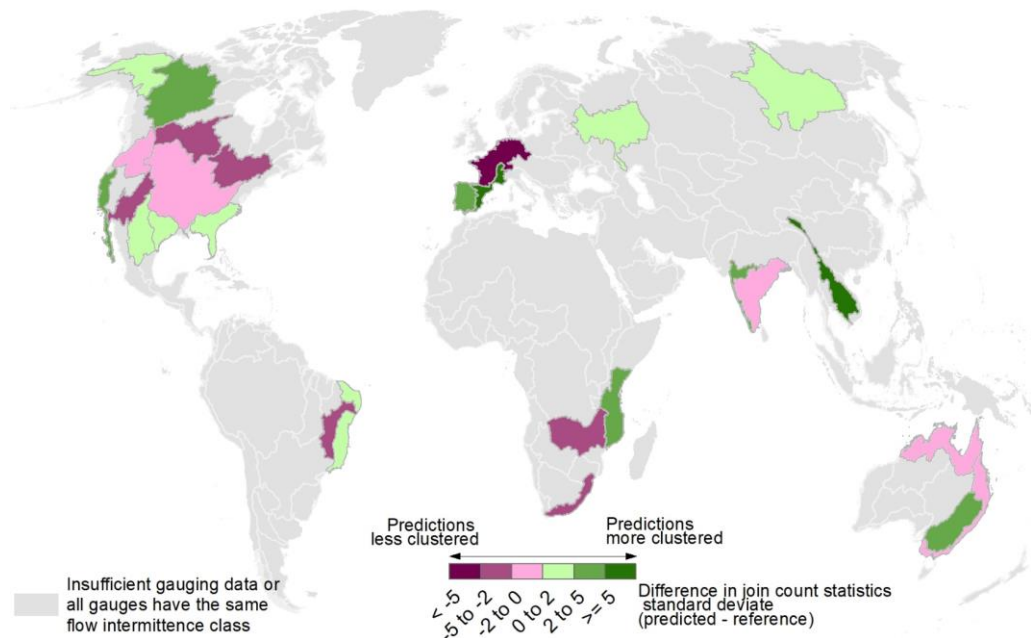


Figure 2.S14. Comparison of clustering between the predicted flow intermittency class of gauging stations and their observed distribution.

(a) Scatterplot (black line is 1:1 line) and (b) map comparing join-count statistics between predictions and the observed distribution of flow intermittency among gauging stations. The standard deviate is the standard score between the estimated join-count statistics and the join-count statistics that would be obtained based on a random spatial distribution of flow intermittency classes, using 1000 permutations. Mapping software: ArcMapTM (ESRI).

Sensitivity analysis of RF predictive performance with respect to the choice of probability threshold

We estimated the probability of flow intermittence for each gauging station included in the training/ testing dataset based on a twice-repeated 3-fold CV. All stations with a resulting probability $\geq P_{threshold}$ for every $P_{threshold}$ in (0.25, 0.26, 0.27, ..., 0.74, 0.75) were iteratively classified to be non-perennial (or perennial otherwise). We then computed a set of performance metrics based on the predicted class of all stations for each combination of $P_{threshold}$ gauges $MAF \geq 10 \text{ m}^3 \text{ s}^{-1}$ and $P_{threshold}$ gauges $MAF < 10 \text{ m}^3 \text{ s}^{-1}$.

There was no overlap between the two MAF size classes for this sensitivity analysis (in contrast to the rest of model training and testing) because the probability of flow intermittence predicted by the two RF sub-model for gauges with $1 \text{ m}^3 \text{ s}^{-1} \leq MAF < 10 \text{ m}^3 \text{ s}^{-1}$ was first averaged before being converted to a categorical flow intermittence class.

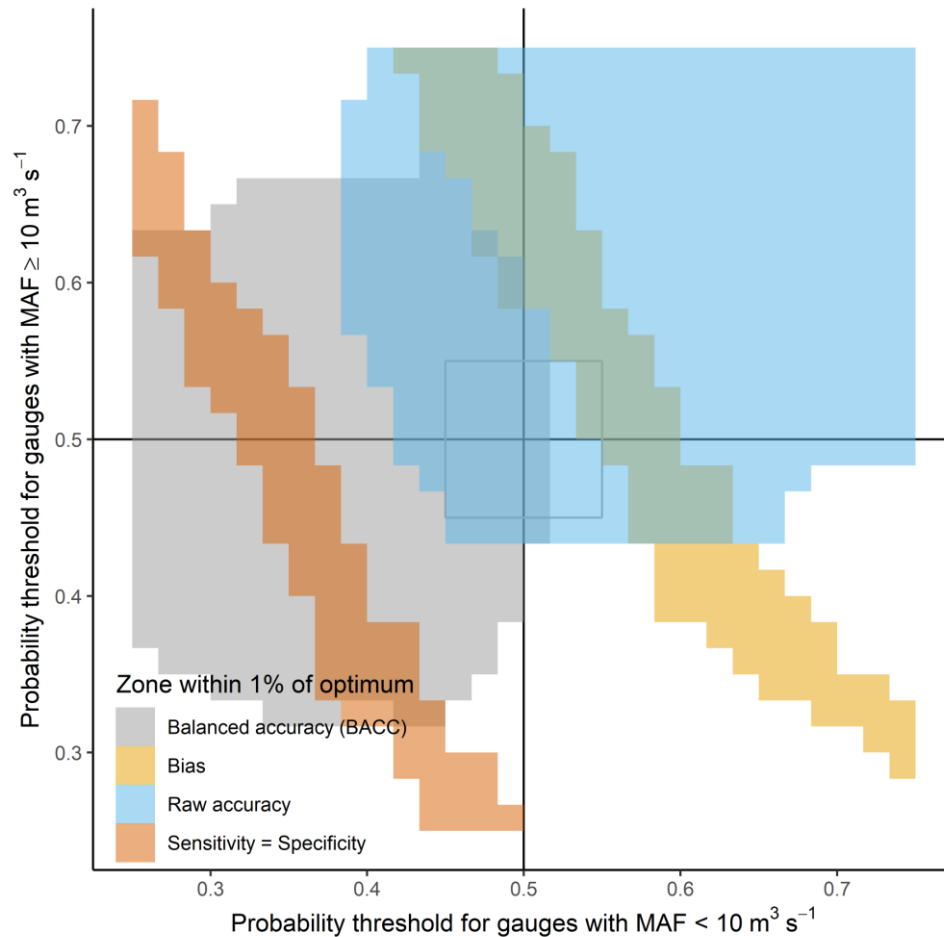


Figure 2.S15. Sensitivity analysis of RF predictive performance with respect to the choice of probability threshold.

The colored zones in the graph show the range of probability thresholds for which each performance metric is within 1% of the optimum value of that metric:

- The *grey zone* shows the range of probability thresholds for which BACC (balanced accuracy, whereby each sample is weighted according to the inverse prevalence of its true class) is between 90% and 91%.
- The *blue zone* shows the range of probability thresholds for which accuracy (percent of correctly classified gauges) is between 92% and 93%.
- The *yellow zone* shows the range of probability thresholds for which bias (predicted – observed % of non-perennial gauges) is between -1% and 1%.
- The *orange zone* shows the range of probability thresholds for which sensitivity-specificity is between -1% and 1%.

The horizontal and vertical black lines show where the probability thresholds for the respective MAF size classes are 0.5, respectively, which represents the thresholds used to classify global reaches in the final models. This threshold was chosen because no single threshold could optimize all four performance metrics. In addition to being an algorithmically intuitive threshold (see **Section III.b - Comparison of RF algorithms** for a description of how the RF model computes the predicted probability), 0.5 hence represents a satisfactory compromise. When adjusting the probability threshold between 0.45 and 0.55, the RF-predicted (i.e., non-extrapolated) prevalence of IRES across the global river network varies from 36% to 48% (compared to 41% with a 0.5 threshold).

2.9.5. Extrapolation of the prevalence of IRES

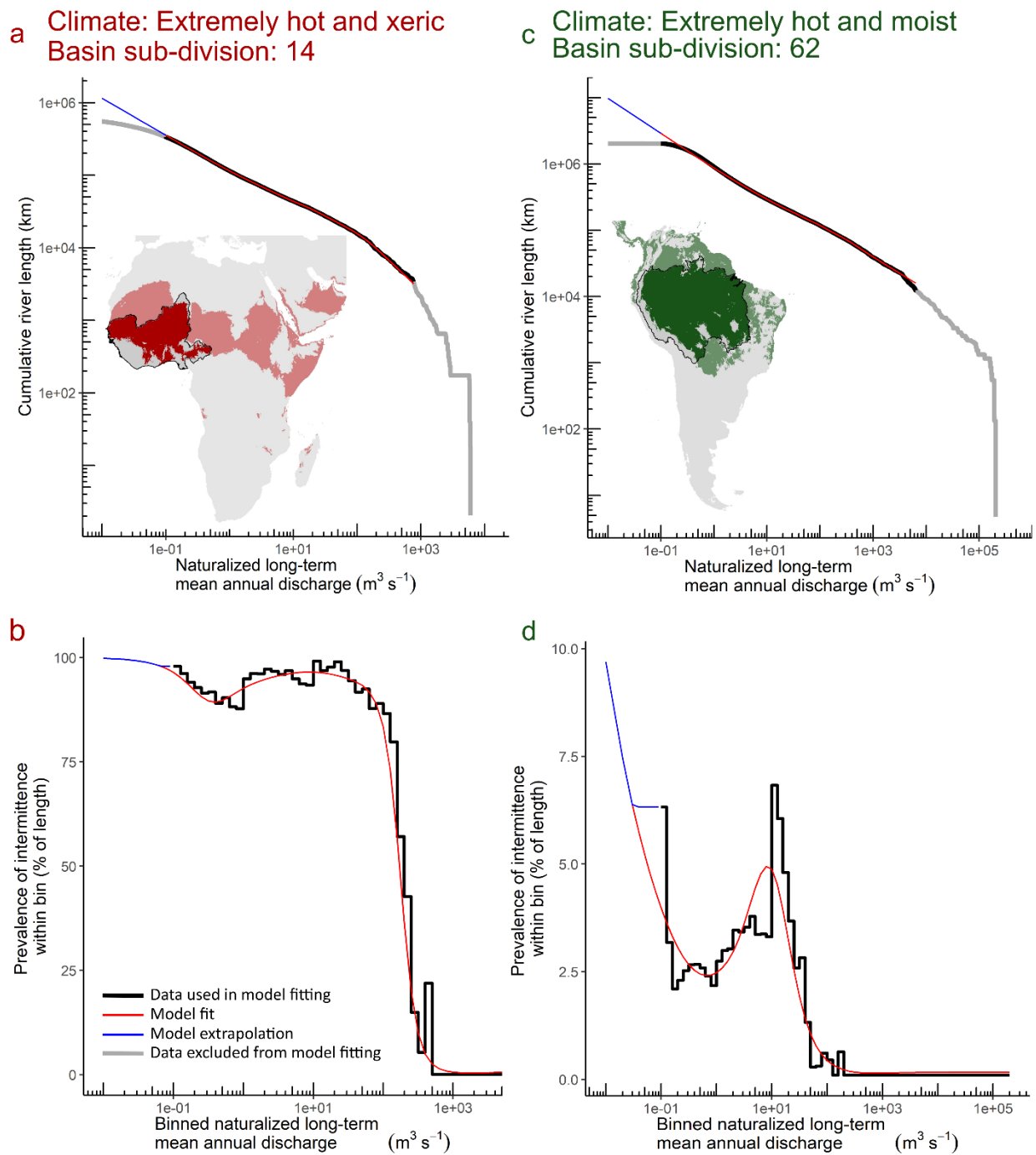


Figure 2.S16. Extrapolation of cumulative river length and prevalence of flow intermittence performed with Generalized Additive Models (GAMs) for two examples of basin-climate subunits.

In panels (a) and (c), the red and green areas represent individual climate zones, and the black outlines represent the investigated sub-basins. The prevalence of flow intermittence in the lowest mean annual flow bin was directly extrapolated to smaller bins when the extrapolated prevalence was lower than it. Mapping software: ArcMap (ESRI).

2.9.6. Pre-processing for model comparisons

Comparisons of the prevalence of flow intermittence at national scales

United States

In the U.S. National Hydrographic Dataset Plus (NHDPlus) at medium-resolution, Version 2 (**Extended Data Figure 2.S3**, for data source see **Extended Data Figure 2.S7b**), most flow lines were classified into two categories based on their “FCODE” attribute: perennial (FCODE = 46006), or non-perennial (FCODE = 46003 – intermittent, or 46007 – ephemeral). A large proportion of river reaches in the NHDPlus dataset are also classified as ‘artificial path’ (FCODE = 55800), which encompasses all drainage lines traversing polygon features in the original paper maps. This category therefore includes large streams and rivers, and the centerlines of lakes (topological representation of flow connection despite the absence of running water to guarantee river network continuity). The proportion of river reaches that are classified as ‘artificial path’ increases with river size. Although most drainage lines classified as ‘artificial path’ in the NHDPlus dataset are perennial, a significant proportion of them are non-perennial, yet there is no flow intermittence attribute for this category. A small proportion of river reaches also does not include an explicit hydrographic category (FCODE = 46000 – river). Therefore, we computed a range for the prevalence of flow intermittence: the lower end of the range includes all non-classified reaches and artificial paths as perennial, while the higher end of the range excludes them altogether.

Australia

In the Australian hydrological geospatial fabric (Geofabric) dataset (**Extended Data Figure 2.S3**, for data source see **Extended Data Figure 2.S7b**), all flow lines are already classified in two categories based on their ‘perenniality’ attribute: perennial or non-perennial. However, no discharge attribute is available for reaches in this dataset, only drainage area. Therefore, all comparisons between the Australian dataset and the global predictions for RiverATLAS are for reaches with a drainage area $\geq 10 \text{ km}^2$. The Australian Geofabric dataset also does not depict streams in large swaths of the desert regions. Therefore, quantitative comparisons mentioned in the main text and shown in **Extended Data Figure 2.S5** were only made for sub-basins where reaches are mapped in the Australian Geofabric dataset (based on BasinATLAS level 12 sub-basins, average area in Australia = 133 km^2).

Comparisons with local on-the-ground visual observations of flow intermittence

U.S. Pacific Northwest

For the U.S. Pacific Northwest, we used 5,372 observations across 3,725 reaches (3,547 perennial, 178 non-perennial) from a larger dataset of 24,316 stream observations (McShane et al., 2017) that occurred from July 1st to October 1st, between 1977 and 2016. The source dataset is a compilation of 11 smaller datasets from independent projects that include aquatic species habitat surveys, wet/dry stream channel mapping, beneficial use reconnaissance surveys, or were collected specifically for the PROSPER intermittent river mapping project (Jaeger et al., 2019; McShane et al., 2017). Streamflow observations included one-time surveys and repeat surveys extending over several years, as well as discrete locations or continuous sections of a stream channel reach (see Jaeger et al., 2019 for a detailed description). This dataset was pre-processed as follows:

- i) We used the same subset of observations as selected by Jaeger et al. (2019) to which we added valid observations before 2004 (which Jaeger and colleagues had excluded based on a specific study design). Unique sites (each of which can have multiple observations) were then selected and spatially processed in the subsequent steps.
- ii) The location of the sites had already been quality (QA/QC) checked and associated with the U.S. NHDPlus medium-resolution river network (Version 2) by Jaeger et al. (2019). Therefore, we extracted each site's drainage area from a grid of contributing area used in Jaeger et al. (2019; one of the "Continuous Parameter Grids"). This grid was generated by Sando et al. (2018) based on flow direction and unweighted flow accumulation rasters from the NHDPlus (medium-resolution, Version 2).
- iii) Each site's point location was then associated with the nearest river reach in RiverATLAS. We automatically removed sites for which the NHDPlus-derived drainage area was less than 10 km², those located over 500 m away from a RiverATLAS reach, and those for which the ratio of RiverATLAS drainage area to NHDPlus-derived drainage area was greater than 3.
- iv) We manually inspected, and corrected if appropriate, the location of the remaining sites if the nearest reach was located more than 200 meters from the original site position or if the drainage area at the location of the site on the reach differed by more than 10% between RiverATLAS and NHDPlus-derived drainage area. Manual inspection involved

verifying that the reach a site had been associated with in the RiverATLAS digital river network corresponded to the actual waterway the station was located on, based on NHDPlus high-resolution topographic maps and high-resolution satellite imagery (ESRI ArcGIS basemaps). Through manual inspection, we identified and then deleted sites on side channels and bifurcations, sites on a nearby tributary of a RiverATLAS reach rather than on the reach itself, sites on streams too small to be represented in the RiverATLAS network, and sites in areas where the real drainage patterns were too complex to reliably match with the RiverATLAS network (e.g., in very low relief areas).

Out of 24,316 initial observations across 9,851 unique sites, we excluded nearly 18,000 observations across about 6,000 sites through steps iii and iv (because most sites were located on reaches too small to be represented in RiverATLAS). Out of the remaining 3,725 unique sites (that had been snapped to the nearest RiverATLAS river reach), we inspected and left unchanged the position of 2,410 sites, and inspected and manually corrected the location of 441 sites.

Note that in this dataset, infrequent, discrete observations of flow state may tend to underestimate the prevalence of intermittence compared to more continuous observations of flow (i.e., at gauging stations) or more frequent observations (i.e., biweekly or monthly ONDE observations in France). This is particularly the case for watercourses that flow most of the year and only seasonally cease to flow, which are common in this region. For this region, the probability that flow cessation is observed at a given reach therefore tends to increase with the number of observations — which we (superficially) confirmed by fitting a logistic regression to all valid observations after June in the dataset from McShane et al. (2017), such that:

$$E\left(\log\left[\frac{P(class=non-perennial)}{1-P(class=non-perennial)}\right]\right) = -2.98 + 0.30 \cdot \text{number of observations} \quad (\text{Equation S2})$$

Both coefficients were significant (p -value < 0.001). This relationship translates to an expected increase in $P(class = non - perennial)$, i.e., the expected probability that a reach be classified as non-perennial, from 0.06 with only one observation, to 0.19 with five observations, and 0.51 with ten observations.

France

For France, we used 124,112 observations across 2,297 reaches (878 perennial, 1,419 non-perennial) from a larger set of 176,973 observations at approximately 3,300 sites uniformly distributed across France from the national river drying observatory (ONDE) network (Nowak & Durozoi, 2014). The ONDE network provides a stable set of sites on river and stream reaches of Strahler orders under five which, since 2012, have been inspected by agency employees from the French Office for Biodiversity (OFB) at least monthly between May and September. This dataset was pre-processed as follows:

- i) ONDE ground observations do not include information on the drainage area, discharge, or general size of the reach with which they are associated, making a direct association between these point observations to the RiverATLAS global river network difficult. However, most sites have an identification number from the French national hydrographic network, the Carthage® database (CARTographie THématique des AGences de l'Eau; resolution ≈ 35 m). Therefore, each unique site was first associated with the Carthage river network (based on the common identification field between the two databases, as well as river name and spatial proximity in the absence of a match based on the identification field). All sites whose initial position was over 10 meters from the Carthage reach with which they were associated by identification number were inspected. A site was deleted if it could not be associated with a Carthage reach or if it was located more than 100 meters from the associated Carthage reach.
- ii) Following this point-to-line association, all identified Carthage reach-sites (i.e., line segments) were associated with RiverATLAS reaches. The Carthage database does not include information on the drainage area or discharge of each reach. Therefore, a custom network-matching tool was developed to assess the degree of similarity between each Carthage reach-site and all RiverATLAS reaches within 1000 m, based on three main criteria: the difference in average azimuth between the two lines as averaged across all 100-m subsegments of the lines, the average distance of every 100-m subsegment of RiverATLAS reaches to the nearest location on the Carthage reach-site, and the average distance of every 100-m subsegment of RiverATLAS reaches to the original point-position of the ground observation site. Based on this procedure, a RiverATLAS reach was presumptively associated with each Carthage reach-site.

iii) We then manually inspected, and corrected if needed, the location of every original observation site based on the three criteria described in step (ii), visual correspondence between the Carthage and RiverATLAS river networks, as well as topographic maps and satellite imagery at a scale ranging from 1:25,000 to 1:50,000. We used the same criteria as for inspecting sites from the U.S. Pacific Northwest, excluding Carthage reaches whose correspondence to RiverATLAS remained unclear (due to complex channel patterns), those on tributaries rather than RiverATLAS reaches, or those too small to be represented in RiverATLAS. We also excluded all sites for which less than 20 observations were available (31 or 1.5% of the total dataset).

Method of comparison

Following this data formatting and harmonization process, we assessed the degree of agreement at the river reach level between the flow intermittence status predicted by our model and that reported by the two sets of visual observations (U.S. Pacific Northwest and France). We considered that a site was non-perennial if it was reported dry or without visible flow for a least one observation. We considered that a RiverATLAS reach was observed to be non-perennial if at least one site associated with it was considered non-perennial.

Classification accuracy was assessed with the same metrics as for gauging stations (Balanced classification ACCuracy or BACC, conventional classification accuracy, sensitivity, and specificity). We also assessed whether intermittence prediction residuals covaried with the number of field observations per site, the percentage of dry or no-flow observations, the human population density in the local catchment directly draining to each reach (as a proxy for potential anthropogenic effects), the RiverATLAS reach pourpoint discharge, and the relative position of the observation sites on the RiverATLAS reach (i.e., how far upstream from the reach pourpoint the site lies), but found no significant patterns.

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2.11. Connecting statement Chapter 2 to Chapter 3

In the previous chapter, I developed a global model for estimating the natural prevalence and distribution of non-perennial rivers and streams (NPRs) across the global river network. This chapter contributes to addressing one of the three gaps I endeavored to address in this thesis — the lack of a global hydrological foundation for the science and management of NPRs. Chapter 3 further addresses this gap by evaluating and classifying the global diversity of natural flow intermittence regimes. This classification provides a hydrological organizing framework that can guide scientific inquiry, modelling, and hypotheses on the processes underlying flow intermittence, and to identify management units that can serve for monitoring, water resource planning, and conservation efforts like environmental flow design.

Chapter 3

Global hydrological diversity of non-perennial rivers and streams

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3.1. Abstract

Non-perennial river and stream reaches (NPRs), which recurrently cease to flow or dry, are integral to river networks globally and crucially contribute to their biodiversity, biogeochemical functioning, and ecosystem services. Yet their hydrological diversity remains poorly understood. This study aims to address this gap by providing a classification of NPR flow intermittence regimes on a global scale. Leveraging long-term daily discharge data from 10,740 gauging stations worldwide, we first identified reliable no-flow records with limited human influence, which yielded 690 time series across 33 countries for subsequent analysis. Through multivariate hierarchical clustering, we delineated nine distinct groups of NPRs based on 14 flow intermittence metrics reflecting the duration, frequency, timing, and climate dependence of no-flow events, as well as overall discharge variability at seasonal and flow-event scales. This classification reveals ecosystems ranging from near-perennial rivers that cease to flow exclusively during droughts to mainly terrestrial systems shaped by occasional water flow. Furthermore, it demonstrates the importance of moving beyond unidimensional characterizations of flow intermittence to understand its diverse impacts on biodiversity, biogeochemistry, and ecosystem services. While an important stepping-stone, this classification is limited by the sample of gauging stations used in its development, which is insufficiently representative of the global distribution of NPRs, both geographically and hydro-environmentally. Future efforts are needed to strategically add new hydrometric records, and to extrapolate this classification for inferring the hydrological class of every river reach in the global river network. The resulting map could bolster global scientific research on the different types of NPRs and inform management strategies for ecosystem conservation and sustainable water resource management.

3.2. Introduction

The majority of rivers and streams on Earth periodically cease to flow and lose most or all surface water (Messenger et al., 2021). These non-perennial reaches (NPRs) critically contribute to the aquatic and terrestrial biodiversity (Crabot et al., 2021; Leigh & Datry, 2017; Sánchez-Montoya et al., 2023), biogeochemical cycles (Datry, Foulquier, et al., 2018; Marcé et al., 2019) and ecosystem services supported by global river networks (Datry, Boulton, et al., 2018; Datry et al., 2023). In terms of biodiversity, for example, reaches that cycle through flowing, non-flowing and dry phases usually exhibit lower species diversity than perennial reaches (Leigh & Datry, 2017) but promote catchment-wide biodiversity by creating a dynamic mosaic of aquatic and terrestrial habitat across space and time (Datry et al., 2014, 2023).

While historically overlooked by the scientific community, NPRs have recently garnered increased scientific interest, yielding a rapidly growing body of knowledge across disciplines (Busch et al., 2020). However, our understanding of NPRs remains biased towards a few regions in semi-arid and Mediterranean regions of developed countries (Krabbenhof et al., 2022; Leigh et al., 2016; Stubbington et al., 2017). This disproportionate focus on a reduced set of regions obscures the wide gamut of ecosystems that NPRs encompass. For example, seasonal drying is widespread in tropical streams (Duvert et al., 2022; Messenger et al., 2021) and strongly determines the ecology and biogeochemistry of those environments (RamyaPriya & Elango, 2021; Valente-Neto et al., 2020). The patterns and processes induced by this type of drying markedly differ from those observed in freezing watercourses across high-latitude and alpine environments (Tolonen et al. 2019). Yet our understanding of NPRs is limited in these climates and others, even in terms of basic hydrology.

The natural frequency, duration and timing of flow cessation, as well as the rate of drying and rewetting, govern the ecological structure and functioning of NPRs (Datry, Foulquier, et al., 2018; Leigh & Datry, 2017; Messenger et al., 2021; Price et al., *In Review*). The flow regime of rivers has shaped the biodiversity of aquatic and terrestrial species over evolutionary times from the catchment to global scales (Lytle & Poff, 2004). Hydrological alterations can thus fundamentally re-organize biotic communities, impacting riverine biogeochemical fluxes and ecosystem services (M. Palmer & Ruhi, 2019; Poff et al., 1997; Richter et al., 1996). For example, increasing drying duration or frequency can lead to a drastic decrease in

taxonomic and functional richness (Crabot et al., 2021; Leigh & Datry, 2017). However, no study to date has systematically quantified the various facets of NPR flow regimes across global biomes and climates, which represents a critical gap for understanding and protecting river networks worldwide.

The hydrological fingerprint of a river or stream can be described by hundreds of metrics, from mean annual discharge to the interannual standard deviation in the calendar day of maximum flow (Eng et al., 2017). A common way to make sense of this complexity is to group rivers and streams that are most hydrologically similar into distinct categories. Just like the Köppen climate classification, which integrates multiple aspects of temperature, precipitation and vegetation (Koppen, 1936), hydrological classifications identify the essential features that differentiate flow regimes (Olden et al., 2012). In doing so, classifications provide an organizing framework that guides scientific inquiry and hypotheses on the processes underlying flow regimes in different classes. Such a framework also identifies watercourses within which species may respond similarly to flow alterations (Poff et al., 2010; Tadaki et al., 2014), and enables regionalization of hydrologic model parameters and improved discharge prediction in ungauged catchments (Wagener et al., 2007). From a management perspective, hydrological classifications delineate potential management units among which resources or sampling sites can be strategically allocated to maximize biophysical representativeness in the spatial design of monitoring programmes, field sampling, and protected areas (Higgins et al., 2005; Kennard, Pusey, et al., 2010).

Several river classifications already include non-perennial categories, yet river typologies rarely account for multiple facets of flow intermittence. At the national scale, multiple types of non-perennial watercourses have been identified for Australia (Kennard, Pusey, et al., 2010), the United States (McManamay & Derolph, 2019), Iran (Tavassoli et al., 2014), and Burkina Faso (Perez-Saez et al., 2017), for example. Some classifications have also focused exclusively on mapping the diversity of flow intermittence regimes in a region, such as in mainland France (Snelder et al., 2013), the U.S. (Eng et al., 2016; Hammond et al., 2021; Jaeger et al., 2019; Price et al., 2021), and eastern Australia (Yu et al., 2019). In most hydrological classifications however, flow intermittence is either ignored, expressed through one single non-perennial river type, or quantified only through the annual number of no-flow days or months, thus overlooking the various components of flow intermittence

regimes. For instance, none of the 13 non-Mediterranean European countries surveyed by (Stubbington et al., 2018) recognized flow permanence in river typologies for ecological status assessment as part of the European Water Framework Directive. Global river classifications suffer from the same limitations, excluding flow intermittence as a clustering criterion (Finlayson & McMahon, 1988; Haines et al., 1988; Ouellet Dallaire et al., 2019) or using a single metric of intermittence (Poff et al., 2006; Puckridge et al., 1998). Other international classification efforts that specifically focus on the drying regime lack consistent global coverage (Sauquet et al., 2021). Finally, Messenger et al. (2021; Chapter 2) estimated the natural global distribution of non-perennial rivers, but only distinguished perennial from non-perennial reaches that cease to flow at least 1 or at least 30 days per year. Beyond knowing *whether* and *where* rivers and streams cease to flow, a classification of the types of NPR on Earth is thus also required to determine *when* and *how*.

The aim of this study was to quantify the hydrological diversity of non-perennial rivers and streams by producing a global classification of flow intermittence regimes minimally influenced by anthropogenic activities. Using long-term time series of daily discharge from a global network of 10,740 *in situ* flow gauging stations, we first identified periods of reliable hydrometric records for NPRs with limited human influence, measured by the population densities, extent of crops and built-up areas, and volume of reservoirs upstream of stations. We then selected gauging stations with at least 15 years of complete daily records, yielding 690 time series for subsequent analysis. Through multivariate hierarchical clustering, we delineated nine distinct groups (or classes) of NPRs in terms of long-term intra- and interannual duration, frequency, timing, and climate dependence of no-flow events, as well the rate of change in discharge magnitude at the seasonal and flow-event scales. Here we define no-flow events as all phenomena potentially leading to zero-flow readings at gauging stations, including drying, full-channel freezing and flow cessation without complete loss of surface liquid water. We then analyzed the environmental characteristics associated with each group based on the climate, physiography, lithology, hydrography and land cover upstream of gauging stations. This last analysis is a first step towards developing a predictive model that would infer the class membership of all ungauged river reaches globally. To this end, we also identified global regions that were under-represented by the gauging stations used for our analysis to help target future additions to our sample of the global hydrometric network.

This classification did not aim to produce geographically contiguous groups, but instead to identify and describe hydrological commonalities in flow intermittence regimes at the river reach scale among regions. These commonalities may be used to understand processes that govern the hydrology of NPRs across continents and to leverage knowledge from well-studied river basins to support scientific studies and management of NPRs in understudied reaches of the same hydrological class elsewhere.

3.3. Data and Methods

3.3.1. Selection and pre-processing of gauging stations and discharge data

We relied on the (Global Runoff Data Centre; GRDC, 2024) database as our main source of global long-term daily discharge data. After downloading all available time series data (as of January 2024), we selected and quality-checked each record in terms of geographic location and discharge data, and linked the remaining stations to a large set of hydro-environmental variables. This procedure is described in the following sub-sections.

Spatial selection and pre-processing

We first removed all stations with daily data for less than 15 years, and those with data for less than 25 years and more than 50% of missing daily data across the recording period. We then selected stations that had not already been geographically validated by Messenger et al. (2021) and associated each of them to a river reach in the RiverATLAS database using the procedure described in (**Chapter 2, Supplementary Information section 2.9.2**). RiverATLAS is a digital representation of the global river network built on the hydrographic database HydroSHEDS (Lehner et al., 2008; Linke et al., 2019). Rivers are delineated from drainage direction and flow accumulation maps derived from elevation data at a pixel resolution of 3 arcseconds (~90 m at the equator) and subsequently upscaled to 15 arcseconds (~500 m at the equator). This linkage enabled us to ensure that gauging stations were correctly located by comparing the reported catchment area and mean annual low recorded at the station to the equivalent estimates from global topographic data and hydrological estimates for the corresponding RiverATLAS reach. Furthermore, RiverATLAS provides hydro-environmental information across the entire upstream drainage area of every reach, which we used to analyze the environmental characteristics of hydrological classes. In total, we quality-checked the geographic location and linked 1372 stations to RiverATLAS, in addition to the 5914 GRDC stations previously formatted by Messenger et al. (2021).

Selection of minimally influenced stations

To distinguish when anthropogenic alterations other than climate change began to significantly influence the flow regime recorded at gauging stations, we compiled time series of human activities in the drainage area upstream of each station, including agriculture, urbanization, and flow regulation by reservoirs. We computed the degree of regulation (DOR; Lehner et al., 2011) by upstream reservoirs from 1900 to 2020 in five-year intervals. Here, DOR expresses the ratio between the volume of over 35,000 upstream reservoirs referenced by the Global Dam Watch dataset (GDW; Lehner et al. *in review*; Mulligan et al., 2021) and the long-term naturalized mean annual discharge (that is, without anthropogenic water use in the form of abstractions or impoundments) modeled by the WaterGAP global hydrological model (Alcamo et al., 2003; Müller Schmied et al., 2014). If the building date of a reservoir was not available, we set the building date as 1930, when only 2% of current estimated reservoir water storage capacity had been built (Lehner et al. *in review*).

The upstream percent area under crop cultivation was estimated from 1900 to 2015, in 10-year intervals until 2000 and then in 5-year intervals, based on the History Database of the Global Environment (HYDE version 3.2; Klein Goldewijk et al., 2017). The upstream population density and percent built-up area (“any roofed structure erected above ground for any use”) were calculated from 1975 to 2020 in 5-year intervals from the Global Human Settlement Layer (GHSL) project estimates (Pesaresi & Politis, 2023; Schiavina et al., 2023). These datasets (GDW, HYDE, and GHSL) were selected for their combination of global and temporal coverage, spatial resolution and spatiotemporal consistency.

All four layers (reservoirs, crops, population densities, and built-up area) were pre-processed from their native format and spatial resolution (ranging from 3 arc-sec for GHSL to 5 arc-min for HYDE, equivalent to 90 m and 9 km at the equator, respectively) to a standardized grid format with the same resolution of 15 arc-second (~500 m). The goal of this standardization was to ensure spatial congruency between these variables and drainage direction from HydroSHEDS for subsequent computation of upstream statistics. See Linke et al. (2019) for details on this overall approach, which was implemented in producing RiverATLAS.

We only included a year of discharge records in subsequent analyses if: (i) less than 2% of the naturalized mean annual discharge at the gauging station was regulated by upstream reservoirs, and (ii) less than 25% of its upstream catchment was cultivated with crops, (iii)

less than 1% was built-up, and (iv) if it was populated by less than 100 people/km² (i.e., the lower end of a “low-density rural area” of the urbanisation classification scheme used by international institutions for global statistical comparisons of the urban-rural continuum; OECD et al., 2021). In years between the 5- or 10-year intervals of the source data, and for gauging records extending before the available periods of data on human influence, we conservatively assumed that the value for each variable was equal to the next available value. For instance, if 0.5% of the upstream area of a given gauging station was built-up in 1990 and 1.3% was built up in 1995, we assumed that 1.3% was built up from 1991 onwards. For records available after the last available year of anthropogenic data, we extended the variable values forward until the end of the discharge time series. Considering that each selected time series was subsequently inspected over its entire selected length for visible anthropogenic influences on the recorded discharge, these thresholds were only applied as initial filters.

Ancillary climatic data

We computed time series of drought indices and temperature to differentiate human-induced and erroneous zero-flow values on the one hand from climate-induced flow cessation on the other hand. These variables also served to quantify the climate-dependence of no-flow events in our hydrological classification.

Zero-flow values recorded at hydrometric gauging stations are often unrelated to natural flow cessation (Zimmer et al., 2020). Flow may be discontinued by human diversions or withdrawals, and zero-flow readings themselves may be erroneous; discharge measurements under low-flow conditions are notoriously difficult (Seybold et al., 2023). Sources of error in zero-flow readings are diverse and include, among others, frozen surface water, inadequate gauge placement, instrument malfunction or damage, rating curve uncertainties, and post-processing errors like typos during data entry or rounding (Messenger et al., 2021; Wilby et al., 2017; Zimmer et al., 2020). Such erroneous values can easily be detected if occurring abruptly in normally perennial watercourses, or outside of the usual dry or cold period in seasonal flow regimes. However, drying during severe droughts or freezing during abnormally cold events, respectively, may also lead to exceptional flow cessation in terms of timing and duration, hence our use of ancillary data to detect these phenomena.

We calculated the average Palmer Drought Severity Index (PDSI) in the upstream area of each gauging station for every 3-month block and the maximum monthly temperature at the location of each station from 1958 to 2019 with the TerraClimate dataset (Abatzoglou et al., 2018). TerraClimate consists of global climate and climatic water balance time series at a monthly time step and a spatial resolution of 2.5 arc-min (~4 km at the equator). PDSI is a dimensionless cumulative drought index that quantifies deviations in soil moisture based on temperature and precipitation (W. C. Palmer, 1965). It ranges from -10 to 10 with values below -2 representing drought conditions and values below -3 and -4 reflecting severe to extreme drought, respectively. While standard PDSI as used here relies on a simplistic water balance model and is limited for cold climates by assuming that all precipitation is liquid (van der Schrier et al., 2013), this dataset offered a suitable spatial and temporal resolution for this study.

Streamflow gauging stations: quality-checking of discharge information

We devised an extensive protocol to flag and remove erroneous discharge records when possible, or to fully exclude those time series deemed too unreliable. A semi-automated approach was implemented by pre-identifying potentially anomalous values based on multiple criteria and models, and using those flags to aid visual examination and interactive deletion of records from every time series with at least one discharge value at or under $0.01 \text{ m}^3 \text{ s}^{-1}$ (10 L s^{-1}). This methodology followed the overall framework for automated anomaly detection introduced by (Leigh et al., 2019), complemented by visual inspection of streamflow records, a common practice for hydrometric data quality checking (Strohmenger et al., 2023). A complete description of the methodology is available in **Supplementary Information section 3.6.1**.

Selection criteria for pre-processed gauging records

We imputed existing or new gaps (from data cleaning) in the clean time series spanning a maximum of 5 consecutive days by interpolation using robust Seasonal Trend Decomposition using Loess (STL; Hyndman et al., 2017). Only discharge time series deemed sufficiently reliable and with at least 15 complete calendar years of data were used in subsequent steps. This criterion of 15 years was chosen based on the sensitivity analysis of (Kennard, Mackay, et al., 2010) as the minimum length of discharge record required to obtain stable estimates of hydrologic metrics for accurately differentiating flow regimes. We considered a year of

data to be complete if there was no remaining missing day of data from January 1st to December 31st after the interpolation procedure.

3.3.2. Hydrologic metrics characterising flow intermittence regimes

For each discharge time series, we computed 15 hydrologic metrics used by Sauquet et al. (2021) to describe the duration, frequency, timing, and rate of change of no-flow periods, which we complemented with four metrics reflecting the climate dependence of intermittence (**Table 3.1**). We considered all daily discharge values at or below $0.001 \text{ m}^3 \text{ s}^{-1}$ as no-flow days and analyzed a gauging station record if it included at least one no-flow day after the initial pre-processing described in the previous section. A no-flow event includes a single no-flow day or a period of consecutive no-flow days. All metrics were computed with custom scripts. A complete description of the meaning and calculation of each metric is available in **Supplementary Information section 3.S2**.

3.3.3. Hydrological classification approach

We used hierarchical agglomerative clustering to identify classes of rivers that were most similar to each other, and most dissimilar to rivers in other classes, in terms of their hydrologic metrics of flow intermittence (**Table 3.1**; Gordon, 1987). Hierarchical agglomerative clustering is commonly used for hydrological classifications because it does not depend on random initial conditions (as opposed to partitional approaches like *k*-means clustering) and yields a dendrogram (tree-like structure) that permits intuitive interpretation of the relative similarity of flow regimes among classes (Olden et al., 2012). Prior to clustering, we evaluated the correlation among hydrologic metrics using Spearman's coefficient (**Supplementary Figure 3.S15**) and selected a subset of non-redundant metrics (in bold italicized font in **Table 3.1**). Each hydrologic metric (*X*) was then transformed to approach normality and z-standardized. We applied a Box Cox transformation to $X + 0.5 * \min(X)$ with the exponent $\lambda \in \{-1, -0.5, 0, 0.5, 1, 1.5, 2\}$ that maximized the profile log-likelihood of a linear model fitted to data. Round numbers were used for λ to decrease the sensitivity of this transformation exponent to minor changes in the input data. The dissimilarity among stations was then computed based on the formatted hydrologic metrics as the pairwise multivariate Euclidean distance.

Table 3.1. Metrics used to describe the flow intermittence regime of gauging stations.

Adapted from Sauquet et al. (2021), see **Supplementary Information section 3.S2** for details on computing each metric. Metrics in bold and italicized were used in the hydrological classification.

Aspect	Name	Definition
Intermittence	F0	No-flow probability defined by the average number of days with no flow per year (day yr^{-1})
Duration	<i>meanD</i> , <i>medianD</i>, <i>sD</i>	Mean, median and standard deviation of the duration of no-flow events (day)
	<i>D80</i>	Duration of the longest no-flow event during the year with an empirical return period of 5 years (day)
Frequency	<i>meanN</i> , <i>medianN</i>, <i>sdN</i>	Mean, median and standard deviation of the number of no-flow events per year (yr^{-1})
Timing	<i>̑</i>, <i>r</i>	Mean timing of no-flow days and the dispersion around that timing, based on circular statistics (dimensionless)
	<i>Sd6</i>	Seasonal predictability of dry periods (dimensionless)
	<i>Drec</i>	Seasonal recession time scale (day)
Rate of change	<i>Ic</i>	Concavity index derived from the flow duration curve (dimensionless)
	<i>BFI</i>	Baseflow index (dimensionless)
	<i>medianDr</i>	Median duration of runoff event (day)
Climate dependence	<i>Fper</i>, <i>FperM10</i>	Percentage of no-flow days in freezing temperatures, that is, occurring during a month with a maximum monthly temperature at or below 0°C and -10°C, respectively.
	<i>PDSIdiff</i>	Difference in median Palmer Drought severity Index (PDSI) during flow days and no-flow days
	<i>P90PDSI</i>	90 th percentile of the Palmer Drought Severity Index (PDSI) during no-flow days

We implemented Ward's minimum-variance criterion as the clustering algorithm after benchmarking it against Unweighted Pair Group Method with Arithmetic mean (UPGMA) and median clustering (Gordon, 1987). All three methods are space-conserving in that the length of the branches of resulting dendrogram approximates the original pairwise distance among observations (i.e., Euclidean distance here); this correspondence in the representation of multivariate distance is measured by the cophenetic correlation coefficient. UPGMA yielded the highest cophenetic correlation, but produced multiple small clusters composed of a handful of gauging stations that were unstable to small variations in the sample of gauging stations (see Methods section on cluster stability). Consequently, Ward's method was used for the clustering presented here.

We set the final number of classes such that an additional class would not yield a substantial gain in within-cluster similarity, although determining what a substantial gain consists of is subjective (Olden *et al.*, 2012). It was identified by examining where the scree plot of the resultant dendrogram representing the average within-cluster dissimilarity (**Supplementary Figure S17**) formed an “elbow” (Cattell, 1966). We also assessed the interpretability of the distribution of hydrologic metrics across the resulting groups of stations.

3.3.4. Variable importance

The relative importance of individual hydrologic metrics in determining the cluster solution was measured with a simple permutation-based approach similar to that used in supervised classification (Breiman, 2001). For every metric, its values were first randomly shuffled among gauging stations, the pairwise Euclidean distance among stations was then re-computed, clustering was performed on that new distance matrix, and the same number of classes were delineated as the original clustering solution. We evaluated the similarity between the original and new clusters with the Adjusted Rand Index (ARI; Hubert & Arabie, 1985). The ARI measures the proportion of gauging stations that are in the same clusters across the two solutions and the proportion of gauging stations in different clusters, accounting for the degree of similarity attributable to randomness alone. This procedure was performed 500 times for each metric, and the average ARI was computed across all permutations of that metric. An average ARI value of 1 indicates perfect agreement between the original and reshuffled clusterings, 0 indicates random agreement, and -1 indicates completely different clusterings. The lower the average ARI associated with a hydrologic metric, the more important that metric is in determining the original cluster solution.

3.3.5. Cluster stability

Cluster stability was assessed as the consistency of individual clusters with small random variations in the set of input gauging stations. This approach is implemented in the *fpc* package in R, following Hennig (2007). The clustering procedure is performed repeatedly with 500 different bootstrap samples (with replacement) of the original set of gauging stations, each time measuring the Jaccard coefficient between each original cluster and the most similar cluster in the new solution (i.e., based on resampled data). The Jaccard coefficient is similar to ARI in that it compares the similarity among clustering solutions but focuses on comparing individual clusters rather than the overall clustering structure. The

mean of the Jaccard coefficient value across all iterations represents the stability of the cluster (Hennig, 2008). A value ≤ 0.5 indicates an unstable cluster which “dissolves” with small changes to the input data, between 0.6 and 0.75 indicates a meaningful yet potentially unstable pattern in the data, and a value > 0.75 denotes a stable cluster (Hennig, 2008).

3.3.6. Hydro-environmental correlates of flow intermittence regimes

We examined the environmental characteristics associated with flow regime classes by training a recursive decision tree to predict the class of gauging stations based on 68 hydro-environmental predictors (**Table 3.2**). Such supervised classifications trees can represent nonlinear relationships, are invariant to monotonic transformations of the independent data, and can handle numerous intercorrelated variables (Breiman et al., 1984). To cope with the uneven number of stations among classes in tree building, we assigned to each observation a weight whose value was inversely proportional to the number of gauging stations in that observation’s hydrological class (Japkowicz & Stephen, 2002). The goal of this analysis was explanatory, to tease out the processes associated with the observed groupings, rather than predictive (Shmueli, 2010).

3.3.7. Analysis of gauge representativeness

The gauging stations used in this analysis represent a small subset of the global hydrometric network (Riggs et al., 2023), which itself is biased towards large perennial rivers in human-dominated watersheds (Krabbenhoft et al., 2022). But collecting, harmonizing, and quality-checking hydrometric data from individual data providers is time consuming (Do et al., 2018). Therefore, we quantified potential biases in the environmental distribution of our sample of stations compared to the distribution of all NPRs globally to help target future compilation efforts. We first measured the univariate difference in the statistical distribution of the gauges versus all NPRs for each of 13 hydro-environmental variables (variables with an asterisk in **Table 3.2**). Following the same approach as Krabbenhoft et al. (2022), we used the 2-Wasserstein distance for this analysis (Dobrushin, 1970; Schefzik et al., 2021). The 2-Wasserstein distance integrates differences in location, size and shape of the distributions (Schefzik et al., 2021), yielding an overall measure of distribution difference that can be used to compare the relative level of bias according to each variable (Krabbenhoft et al., 2022). Global NPRs included all reaches in RiverATLAS with a $> 50\%$ probability to cease flowing at least one day per year on interannual average, according to Messenger et al. (2021).

Table 3.2. Hydro-environmental characteristics used to assess the environmental characteristics associated with flow intermittence regime classes and the distribution bias in the set of gauging stations used in the classification.

A subset of variables, marked with * were used in assessing bias. Attributes abbreviations refer to *T*: temperature, *P*: precipitation, *Q*: discharge. Spatial representations refer to: *p* (derived at the pour point of the river reach), *c* (derived within the local catchment that drains directly into the reach), or *u* (derived within the total drainage area upstream of reach pour point). Abbreviations for aggregation methods (*Aggreg.*) refer to: *avg*: average, *maj*: majority, *min*: minimum, *max*: maximum. See Linke et al. (2019) and Messenger et al. (2021) for a full description of the methodology to calculate the variables

Category	Attribute	Spatial Aggreg.		Source
Climate	Annual mean air T*	c, u	avg	WorldClim v2 (Fick & Hijmans, 2017)
Climate	Mean diurnal range (BIO2)	c, u	avg	WorldClim v2 (Fick & Hijmans, 2017)
Climate	Isothermality — (BIO2/BIO7) ×100	c, u	avg	WorldClim v2 (Fick & Hijmans, 2017)
Climate	Air T seasonality (SD ×100)	c, u	avg	WorldClim v2 (Fick & Hijmans, 2017)
Climate	Max. air T of warmest month	c, u	avg	WorldClim v2 (Fick & Hijmans, 2017)
Climate	Min. air T of coldest month	c, u	avg	WorldClim v2 (Fick & Hijmans, 2017)
Climate	Air T annual range (BIO7)*	c, u	avg	WorldClim v2 (Fick & Hijmans, 2017)
Climate	Mean air T warmest quarter	c, u	avg	WorldClim v2 (Fick & Hijmans, 2017)
Climate	Mean air T coldest quarter*	c, u	avg	WorldClim v2 (Fick & Hijmans, 2017)
Climate	Annual P*	c, u	avg	WorldClim v2 (Fick & Hijmans, 2017)
Climate	P of wettest month	c, u	avg	WorldClim v2 (Fick & Hijmans, 2017)
Climate	P driest month*	c, u	avg	WorldClim v2 (Fick & Hijmans, 2017)
Climate	P seasonality	c, u	avg	WorldClim v2 (Fick & Hijmans, 2017)
Climate	Global aridity index*	c, u	avg	GAI v2 (Trabucco & Zomer, 2019)
Climate	Snow cover extent*	c, u	annual avg	MODIS/Aqua (Hall & Riggs, 2016)
Climate	Snow cover extent	c	annual max.	MODIS/Aqua (Hall & Riggs, 2016)
Hydrology	Inundation extent	c, u	annual min.	GIEMS-D15 (Fluet-Chouinard et al., 2015)
Hydrology	Inundation extent	c, u	annual max.	GIEMS-D15 (Fluet-Chouinard et al., 2015)
Hydrology	Limnity (percent lake area)*	c, u	% extent	HydroLAKES (Messenger et al., 2016)
Hydrology	Naturalized Q*	p	annual avg	WaterGAP v2.2 (Döll et al., 2003)
Hydrology	Naturalized Q	p	annual min.	WaterGAP v2.2 (Döll et al., 2003)
Hydrology	Naturalized Q	p	annual max.	WaterGAP v2.2 (Döll et al., 2003)
Hydrology	Naturalized Q	p	min/max	WaterGAP v2.2 (Döll et al., 2003)
Hydrology	Naturalized Q	p	min/avg	WaterGAP v2.2 (Döll et al., 2003)
Hydrology	Specific Q* (Q/catchment area)	u	annual avg	WaterGAP v2.2 (Döll et al., 2003)
Hydrology	Specific Q (Q/catchment area)	u	annual min.	WaterGAP v2.2 (Döll et al., 2003)
Landcover	Forest cover extent*	c, u	% extent	GLC2000 (Bartholomé & Belward, 2005)
Landcover	Glacier extent	c, u	% extent	GLIMS (GLIMS and NSIDC, 2012)
Landcover	Land cover classes	c	spatial maj	GLC2000 (Bartholomé & Belward, 2005)
Landcover	Permafrost extent	c, u	% extent	PZI (Gruber, 2012)
Landcover	Potential natural vegetation classes	c	spatial maj	EarthStat (Ramankutty & Foley, 1999)
Physiography	Drainage area*	u	-	HydroSHEDS (Lehner & Grill, 2013)
Soils+Geology	Karst area extent*	c, u	% extent	Rock Outcrops v3.0 (Williams & Ford, 2006)
Soils+Geology	Lithological classes	c	spatial maj	GLiM (Hartmann & Moosdorf, 2012)
Soils+Geology	Clay fraction in soil 0-100 cm	c, u	avg	SoilGrids250m v2 (Hengl et al., 2017)
Soils+Geology	Sand fraction in soil 0-100 cm	c, u	avg	SoilGrids250m v2 (Hengl et al., 2017)
Soils+Geology	Silt fraction in soil 0-100 cm	c, u	avg	SoilGrids250m v2 (Hengl et al., 2017)
Soils+Geology	Soil water content	c, u	annual avg	GSWB (Trabucco & Zomer, 2010)
Soils+Geology	Soil water content	c, u	annual min.	GSWB (Trabucco & Zomer, 2010)

We also assessed locations where the addition of a gauging station in the sample would most contribute to reducing distributional bias. In this case, we improved upon the approach implemented in Krabbenhoft et al. (2022), which consisted of computing for each river reach globally the change in relative univariate bias from adding a station on that reach, averaged across all environmental variables. Bias in that case was computed as the difference in arithmetic mean for a given variable (after transformation and scaling) between the gauging stations and the overall river network (Krabbenhoft et al., 2022). A shortcoming of this method is that it uses the average gain in univariate representativeness across all variables as a proxy for multivariate gain in representativeness, which is the true objective of the analysis. As a simple two-dimensional illustration, adding a gauging station on a large uninfluenced river may be considered low priority by averaging the substantial decrease in overall bias from adding a gauge on an uninfluenced river (which are underrepresented in the global hydrometric network) with the increase in bias from adding a gauge on a large river (which are strongly overrepresented). However, few gauging stations are present on rivers that are both large and uninfluenced (i.e., underrepresented in a multivariate sense). For each ungauged NPR globally, we thus computed the change in similarity between the multivariate distribution of gauging stations (across the 13 variables) and that of all NPRs, expressed by the Kullback-Leibler divergence, if a gauge was placed on that reach. The Kullback-Leibler divergence, also known as relative entropy (Kullback & Leibler, 1951), was calculated with the *rags2ridges* package in R (Peeters et al., 2022).

Both the Wasserstein distance and the Kullback-Leibler divergence were calculated after transforming and standardizing every environmental variable to approach a unit normal distribution. Prior to being transformed, each variable (X) with negative values was shifted for the Box Cox transformation to be applied to strictly positive values (X'). That is to say, with $m(S, n)$ as the n -th smallest element of set S :

If $m(X, 1) \leq 0$:

$$X' = X_{non-negative} + 0.5 \cdot m(X_{non-negative}, 2)$$

$$X_{non-negative} = X - m(X, 1)$$

The transformation exponent λ (in 0.5 increments, see the *Hydrological classification approach* section), and the means and standard deviations used for standardization, were calculated from the distributions of the environmental variables of global NPRs. These same parameters were used in formatting the environmental variables of the gauging stations.

3.4. Results

3.4.1. Global availability of hydrometric data for non-perennial rivers and streams with limited human influence

From the 10,740 gauging stations documented in the GRDC database (as of January 2024), 6715 stations provide daily data for a period spanning at least 15 years and have enough metadata for their location to be ascertained. Of these, 4063 stations monitored discharge under limited anthropogenic influence at some point during their period of record, including 1492 stations on potential NPRs (i.e., that included at least one daily discharge value under $0.01 \text{ m}^3 \text{ s}^{-1}$). Following the removal of anomalous data and infilling of missing data (for maximum gaps of 5 days), a total of 690 stations met our selection criteria of 15 complete years of daily data, no missing value, and at least one value at or under $0.001 \text{ m}^3 \text{ s}^{-1}$. We used this subset of stations for computing hydrologic metrics and developing the hydrological classification. An average ($\pm$ SD) of 45 ($\pm$ 21) complete years of daily discharge data were available from these stations, which were distributed across 33 countries. Nearly all stations were in North America, western Europe, Scandinavia, Brazil, southern Africa, and Australia.

3.4.2. Global flow intermittence regimes: classification and environmental correlates

The selected gauging stations encompassed a wide diversity of flow intermittence regimes (**Figures 3.1-3.3**). For example, whereas some gauging stations recorded a single no-flow event across their entire monitoring period, many monitored flow for less than half of the year and as little as 20 days per year on average (**Figure 3.1**). This sample of stations also demonstrates how flow cessation can occur any time of the year depending on climate, and that the timing of no-flow events may remarkably differ even for NPRs within the same basin (**Figure 3.2**). Maps of the distribution among stations of all hydrological metrics used in the classification are provided in **Supplementary Figures 3.S1 to 3.S15**.

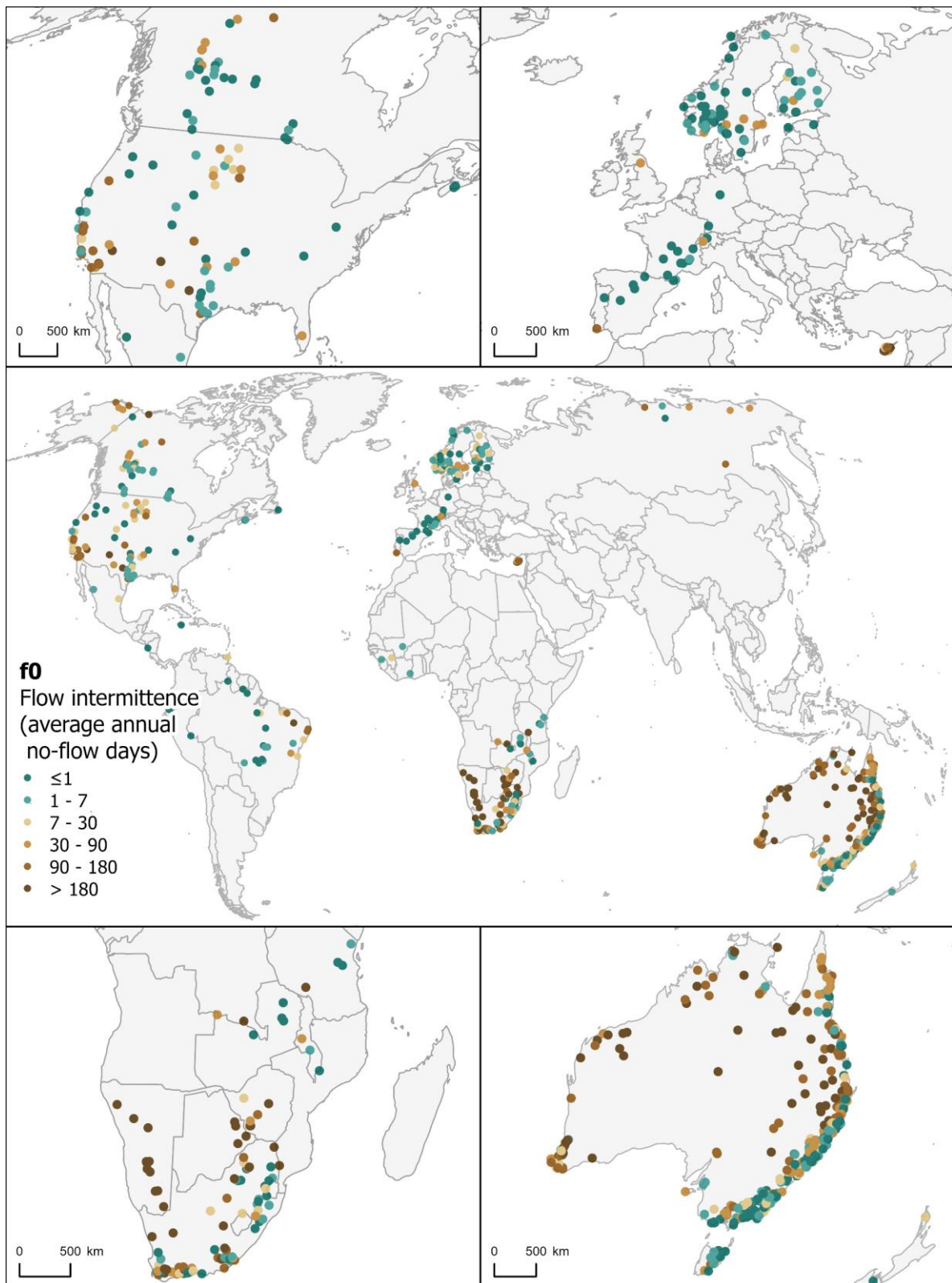


Figure 3.1. Distribution of flow intermittence among gauging stations used in producing the global classification of flow intermittence regimes (n=690).

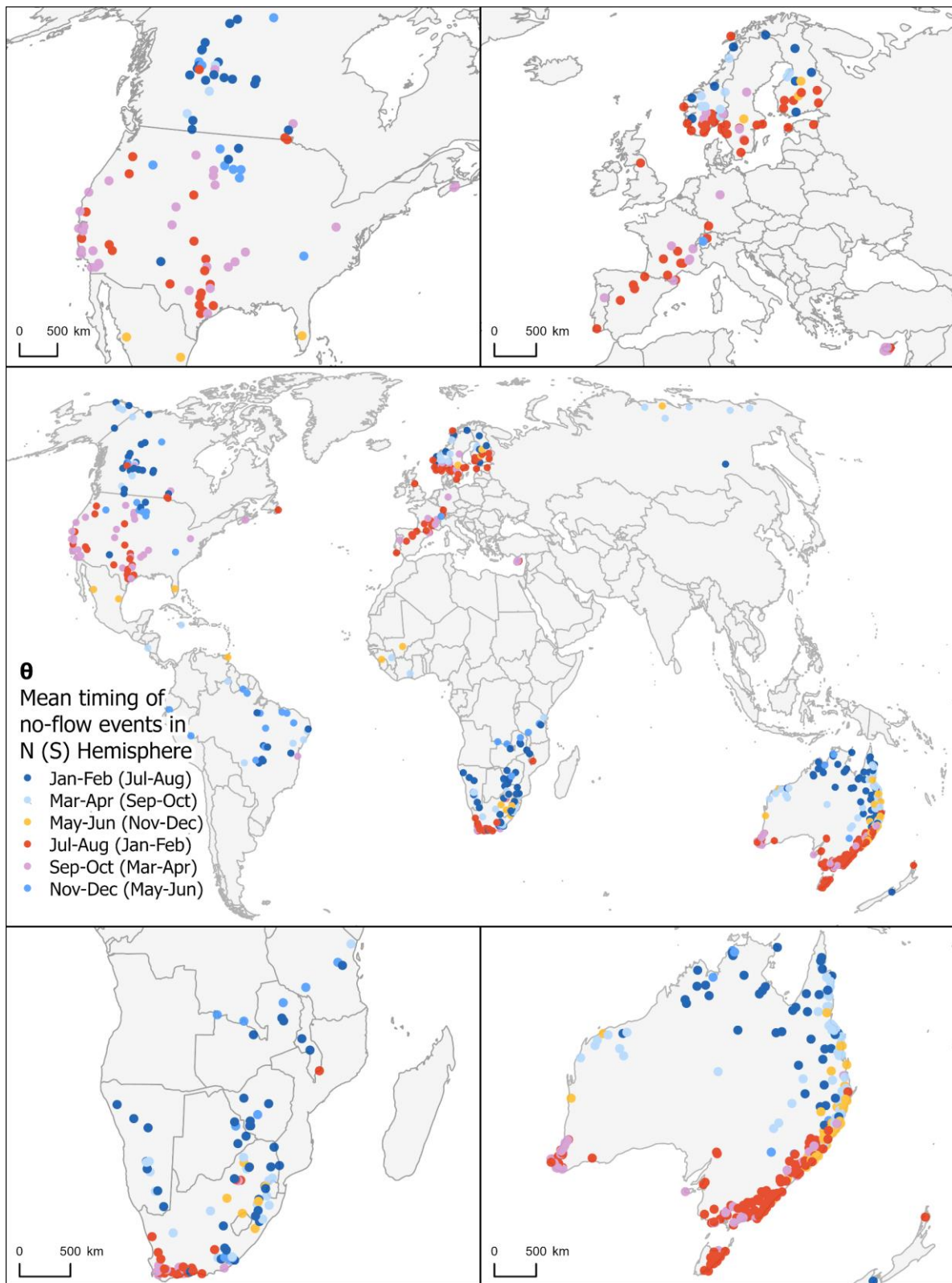


Figure 3.2. Distribution of mean timing of no-flow events among gauging stations used in producing the global classification of flow intermittence regimes (n=690).

We identified nine main classes of flow intermittence regimes globally based on our sample of stations, each represented by 35 (5%) to 151 (22%) stations (**Figure 3.4**). Below, we provide a description of these classes in terms of the distribution of metrics describing the frequency, duration, timing and climate dependence of flow cessation, and the rate of change in discharge across gauging stations representing that regime (**Figure 3.3, Table 3.3, Supplementary Figure 3.S18**). The relative similarity among flow regimes is depicted in the clustering dendrogram (**Supplementary Figure 3.S19**) and the environmental variables associated with each class are shown in **Figure 3.5** (boxplots) and **Supplementary Figure 3.S20** (classification tree).

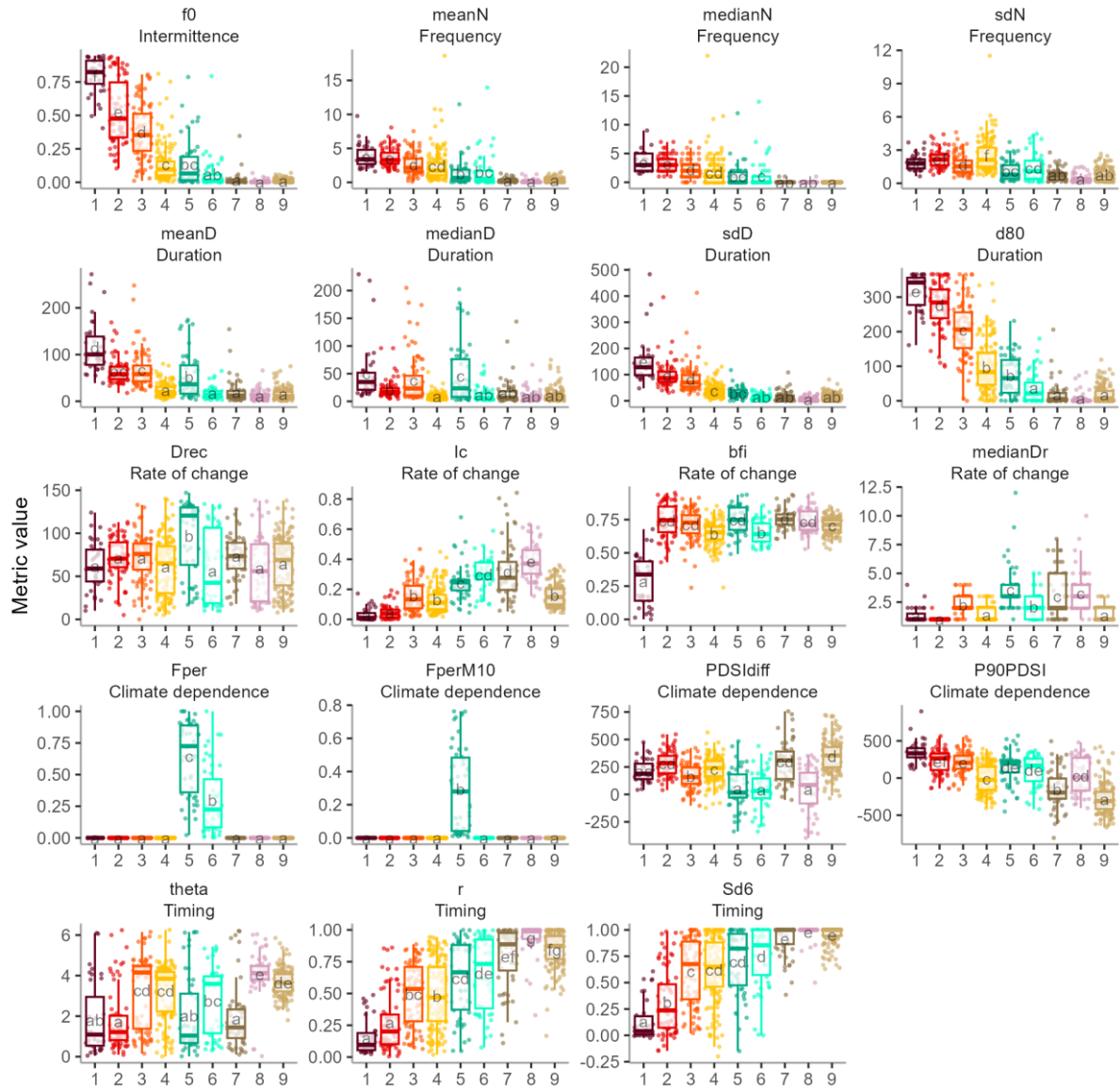


Figure 3.3. Boxplot comparison of the hydrologic metrics of gauging stations by flow intermittence regime class. Boxplots represent the median (horizontal line), 25th and 75th percentiles (boxes' lower and upper sides, respectively), and 1.5*interquartile range (vertical lines/whiskers) of metrics within each class.

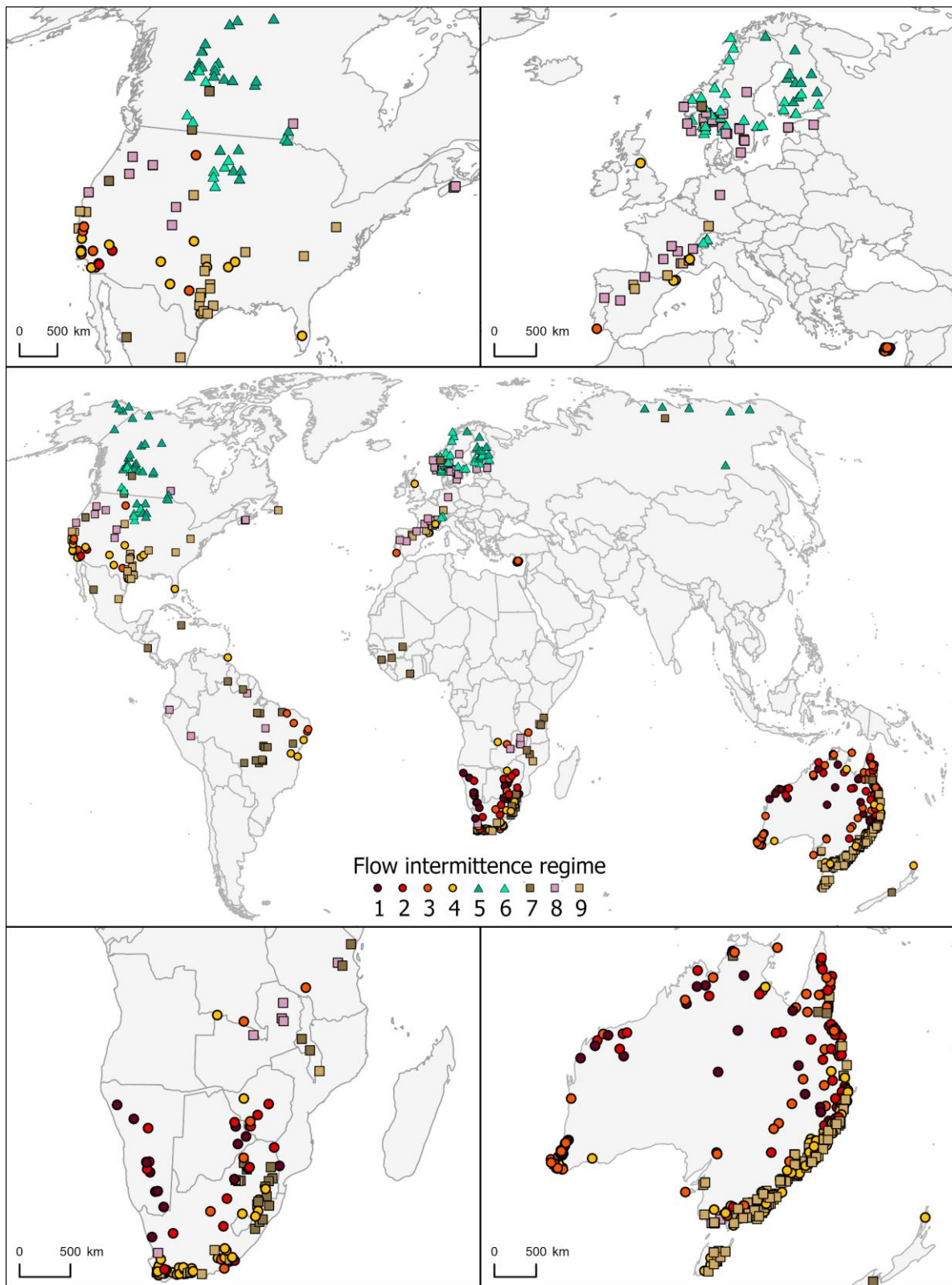


Figure 3.4. Distribution of flow intermittence regimes across global discharge gauging stations.

Several hydrologic metrics exhibit broad trends among classes: flow intermittence decreases from class 1 to class 9 (from nearly 10 months to 2 days per year on average), with rivers undergoing fewer and shorter no-flow events in more defined periods of the year (i.e., stronger seasonality), and displaying more stable flow regimes at the flow-event and seasonal scales. Classes 1 through 6 stop to flow at least once per year and for more than two weeks per year on average, whereas flow cessation is occasional to exceptional in classes 7 through 9. In terms of geographic distribution, classes 1 through 3 are found exclusively in warm to extremely hot climates, classes 5 and 6 in cold climates, while classes 4, 7, 8 and 9 are found in less confined regions. In classes exhibiting high degrees of intermittence, increased flow cessation is not only associated with greater seasonality in precipitation but also larger drainage area and sandier soils (**Figure 3.5**). Beyond these broad trends, each flow intermittence regime differs in nuanced ways. For example, classes 4 and 5 exhibit the same degree of intermittence, undergoing flow cessation 49 days per year on average, but through different mechanisms. Rivers in class 4 drain smaller catchments and stop to flow more frequently and variably than those in class 5 due to a flashier flow regime that is more sensitive to climatic conditions; they also cease to flow for shorter periods on average but with occasional longer dry bouts (> 3 months every 5 years on average). Moreover, flow cessation is less seasonal and vary in its timing across class 4 rivers whereas the great majority of no-flow days (60%) in class 5 rivers occur in cold winter months when air temperatures never go above freezing. Similarly, both classes 5 and 6 are found in climates with extremely cold to cold winters, respectively, associated with high latitudes or high elevation. However, class 6 is comprised of smaller rivers in wetter regions, such that flow intermittence is less severe but may occur both in winter and summer (30% of no-flow days occur in months with air temperatures under 0°C). Classes 7 to 9 all represent rivers with low levels of intermittence (less than a week per year, on average) with strong seasonality. Class 8 rivers are least affected by flow cessation, both in term of frequency and duration, but drying in these watercourses occurs even outside of droughts, during summers. In rivers of classes 7 and 9, by contrast, 90% of no-flow days occur during dry spells (PDSI < -2), with class 9 rivers drying exclusively during summers and class 7 rivers drying more variably across the year and between regions.

Table 3.3. Distribution of hydrologic metrics and environmental variables by flow intermittence regime class.

Values represent the mean (10th-90th percentiles) calculated across all stations belonging to each class. See **Table 3.1** for a description of the hydrologic metrics and **Table 3.2** for a description of the environmental variables. The hydrologic metric θ was not included because the mean could not be meaningfully interpreted. c and u denote spatial statistics computed for the sub-catchment immediately draining to the station and the entire upstream area, respectively.

CI (n)	f0 (days)	meanN (events)	medianN (events)	sdN (events)	meanD (days)	medianD (days)	sdD (days)	d80 (days)	Drec (days)
1 (35)	291 (219-343)	3.8 (2.2-5.7)	3.5 (2-5)	1.9 (1.2-2.8)	115 (61.7-183)	50 (14-86)	150 (88-203)	317 (253-365)	62 (25-94)
2 (70)	194 (96-325)	3.6 (2.0-5.5)	3.2 (2-5)	2.2 (1.3-3.2)	65 (39.2-104)	22 (10-38)	98 (58-138)	276 (187-365)	71 (41-99)
3 (82)	137 (34-250)	2.6 (1.1-4.6)	2.3 (1-4)	1.7 (0.8-3.1)	68 (33.5-106)	39 (8-100)	83 (44-121)	205 (109-314)	71 (36-96)
4 (142)	49 (11-105)	2.4 (0.6-4.9)	1.6 (0-4)	2.5 (1.1-4.2)	24 (10.6-42)	9 (4-14)	39 (15-69)	98 (18-201)	61 (19-103)
5 (50)	49 (2-153)	1.3 (0.06-2.5)	1.1 (0-2)	1.1 (0.2-2.3)	52 (10.6-128)	46 (4-108)	30 (7-57)	74 (1-153)	97 (31-133)
6 (48)	22 (0.6-63)	1.5 (0.02-4.4)	1.2 (0-4)	1.4 (0.2-3.3)	17 (5.7-30)	12 (3-28)	15 (0-32)	38 (0-101)	57 (16-118)
7 (56)	7 (0.3-10)	0.3 (0.04-0.6)	0 (0-0)	0.8 (0.2-1.6)	20 (3.1-42)	16 (2-32)	16 (0-44)	18 (0-40)	74 (45-98)
8 (56)	2 (0.04-5)	0.2 (0.02-0.4)	0 (0-0)	0.4 (0.1-1.0)	12 (1-24)	9 (1-23)	7 (0-21)	7 (0-26)	60 (18-110)
9 (151)	4 (0.2-11)	0.3 (0.03-0.7)	0 (0-0)	0.8 (0.2-1.5)	15 (4-28)	11 (2-23)	15 (0-32)	18 (0-51)	65 (20-101)
All (690)	68 (0.5-230)	1.7 (0.04-4.2)	1.3 (0-4)	1.5 (0.2-3.0)	36 (5.8-80)	20 (3-43)	44 (0.5-105)	103 (0-297)	67 (20-111)
CI (n)	lc	BFI	medianDr (days)	Fper (%)	FperM10 (%)	PDSIdiff	P90PDSI	r	Sd6
1 (35)	0.03 (0.00-0.09)	0.29 (0.04-0.49)	1.3 (1-2)	0 (0-0)	0 (0-0)	2.1 (1.1-3.6)	3.5 (1.7-5.1)	0.2 (0.0-0.4)	0.1 (0.0-0.5)
2 (70)	0.05 (0.00-0.09)	0.74 (0.57-0.90)	1.0 (1-1)	0 (0-0)	0 (0-0)	2.9 (1.4-4.3)	2.2 (0.0-3.9)	0.3 (0.1-0.6)	0.3 (0.0-0.8)
3 (82)	0.16 (0.05-0.31)	0.71 (0.58-0.85)	2.3 (2-3)	0 (0-0)	0 (0-0)	1.6 (0.1-3.0)	2.1 (0.5-4.1)	0.5 (0.1-0.8)	0.6 (0.2-1.0)
4 (142)	0.13 (0.05-0.27)	0.65 (0.53-0.74)	1.4 (1-2)	0 (0-0)	0 (0-0)	2.3 (1.1-3.6)	0.0 (-2.6-2.4)	0.5 (0.1-0.8)	0.6 (0.2-1.0)
5 (50)	0.24 (0.11-0.36)	0.75 (0.63-0.86)	3.6 (2-6)	65 (25-93)	30 (2-70)	0.6 (-1.7-2.9)	1.5 (-1.4-4.0)	0.6 (0.2-0.9)	0.7 (0.3-1.0)
6 (48)	0.30 (0.13-0.40)	0.65 (0.54-0.76)	2.1 (1-3)	30 (3-68)	0 (0-0)	0.5 (-2.1-2.6)	1.1 (-1.9-3.3)	0.7 (0.3-1.0)	0.8 (0.4-1.0)
7 (56)	0.32 (0.13-0.61)	0.76 (0.68-0.84)	3.0 (1-6)	0 (0-0)	0 (0-0)	3.0 (0.8-5.3)	-1.5 (-4.9-2.4)	0.8 (0.4-1.0)	0.9 (0.7-1.0)
8 (56)	0.39 (0.25-0.57)	0.74 (0.65-0.84)	3.3 (2-5)	0 (0-0)	0 (0-0)	0.5 (-2.7-3.0)	0.0 (-2.8-3.1)	0.9 (0.9-1.0)	1.0 (1.0-1.0)
9 (151)	0.16 (0.08-0.27)	0.71 (0.63-0.77)	1.4 (1-2)	0 (0-0)	0 (0-0)	3.5 (1.7-5.5)	-2.8 (-5.0-0.5)	0.8 (0.7-1.0)	1.0 (0.8-1.0)
All (690)	0.18 (0.03-0.36)	0.68 (0.54-0.83)	1.9 (1-4)	7 (0-22)	0 (0-0)	2.2 (0.0-4.2)	0.0 (-3.6-3.3)	0.6 (0.1-1.0)	0.7 (0.1-1.0)
CI (n)	Drainage area (10 ² km ²)	Mean annual Q (m ³ s ⁻¹)	Mean T coldest quarter (c, °C)	Max snow cover (c, %)	P driest month (c, mm)	P seasonality (c, CV)	Aridity index (w)	Sand fraction in soil (w, %)	Probability of flow cessation*
1 (35)	83 (1.0-119)	11 (0.1-19)	16 (11-22)	0 (0-0)	7 (0-23)	0.8 (0.4-1.2)	2.1 (0.8-3.2)	58 (43-69)	1.0 (0.9-1.0)
2 (70)	12 (0.8-28)	5 (0.2-9)	17 (11-22)	1 (0-0)	13 (0-28)	0.8 (0.4-1.1)	4.1 (1.6-7.0)	50 (38-62)	0.9 (0.6-1.0)
3 (82)	95 (0.8-227)	26 (0.3-64)	14 (9-23)	1 (0-1)	12 (1-26)	0.8 (0.4-1.1)	4.2 (2.2-6.8)	53 (38-68)	0.8 (0.6-1.0)
4 (142)	11 (0.5-22)	4 (0.1-7)	11 (6-17)	2 (0-2)	30 (7-50)	0.5 (0.2-0.8)	5.4 (2.5-8.0)	48 (36-62)	0.8 (0.4-1.0)
5 (50)	175 (0.4-310)	83 (0.3-160)	-18 (-29--8)	93 (63-100)	15 (5-25)	0.6 (0.4-0.7)	5.7 (3.0-7.5)	37 (22-54)	0.7 (0.5-1.0)
6 (48)	17 (0.01-44)	4 (0.2-10)	-6 (-10--2)	89 (53-100)	40 (8-76)	0.4 (0.3-0.7)	13.3 (2.5-23.8)	46 (25-63)	0.4 (0.0-1.0)
7 (56)	76 (0.6-84)	53 (0.3-143)	16 (9-25)	9 (0-3)	16 (2-38)	0.7 (0.4-1.1)	7.6 (3.9-11.0)	44 (31-57)	0.4 (0.0-0.8)
8 (56)	15 (0.4-72)	14 (0.4-32)	3 (-6-17)	53 (0-99)	35 (5-56)	0.4 (0.2-0.8)	10.0 (5.0-13.9)	47 (30-61)	0.2 (0.0-0.6)
9 (151)	9 (0.4-26)	5 (0.2-14)	9 (6-14)	6 (0-18)	40 (21-55)	0.3 (0.2-0.5)	7.1 (4.1-9.6)	47 (35-59)	0.5 (0.2-0.9)

*Probability of flow cessation for at least one day per year, on inter-annual average, estimated by Messenger et al. (2021)

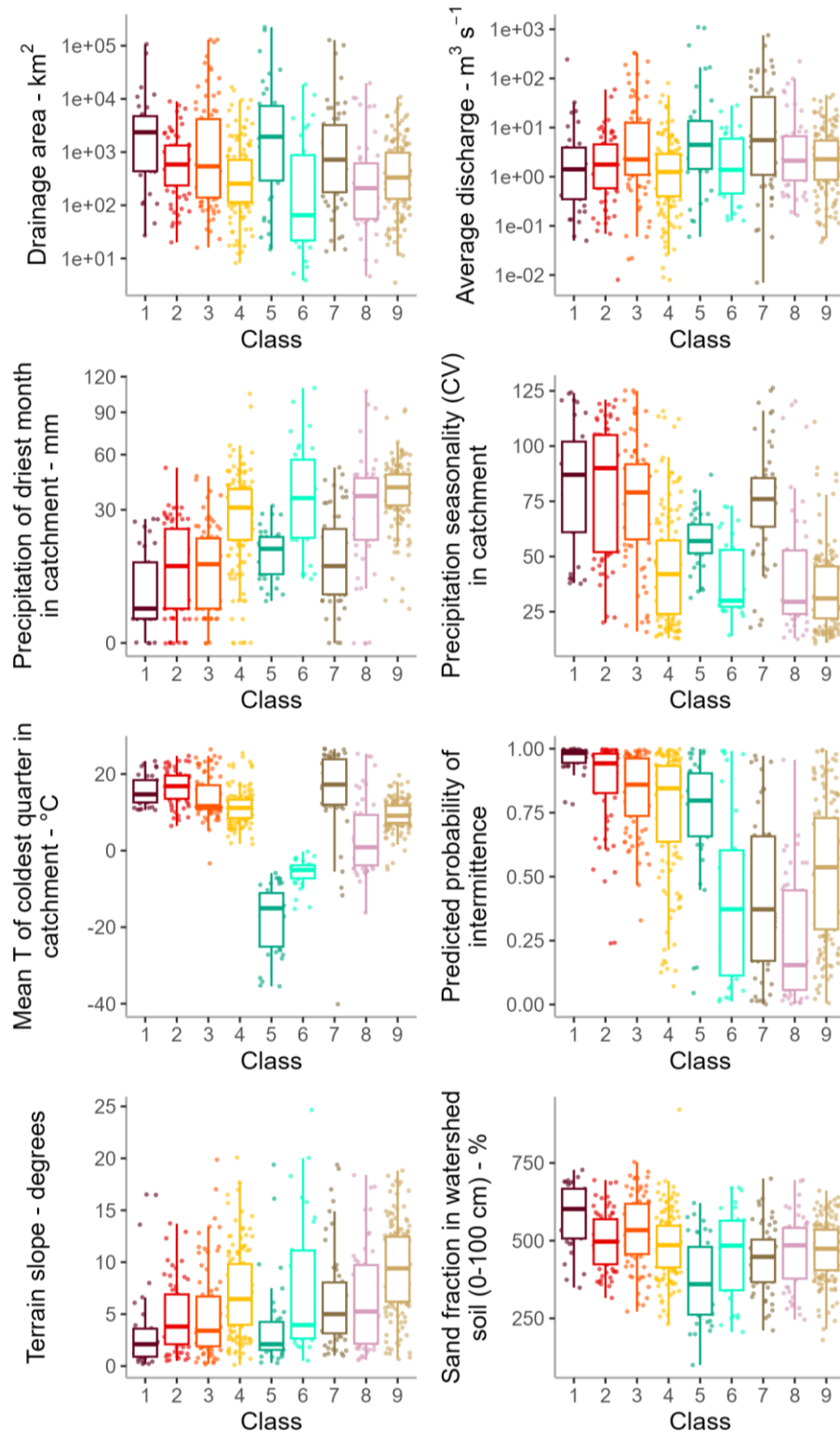


Figure 3.5. Boxplot comparison of selected environmental characteristics associated with global flow intermittence regime classes. Boxplots represent median (horizontal line), 25th and 75th percentiles (boxes' lower and upper sides, respectively), and 1.5*interquartile range (vertical lines/whiskers).

3.4.3. Sensitivity analysis

All hydrologic metrics substantially and equally contributed to determining the final classification (**Figure 3.6**). Random permutation (reshuffling) of the values of any one metric led to significantly different clustering solutions ($ARI \leq 0.6$). The uniformity in contribution largely stems from equally weighting all metrics in the computation of pairwise Euclidean distance among stations. This result nonetheless shows that each metric carries unique information and contributed to delineating flow intermittence regimes.

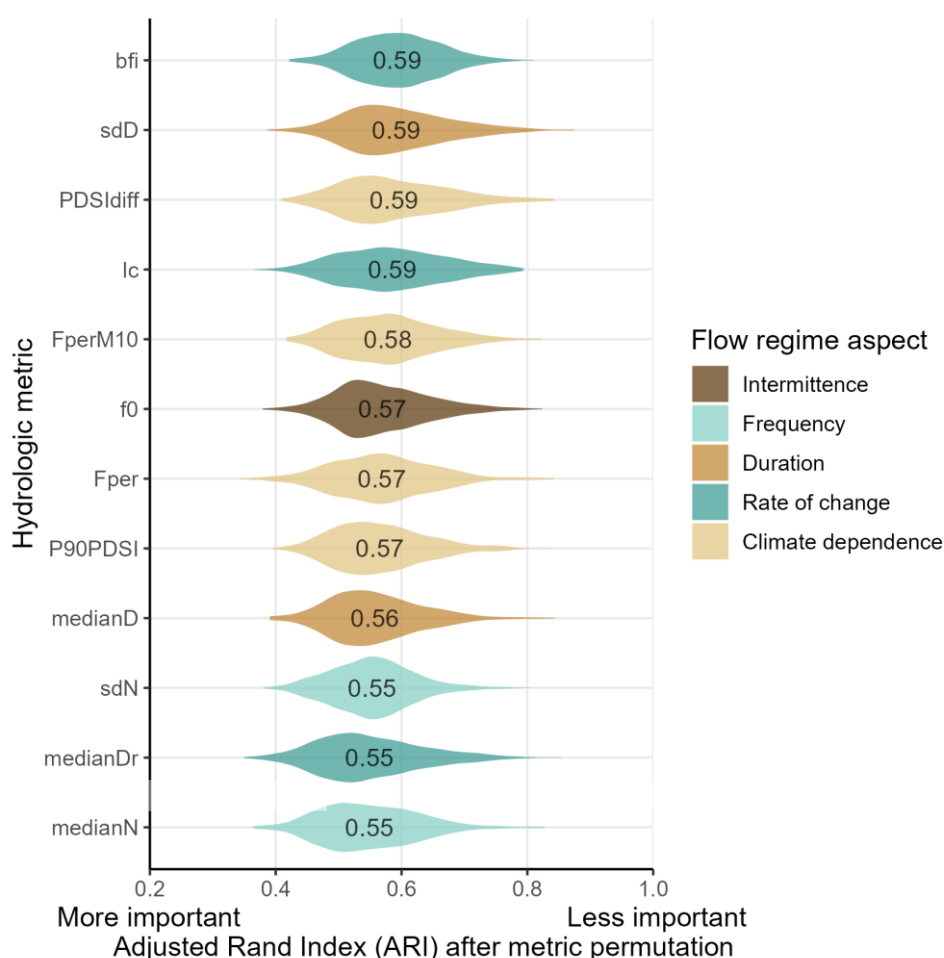


Figure 3.6. Importance of hydrologic metrics in determining the clustering solution.

The violin plots show the distribution of Adjusted Rand Index (ARI) values for each hydrologic metric across 500 random reshuffling of the metric values. A lower ARI value reflects greater difference in the clustering and thus suggests that the metric is more important in determining the clustering solution. The numbers at the center of the violin plots are the mean ARI value for that metric. See Methods section *Cluster stability* for more details on this analysis.

Bootstrap resampling and re-clustering gauging stations leads to new classes with limited similarity compared to the classes we have identified, suggesting that most of these original classes are relative unstable. Although class 5 is highly stable, with an average Jaccard similarity of 1.0 across 100 bootstrap resampling and re-clustering iterations, and classes 4

and 6 are moderately stable (average Jaccard similarity ~ 0.7 for both classes), all other classes usually dissolved after random resampling of gauging stations (Jaccard similarity < 0.5 for the majority of bootstrap samples; Hennig, 2008). This observed instability was not related to our chosen number of classes because at least half of identified classes were unstable whenever stations were grouped in more than three clusters.

3.4.4. Representativeness of gauging stations

The gauging stations used in our hydrological classification represent a biased sample of global NPRs. Our univariate assessment of station representativeness showed that medium- to large-sized rivers, those draining forested catchments, in warm temperate climates, and/or with low air temperature seasonality, are currently over-represented (**Figure 3.7**). River size, forest cover, precipitation of the driest month, and slope stand out as the variables with the highest distributional difference between gauging stations and global NPRs. NPRs in more arid climates, whether cold or hot, are especially underrepresented, as well as those draining catchments fully underlain by karst.

In addition to this univariate assessment, the multivariate comparison of gauging stations compared to global NPRs allowed us to map where adding a station would increase the representativeness of our sample (**Figure 3.8**). Adding records from stations in mountainous and desert regions in general, in the Sahel, central Mexico, northwestern India and Pakistan, in the steppes of Mongolia, the prairies of North America and Argentinian pampa, and in the Canadian and Russian Arctic, for example, would all bring a greater diversity of NPRs in our sample and potentially uncover new flow intermittence regimes. In some regions (e.g., northwestern Brazil), adding a station on a small river or stream would decrease bias, whereas doing so on a large river would increase it, highlighting the added value of performing a multivariate assessment.

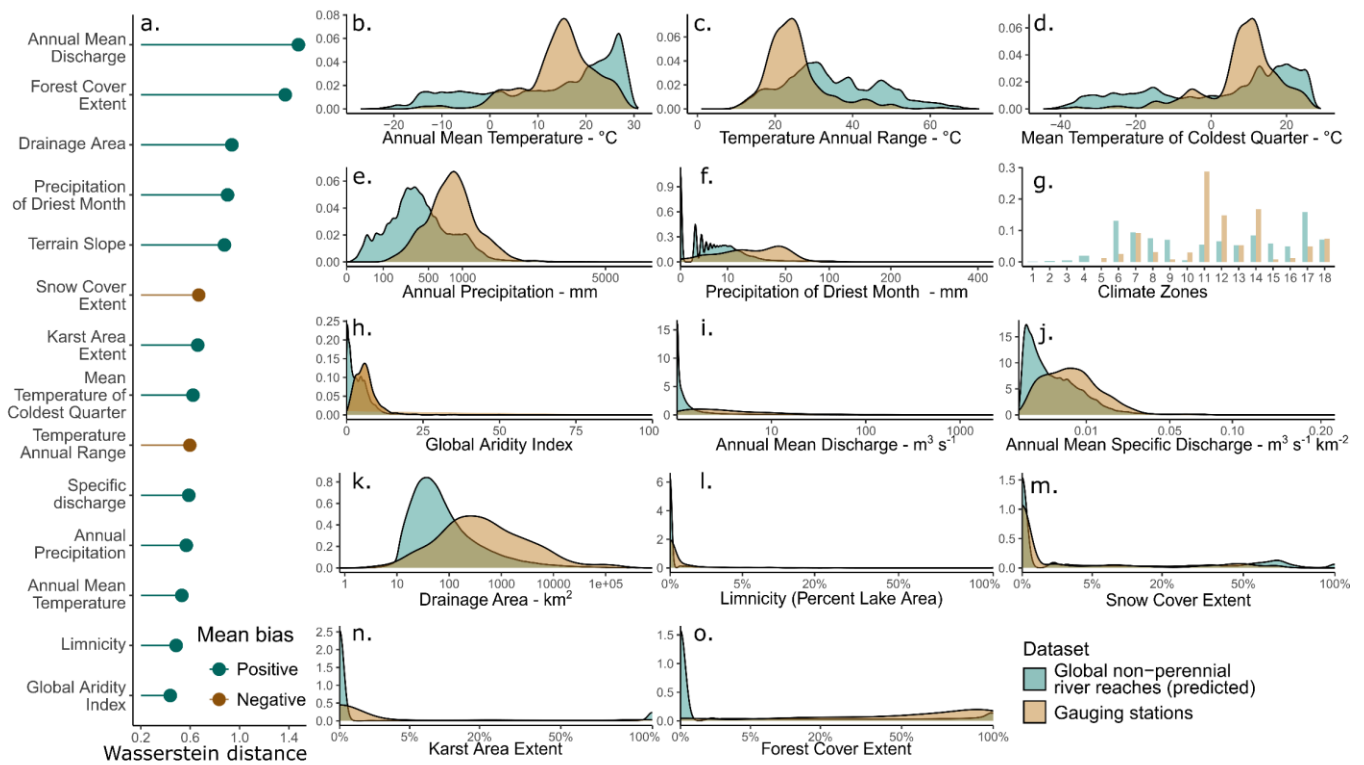
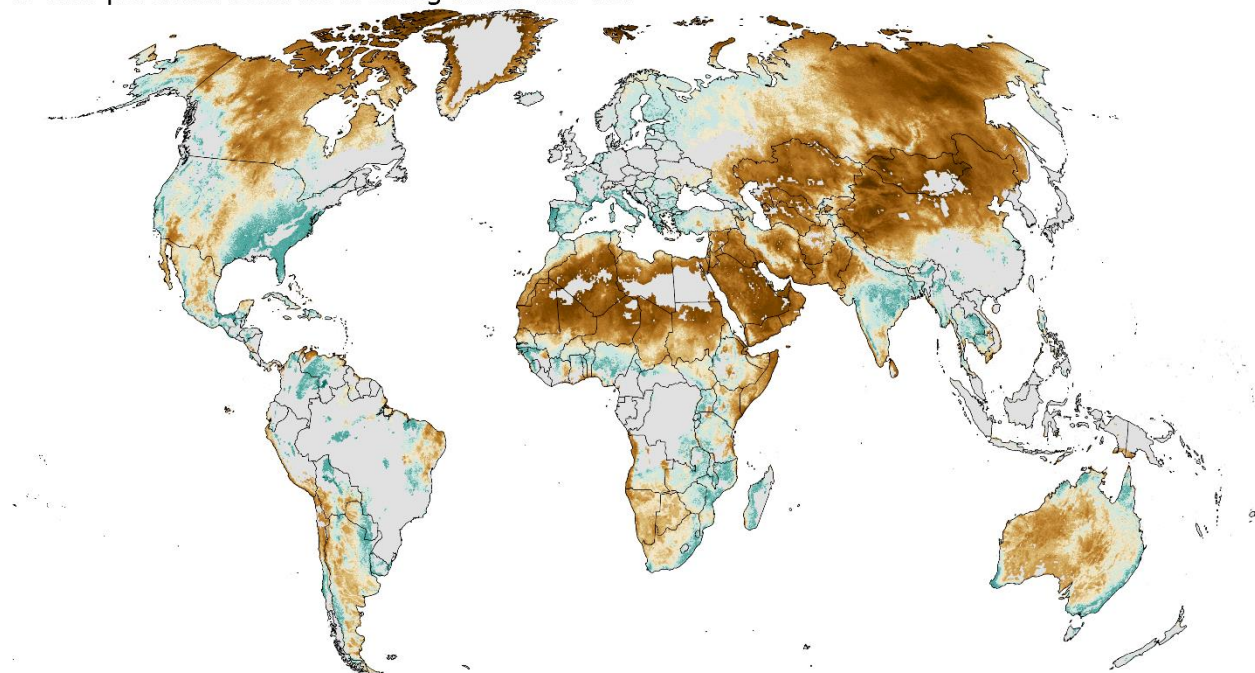


Figure 3.7. Environmental representativeness of gauging stations used in the classification of flow intermittence regimes compared to all global non-perennial river reaches (NPRs).

The Wasserstein distance (a) expresses differences in the location, size and shape of the univariate distributions of gauging stations ($n=690$) compared to global NPRs ($n=3.8 \times 10^6$), yielding an overall measure of distribution difference. Mean bias is the difference in means among each pair of distributions (stations and global NPRs). The distribution plots (b-o) show empirical probability density functions for all variables, aside from climate zones (g) for which the relative frequency distribution is shown. All variables were averaged across the total drainage area upstream of the reach pour point associated with each gauging station or river reach, respectively. See **Table 3.2** for a description of the variables and **Extended Data Figure 2.S1a in Chapter 2** for a description of the climate zones (Metzger et al., 2013). Global NPRs include all reaches predicted to have a probability ≥ 0.5 to naturally stop to flow at least one day per year, on interannual average, including those currently under anthropogenic influence (Messager et al. 2021).

a. Non-perennial reaches draining under 100 km²



b. Non-perennial reaches draining over 100 km²

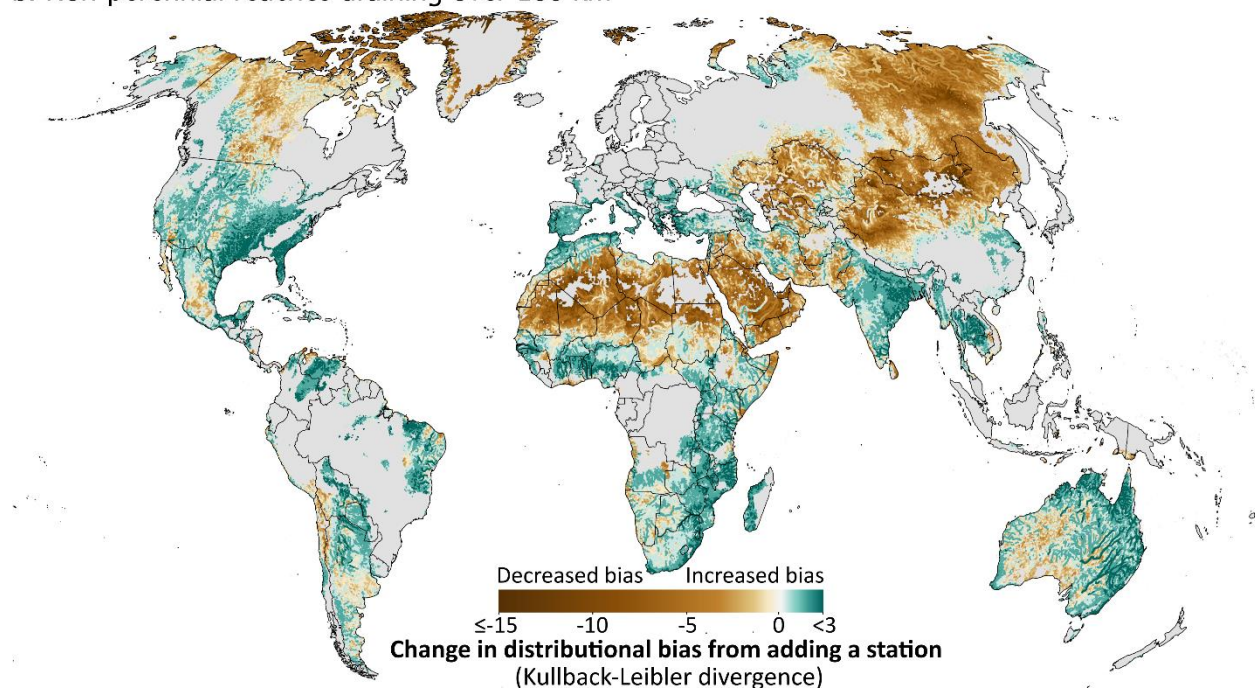


Figure 3.8. Estimated global change in multivariate environmental representativeness of gauging stations from adding a new station.

Marginal change in Kullback-Leibler divergence between the multivariate distributions of gauging stations and global NPRs from adding a discharge time series record from a gauging station on each NPR without a station in this study, based on variables shown in **Figure 3.7a**. Mapped NPRs include all reaches with a modeled natural mean annual discharge over 0.1 m³ s⁻¹ and probability ≥ 0.5 to naturally stop to flow at least one day per year, on interannual average, including those currently under anthropogenic influence (Messenger et al. 2021). Grey areas represent land areas where there are no mapped NPRs with a natural mean annual discharge over 0.1 m³ s⁻¹.

3.5. Discussion

Despite growing acknowledgement of the global prevalence and importance of non-perennial river and streams, our grasp of their hydrological diversity remains rudimentary and biased. Here we delineate nine global hydrological types of NPRs which differ in how often, how long, when and why they stop to flow. This classification spans ecosystems close to the opposite ends of the freshwater-terrestrial spectrum, from near-perennial rivers that never dry outside of severe droughts (class 9) to mainly terrestrial ecosystems shaped by occasional and short-lived water flow (class 1). By quantifying how two rivers may stop flowing for the same length of time but different reasons (e.g., classes 4 and 5), our analysis highlights the importance of moving beyond a unidimensional characterization of flow intermittence to understand the diversity of ways it influences biodiversity, biogeochemistry, and ecosystem services. Additionally, that gauging stations within the same hydrographic basin could belong to different flow intermittence classes shows the relevance of conducting analyses at the scale of river reaches to better capture sub-regional and river size variability in flow regimes.

A classification is a model, so all classifications are wrong, but some are useful (Box et al., 2005). Our hydrological classification did not aim to unveil truly discrete entities the way phylogenetic classification organizes organisms within groups based on actual common ancestry. The goal of hydrological classifications is rather to reduce the multidimensional complexity of hydrological signatures into a synthetic mental model that can be effectively understood, communicated and managed (Tadaki et al., 2014). Coarser classifications may group hydrological patterns that match really distinct processes (e.g., pluvial vs. nival regimes), but finer classifications usually identify groups that stretch along a gradient in contribution from interacting drivers. In the absence of true groupings and despite the existence of guidelines and common practices (Olden et al., 2012), hydrological classification involves a multitude of subjective choices with trade-offs, such as the selection and pre-processing of input data, which metrics, transformations, weights, algorithms and associated parameters to use, or the number of final clusters to present (Peñas et al., 2014, 2016). Here we tried to simultaneously maximize the use of limited data while computing reliable metrics upon which to group data, and to build a parsimonious classification that reflects the underlying structure of the data while effectively reducing complexity.

The intended scientific and management applications of a classification also shape the decisions made during its development (Tadaki et al., 2014). For example, we intentionally implemented a hierarchical classification algorithm to express the relative dissimilarity among classes; we expect that a greater number of classes could be delineated after adding gauging stations, and that varying levels of detail, based on meta-classes, could be catered to different applications – the same way biomes, taxonomic clades, or climates can be successively disaggregated for different uses. Another key choice that we made was to not include metrics of river magnitude. This was meant to evaluate whether flow intermittence regimes inherently varied by river size and showed that, although classes differ in drainage area, these differences do not appear to be a primary determinant of the groupings.

In terms of scientific applications, we hope that our classification will provide a template to generate hypotheses regarding common hydrological processes characterizing NPRs within and among classes (Shanafield et al., 2021), and their consequences on biota, ecosystem processes, and contributions to people. If used to predict the flow intermittence class of all global NPRs, this classification could help improve predictions of flow intermittence in ungauged reaches by physically-based models as well, a notorious challenge in hydrological modeling (Mimeau et al., 2024). In terms of management applications, this classification could be used to establish reference ecological conditions for biomonitoring adapted to the unique hydrology of NPRs, for the Water Framework Directive for example, or as the basis for a new global river health monitoring (Kuehne et al., 2023; Stubbington et al., 2018). It could serve to assess the representativeness of global protected areas, providing a basis for systematic conservation planning of NPRs (Linke et al., 2011). Furthermore, extrapolating flow intermittence classes developed from gauging stations with limited anthropogenic influences to reaches whose hydrology is influenced by human activities could also shed light on what the flow regime would be like in the absence of flow alteration. Finally, such a hydrological classification is one of the pre-requisites for determining and implementing the amount of water required to sustain NPR ecosystems at regional scales with the Ecological Limits of Hydrologic Alteration (ELOHA) framework (Poff et al., 2010). Assuming that hydrological classes comprise watercourses in which ecosystems respond similarly to changes in hydrology, the relationships between flow alteration (e.g., change in summer no-flow duration) and ecological metrics (e.g., salmon juvenile abundance) determined for a

limited set of rivers could hence be presumptively applied to other rivers of the same type in the region (Arthington et al., 2006; Harris et al., 2000; Poff et al., 2010).

The first and only major attempt until now to hydrologically classify flow intermittence regimes at the global scale, by Sauquet et al. (2021), analyzed 471 unregulated NPRs distributed across four countries — Australia, the UK, France, and the conterminous US. This classification was then used for trend detection in the annual frequency of flow cessation events by flow intermittence regime and region. Our classification drew substantially from this study, notably by using the same set of core metrics to characterize flow intermittence regimes, with the aim to expand their approach beyond these select regions. Despite using separate sets of gauges and slightly different classifying metrics, both clustering analyses yielded nine flow intermittence classes, with apparent overlap in their characteristics. For instance, strongly intermittent classes 7 and 8 in Sauquet et al. appear to overlap with classes 2 and 3 from our study whereas near-perennial classes 1 and 2 from Sauquet et al. approximate classes 8 and 9 here; class 5 in their study, which exclusively occur in the US interior with cold winters, overlaps with both classes 5 and 6 in this study. Notwithstanding these similarities, our study differs from Sauquet et al. in several ways. First, Sauquet et al. exclusively used gauging stations from nationwide reference hydrometric networks, each of which had undergone its own intensive screening procedure prior to the study (e.g., Barker et al., 2019; Falcone et al., 2010), and only kept records with at least 30 years of data from 1970 to 2018. By contrast, we tried to apply uniform criteria to identify the periods with limited human influence within each daily discharge time series provided in the GRDC database, and used the remainder if it comprised at least 15 years of data from 1898 to 2022. Our approach aimed to exclude periods with anthropogenically altered discharge while maximizing the number of gauging stations for analysis, because most hydrometric networks worldwide lack pre-screened reference subsets of stations and tend to have shorter time series with larger gaps than those studied by Sauquet et al. Including shorter time series across a longer period served the same purpose, and was deemed acceptable considering that we did not aim to analyze temporal trends in flow intermittence regimes. That said, 78% of discharge time series classified in our study included at least 30 years of data. Furthermore, we explicitly included an indicator of the climate-dependence of zero-flow records (PDSIdiff and P90PDSI, see **Table 3.1**) to differentiate watercourses whose flow cessation during the period of record may not represent longer-term patterns due to

abnormally dry or wet conditions. The second major difference between our classification and that of Sauquet et al. is that our assessment of climate dependence was exclusively focused on flow cessation and was directly incorporated into the classification. That is to say, we quantified climatic conditions and air temperature only during no-flow days rather than for analyzing overall conditions at the sites, and used those metrics of climate dependence as inputs to the hydrological classification rather than for a post-hoc analysis. This inclusion was meant to differentiate flow intermittence regimes driven by drying from those dominated by freezing (or both), those where flow cessation results from abnormal conditions, and to cope with the variable periods of record (as mentioned in the previous paragraph).

Several methodological limitations in the development of this classification warrant improvements prior to dissemination. First, and most importantly, the sample of gauging stations used in its development is small and biased, leading to the under-representation of excessively large regions (**Figure 3.7**) and potential omission of entire flow regimes. Using the GRDC database allowed us to develop a robust classification workflow, which we hope to build upon with additional data, whose collection will be guided by our gap analysis. Second, the criteria we used for filtering out gauging stations with human-altered flow regime were admittedly arbitrary and aimed at excluding the most influenced NPRs while retaining a sufficient sample size for the classification (**Supplementary Figure 3.S16**). Considering the ubiquitous impact of human activities, this approach allowed us to utilize portions of hydrometric records prior to major changes in river catchments while accounting for differences in the timeline of impacts across regions. It represents a notable advance compared to most global hydrological studies that discard entire time series based on present-day conditions and thus lose valuable data. Nonetheless, we plan to develop a quantitative model to identify the proxy variables and criteria applicable at the global scales that can best reproduce the expert-driven screening of gauging stations underpinning reference national hydrometric networks. To this end, we will collect hydrometric data directly from national data providers and request all ancillary data (e.g., rating curve data) and metadata (e.g., flags identifying days when the water is frozen, explicit mentions of human alteration). This information will not only allow us to evaluate the suitability of stations in terms of human influence but also to support quality-checking of the discharge time series themselves. Indeed, the absence of such ancillary data forced us to adopt a

conservative approach in excluding no-flow discharge records. Third, our use of discharge records of different lengths and across a period spanning more than 100 years, while necessary considering the limiting size of our sample, may lead to confounding temporal patterns in flow intermittence that were insufficiently captured by the inclusion of the drought-dependence metrics. With more gauging stations to pull from, future iterations may use only longer time series and include metrics that further capture interannual regime stability (e.g., trends, change points, alternative stable states), whether natural or induced by climate change (Verdon-Kidd et al., 2023; Zipper et al., 2022). Fourth, and last, additional sensitivity analysis is needed to explain the high instability of several clusters revealed by bootstrap sampling (see Results section *Sensitivity analysis*). Whereas this lack of stability may simply underline that flow intermittence regimes fall along a gradient rather than in truly discrete types, future analyses could test how cluster stability changes with additional gauging stations, other clustering algorithms, or when adding and removing hydrological metrics.

Beyond these methodological improvements, we plan several additional analyses for increasing the scope of this classification. We developed this classification as a preliminary exploration of the diversity of flow intermittence regimes in NPRs. We deliberately chose this reduced focus on flow intermittence as a master variable determining their ecological and socio-cultural structure and functions (Datry et al., 2023; Poff et al., 1997). However, we plan to enhance it with the addition of other hydrological metrics unrelated to flow intermittence for understanding the flow regime of NPRs more fully. The predictive performance of these classes to predict biodiversity patterns and discriminate among biotic communities could then be assessed (Puckridge et al., 1998). After the methodological improvements described in the previous sections, we plan to extrapolate this classification and infer the hydrological class of every river reach in the global river network using a supervised classification algorithm trained with ancillary hydro-environmental information (Messenger et al., 2021). Finally, other abiotic factors differentiate rivers in fundamental ways, including their thermal and sedimentary regime, water quality, metabolism or geomorphology, for example (Maheu et al., 2016; Savoy et al., 2019; Tadaki et al., 2014; Wohl et al., 2015), and biotic and socio-cultural aspects, and could be classified. Therefore, we hope to combine the resulting map of hydrological river types with others on water temperature or geomorphology to form a hierarchical multidisciplinary framework as

outlined by Ouellet Dallaire et al. (2019) that would help communicate and manage the diversity of global rivers, including non-perennial ones.

This study provides valuable insights on the global diversity of flow regimes in non-perennial rivers and streams. Yet a river classification is useful insofar as it achieves uptake by scientists, practitioners and policy makers as a common frame of reference, which requires robustness and stability. We believe that the classification results presented here do not achieve these criteria yet, mostly because of the geographic bias of the discharge database. Using the analytical workflow developed here as a solid foundation, we will continue improving the classification to become a global standard for informing the science and management of rivers and streams.

3.6. Supplementary Materials

3.6.1. Selection and pre-processing of gauging stations and discharge data

Differences in hydrometric data compared to Messenger et al. 2021

Similarly to Messenger et al. (2021), we relied on the Global Runoff Data Centre (GRDC, 2024) database as our main source of global long-term daily discharge data. In contrast to that study, however, an updated version of the database was used and pre-processed with a different selection and quality-checking procedure. We also did not include stations from the Global Streamflow Indices and Metadata (GSIM) archive, a compilation of twelve free-to-access national and international streamflow gauging station databases (Do et al., 2018; Gudmundsson et al., 2018). These differences in hydrometric dataset between Messenger et al. (2021) and this study result from divergences of objective among the two studies. Whereas the former aimed to identify non-perennial watercourses as those that ceased to flow at least one day per year on average, here we endeavored to describe the flow intermittence regime of watercourses more fully. Consequently, GSIM could not be used, because it only provides summary indices of discharge time series computed at the yearly, seasonal, and monthly resolution rather than daily data. Our analysis also required ascertaining the validity of all no-flow records and quality-check other aspects of the record beyond no-flow events, rather than only making sure that at least one no-flow day per year was valid on average across the record. This exclusion of GSIM and more stringent quality-checking procedure constrained us to work with a smaller dataset, hence our use of the most recent version of the GRDC database (January 2024) to maximize the number and length of time series available for analysis.

In contrast to Messenger et al. (2021), we also included stations on headwater streams located upstream of the smallest river reaches represented in RiverATLAS (with a mean annual discharge $\geq 0.1 \text{ m}^3 \text{ s}^{-1}$), which tend to be underrepresented in global studies yet comprise a large portion of the global hydrographic network. As opposed to the models used in Messenger et al. (2021), leveraging hydro-environmental data from the larger RiverATLAS watercourse immediately downstream from these stations would not substantially affect our analysis because it did not rely on the modeled discharge estimates from RiverATLAS as a core attribute.

Detailed protocol for quality-checking discharge information

We devised an extensive protocol to flag and remove erroneous discharge records when possible, or to fully exclude those time series deemed too unreliable. A semi-automated approach was implemented by pre-identifying potentially anomalous values based on multiple criteria and models and using those flags to aid visual examination and interactive deletion of records from every time series with at least one discharge value at or under $0.001 \text{ m}^3 \text{ s}^{-1}$ (1 L s^{-1}). Below, we detail our methodology which generally follows the frameworks for automated anomaly detection introduced by Leigh et al. (2019) and the approach for visual inspection of streamflow records used by Strohmenger et al. (2023).

- 1) *Defining users' needs and goal.* Here we aimed to minimize the potential bias in hydrologic metrics describing the various facets of the flow regime induced by erroneous and human-influenced flow records. Using biased metrics to classify gauging stations may create artefactual clusters or assign stations to the wrong cluster.
- 2) *Identifying data characteristics.* Global streamflow records represent a wicked challenge for data quality checking. They consist of thousands of daily time series, each with several thousand data points, seasonal patterns ranging from inexistent to extreme, and similarly variable inter-annual variations. Discharge records often follow a square-root or log-normal distribution with values spanning from 2 to more than 6 orders of magnitude (e.g., from $0.001 \text{ m}^3 \text{ s}^{-1}$ to $> 1000 \text{ m}^3 \text{ s}^{-1}$ within the same year). Discharge tends to be strongly temporally autocorrelated, particularly during the seasonal flow recession and when baseflow dominates, but floods can cause abrupt increases and decreases in values by multiple orders of magnitude. The number of anomalous values is highly uneven among gauging stations, some time series having no errors while others being almost entirely erroneous due to simplistic interpolation between sparse records or instrumental and data reporting errors. An anomalous flow pattern in one record (e.g., 400 days without flow or a sudden drop in value) may be normal in another. Apparent change points and trends may be attributed to instrumental errors, shifts in river channel form following floods invalidating the rating curve used to compute discharge from water height, or to actual changes in flow regime due to climate change or hysteresis following a severe drought. No ancillary information is provided by data providers to establish context, explain potential changes in monitoring, or flag interpolated data.

Finally, expert knowledge on the processes causing observed anomalous patterns is limited given the diversity of flow regimes, channel forms and instrumentation among records.

- 3) *Defining the possible types of anomalies.* Based on previous studies and our own observations (Leigh et al., 2019; Messenger et al., 2021; Strohmenger et al., 2023; Trambly et al., 2021; Wilby et al., 2017), we sought to identify the following types of anomalies in discharge records:
- (i) Point anomalies: a sudden drop or increase that may be due to water management, the presence of debris in the river, instrument maintenance or technical failures,
 - (ii) Noise: high-frequency oscillations, random or periodic due to perturbation in measurements or hydropeaking, for example,
 - (iii) Constant offset, due to instrument calibration or rating curve bias,
 - (iv) Sudden shifts followed by continued change in range and mean, due to hydraulic changes following floods, for example,
 - (v) Long-term drift from climate change or a lack of instrument calibration,
 - (vi) Step shifts between regular values due to rounding to the nearest cubic foot or to the nearest whole, tenth or hundredth of a cubic meter,
 - (vii) Cropped range: values not exceeding a floor or a ceiling value due to limitations in the measuring range of the instrument (because of the placement of the gauge, or the size of the depth staff or weir) or the rating curve,
 - (viii) Linear interpolation: long periods of abnormally smooth records due to infilling of missing data through linear interpolation, carrying the last value forward, or more advanced time series methods like season-trend decomposition using LOESS (Hyndman & Athanasopoulos, 2018),
 - (ix) Constant values for extended periods, usually due to data entry error or rounding, and often observed at the beginning and end of records,
 - (x) Missing values,
 - (xi) Negative values due to data entry errors or flow reversals.

These anomalies are present across the full range of discharge values but are particularly prevalent and visible for zero-flow values flow.

- 4) *Ranking anomalies by importance.* We primarily concentrated our efforts on ascertaining the validity of no-flow readings and secondarily ensured the reliability of the overall record. Our priority was to spot sudden drops to zero, abrupt increases to non-zero values during no-flow periods, anomalous continuous periods of zero (i.e., at the beginning or end of records), or values just above zero for extended periods yet never reaching zero (e.g., several weeks at $0.002 \text{ m}^3 \text{ s}^{-1}$ for a watercourse with mean annual discharge over $1 \text{ m}^3 \text{ s}^{-1}$). Erroneous peaks and constant values were also easily and systematically removed. The start and end of linearly interpolated periods was most difficult to detect, particularly during flow recession and low-flows which are characterized by a smooth extended decrease in discharge over time. Therefore, periods or records in which an excessive proportion of records seemed interpolated in a way that could affect metrics of flow intermittence (i.e., by failing to measure or exaggerating the duration zero-flows) were removed entirely. We did not address long-term drift given that we could not reliably differentiate calibration errors from the effects of climate change.
- 5) *Select suitable methods for anomaly detection.* We implemented four different approaches to flag potentially anomalous daily discharge values (Q):
- (i) *Hard rules:* we implemented the same automatic flagging as Messenger et al. (2021), inspired by Gudmundsson et al. (2018). We removed negative values and flagged all sequences of identical daily values other than zero spanning at least 10 days, single zero-flow values surrounded by positive or missing values, and daily values if $\log(Q+0.01)$ was larger or smaller than the mean value of $\log(Q+0.01)$ plus or minus at least 6 times the standard deviation of $\log(Q+0.01)$ computed for that calendar day for the entire length of the series. The mean and standard deviation were computed for a 5-day window centred on the calendar day to ensure that enough data are considered. These criteria are discussed in Gudmundsson & Seneviratne (2016) and Klein Tank et al. (2009).
 - (ii) *Multiple Seasonal Trend Decomposition using Loess (MSTL):* a Box Cox transformation was first applied to $Q+0.01$ to make discharge values approach normality. The transformed discharge time series was then decomposed into trend, seasonal and remainder components (Hyndman & Athanasopoulos, 2018). Daily values were flagged as potential outliers if the remainder component of the value (after removing

the trend and seasonal components) was inferior to the first quartile, or superior to the third quartile, of remainder values by at least three times the interquartile range of remainder values. This method was implemented through the *tsoutliers* methods in the *forecast* package in *R* (Hyndman et al., 2017).

(iii) *Autoregressive integrated moving-average (ARIMA) model*: this custom method was developed as a complement to the MSTL method to leverage information from nearby gauges and gain flexibility in the criterion used for anomalous value flagging. An ARIMA model was trained on the transformed discharge, with Fourier series and discharge from a nearby gauge (when available) as external regressors. Fourier series were included to account for annual seasonality in discharge, and the nearby gauge was identified from all gauges within a network distance of 100 km and with at least 75% of overlapping records, selecting the source gauge with the highest cross-correlation in discharge with the target gauging station (across all lag values of the cross-correlation function). The number of Fourier Series was determined by minimizing the Akaike Information Criterion with a maximum of 10 Fourier series for records shorter than 80 years and 3 for longer time series (to avoid excessive computation time). The degree of differencing, and the autoregressive and moving average orders, were automatically determined with the *auto.arima* function of the *forecast* package in *R* (Hyndman et al., 2017). After training the ARIMA model, if model residuals were autocorrelated (based on a Ljung-Box test), we also trained an ARIMA model without discharge from the nearest gauge as an external regressor and selected it if the resulting model residuals were not significantly autocorrelated. Finally, we flagged all Q values that were outside of the 95% confidence interval of the one-step forecast and whose difference from the one-step forecast was outside of the long-term 95% confidence interval for the 7-calendar day period centered on that date. The latter criterion was meant to flag flood peaks that the ARIMA model could not anticipate only during periods of the year when flooding is uncommon.

(iv) *Second-order difference outliers*: this custom method was developed to flag anomalously smooth sequences of daily discharge potentially resulting from missing data infilling through interpolation. Interpolation tends to produce consistent increasing or decreasing trends in the data between data points. Accordingly, we first computed the second-order difference of transformed discharge. We then computed

the coefficient of variation (CV) in differenced discharge within an 11-day moving window across the entire record. We flagged sequences of at least 7 consecutive days whose moving-window CV was below the 10th percentile for that calendar day.

We did not use these methods for automatic outlier removal because their performance substantially varied across flow regimes and would warrant additional fine-tuning by flow regime. Instead, we visually inspected and interactively deleted outliers from every time series with a bespoke application we developed for this purpose. This application enabled us to dynamically zoom in to inspect short periods of record, vary the scale from linear to square-root- and log-transformed, and color code daily values by the type of associated flags (generated by the four methods described above) as well as by maximum monthly air temperature, drought index (PDSI) and anthropogenic variables. We either removed discrete daily values, sequences of daily values, or excluded entire time series from subsequent analysis if they were deemed too unreliable. We also excluded all stations with more than 95% of integer values in their record and periods of records exclusively composed of positive integer and zeros values.

3.6.2. Hydrologic metrics characterising global flow intermittence regimes

Below we provide additional detail for the calculation of each hydrologic metric of flow intermittence. No-flow days include all days with a daily discharge $\leq 0.001 \text{ m}^3\text{s}^{-1}$ (1 L s^{-1}).

Intermittence

FO is the no-flow probability defined by the average number of days with no flow per year (day yr^{-1}). It is computed as the ratio between the total number of no-flow days and the number of years on record.

Duration

No-flow events (*e*) consist of a discrete series of subsequent no-flow days, delimited either by daily discharge values $> 0.001 \text{ m}^3\text{s}^{-1}$ or by the start or end of the discharge time series. A single no-flow event can start and end in different years.

meanD, **medianD**, **sD** are the mean, median and standard deviation of the duration of no-flow events (day), respectively, and are simply computed from the distribution of durations of no-flow events across the entire record.

d80 is the duration of the longest no-flow event during the year with an empirical return period of 5 years (day). It is calculated by:

- i) Identifying continuous blocks of 5 years of daily data
- ii) Calculating the yearly maximum no-flow event duration (days)
- iii) Computing the 80th percentile of yearly maximum no-flow event duration across all years within a 5-year block. This approach aimed exclude isolated years which may represent a bias sample to compute events with a 5-year return period.
- iv) For records that did not have any 5-year block of continuous daily data, d80 was computed as the 80th percentile of the yearly maximum no-flow event duration across all years.

Frequency

meanN, **medianN**, **sdN** are the mean, median and standard deviation of the number of no-flow events per year (yr^{-1}), respectively, and are simply computed from the distribution of yearly number of no-flow events by year across the entire record.

Timing

The mean timing of no-flow events $\bar{\theta}$ and the dispersion around that timing r are both based on circular statistics (dimensionless), whose calculation is detailed in Burn (1997) as follows:

i) the calendar date of each no-flow day i is converted to an angular value θ_i in radians:

$$\theta_i = (\text{calendar date})_d \left(\frac{2\pi}{\text{total number of days that year}} \right)$$

ii) The x - and y -coordinates of the mean no-flow day are then calculated as:

$$\bar{x} = \frac{1}{n} \sum_{i=1}^n \cos(\theta_i)$$

$$\bar{y} = \frac{1}{n} \sum_{i=1}^n \sin(\theta_i)$$

iii) The mean timing of no-flow days is then obtained as:

$$\bar{\theta} = \tan^{-1} \left(\frac{\bar{x}}{\bar{y}} \right)$$

iv) For gauging stations in the southern hemisphere, a correction factor was applied to theta to account for the reversal of calendar days of seasons (i.e., in temperate regions, the meteorological summer starts December 1st instead of June 1st). Because our stations were distributed across all latitudes, we did not apply a single correction factor as Sauquet et al. (2021). To avoid an artificial discontinuity between stations on either side of the equator that may nonetheless exhibit seasonality in flow cessation, we instead computed $\bar{\theta}_{corrected}$ as follows:

$$\bar{\theta}_{corrected} = \begin{cases} \bar{\theta} & \text{if } latitude_{station} > 0 \\ \bar{\theta} - \left(\left(\pi \max \left(-1, \frac{latitude_{station}}{23.5} \right) \right) \% 2\pi \right) & \text{if } latitude_{station} < 0 \end{cases}$$

such that the correction factor in the southern hemisphere increased gradually from 0 at the equator to π at the Tropic of Cancer and beyond, and that the resulting angular value would remain under 2π with the modulo operator %.

r , which measures the interannual regularity in mean annual timing of no-flow days (a value close to one indicates a high concentration around θ while a value close to zero indicates no seasonality) was computed as the norm of the mean vector as:

$$r = \sqrt{\bar{x}^2 + \bar{y}^2}$$

Like Sauquet et al. (2021), the variables $r \times \cos(\bar{\theta}_{corrected})$ and $r \times \sin(\bar{\theta}_{corrected})$ were used instead of r and $\bar{\theta}_{corrected}$ to avoid an artificial break in winter.

sd6, first introduced by Gallart et al. (2012), is the seasonal predictability of dry periods and was computed as follows:

- i) Compute the total number of no-flow days in the 6-month moving window centered around each day in the record.
- ii) Use the calendar day with the most no-flow days within its window, on interannual average, to delimit the “dry period” as the 6-month window centered on that day. Calendar days outside of that window were considered part of the “wet period”.
- iii) The number of months with at least one zero-flow day is computed for each wet and dry period of every year.

$$\text{iv) } \mathbf{sd6} = 1 - \frac{\text{meanF06dm}}{\text{meanF06wm}}$$

where *meanF06dm* and *meanF06wm* are the interannual average number of months with no-flow days for the dry and wet periods, respectively.

Rate of change

Drec, the seasonal recession time scale (days) described in Catalogne (2012), is computed as follows:

- i) Compute the long-term 30-day moving average discharge by calendar day (Q_{m30d} for $d = 1, \dots, 365$).
- ii) Re-organize calendar days by water year so that, for each gauging station, the first day of the water year was the calendar day with the maximum Q_{m30d} , making the beginning of the year the beginning of the falling limb or seasonal recession. Q_{m30d} is used to identify this calendar day rather than the long-term mean average discharge because the latter could be biased by a single large flood.
- iii) Taking the distribution of Q_{m30d} , **Drec** is computed as the number of days between the first calendar day whose Q_{m30d} is equal or below the 90th percentile $P90(Q_{m30d})$, and the first calendar day whose Q_{m30d} is equal or below the median Q_{m30d} .

Ic, the concavity index introduced by Sauquet & Catalogne (2011), reflects the contrast between low-flow and high-flow regimes derived from quantiles of the Flow Duration Curve computed as:

$$Ic = \frac{Q_{10} - Q_{99}}{Q_1 - Q_{99}}$$

The base flow index (BFI), the ratio of baseflow to total flow, was computed following Institute of Hydrology (1980):

- i) divide the time series into non-overlapping 5-day blocks
- ii) compute the minimum discharge in each block
- iii) identify the day of minimum discharge in each block. When multiple days have the same minimum discharge, take the median calendar day of minimum value within the block.
- iv) Identify turning points: days of minimum flow within each 5-day block whose discharge*0.9 is equal or less than the minimum flow in both neighboring 5-day blocks.
- v) Compute daily baseflow as the linearly interpolated value between turning points.
- vi) Constrain daily baseflow (Q_{bf}) to equate the actual daily discharge value (Q) if the linearly interpolated value exceeds the actual discharge value.
- vii) $BFI = \frac{\sum Q_{bf}}{\sum Q}$

The median duration of runoff events (medianDr; Sauquet et al., 2021) was computed as follows:

- i) Computed daily runoff discharge as $Q_r = Q - Q_{bf}$
- ii) Identify $d_{maxQ_r,y}$ the date of maximum runoff discharge, by year. Take the earliest date if multiple dates have runoff discharge equal to that maximum.
- iii) Identify the next date for which $d_{Q_r \leq 0.5maxQ_r,y}$, for each year
- iv) Compute the duration of runoff event for each year as:
$$Dr_y = d_{Q_r \leq 0.5maxQ_r,y} - d_{maxQ_r,y}$$
- i) Compute the median of Dr_y across all years.

Climate dependence

Fper and **FperM10** were computed as the percentage of no-flow days that occurred during a month with a maximum monthly air temperature at or below 0°C and -10°C, respectively, at the location of the gauging station, according to TerraClimate time series (Abatzoglou et al., 2018).

PDSIdiff was computed as follows from TerraClimate spatiotemporal time series of monthly climate and climatic water balance for the global land surface from 1958 to 2019:

- i) Compute the average Palmer Drought Severity Index (PDSI) in every 3-month blocks upstream of each gauging station: $PDSI_{3mo}$
- ii) Compute the median $PDSI_{3mo}$ for flow days and no-flow days, respectively, across the record.
- iii) $PDSIdiff = \text{median}(PDSI_{3mo_flowdays}) - \text{median}(PDSI_{3mo_noflowdays})$

P90PDSI is the 90th percentile of the Palmer Drought Severity Index (PDSI) during no-flow days, $P90(PDSI_{3mo_noflowdays})$

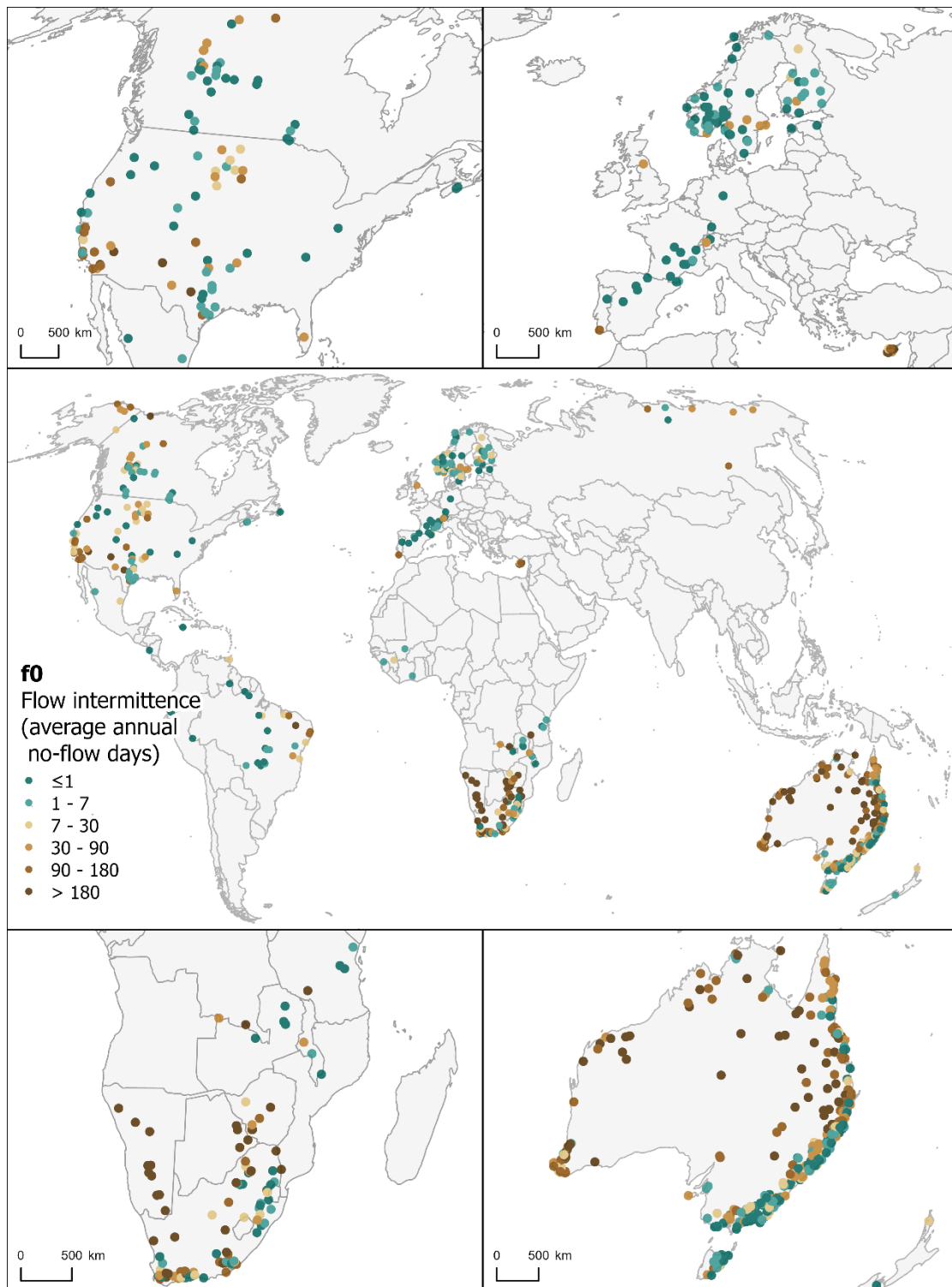


Figure 3.S1. Distribution of flow intermittence (f0) among gauging stations used in producing the global classification of flow intermittence regimes (n=690).

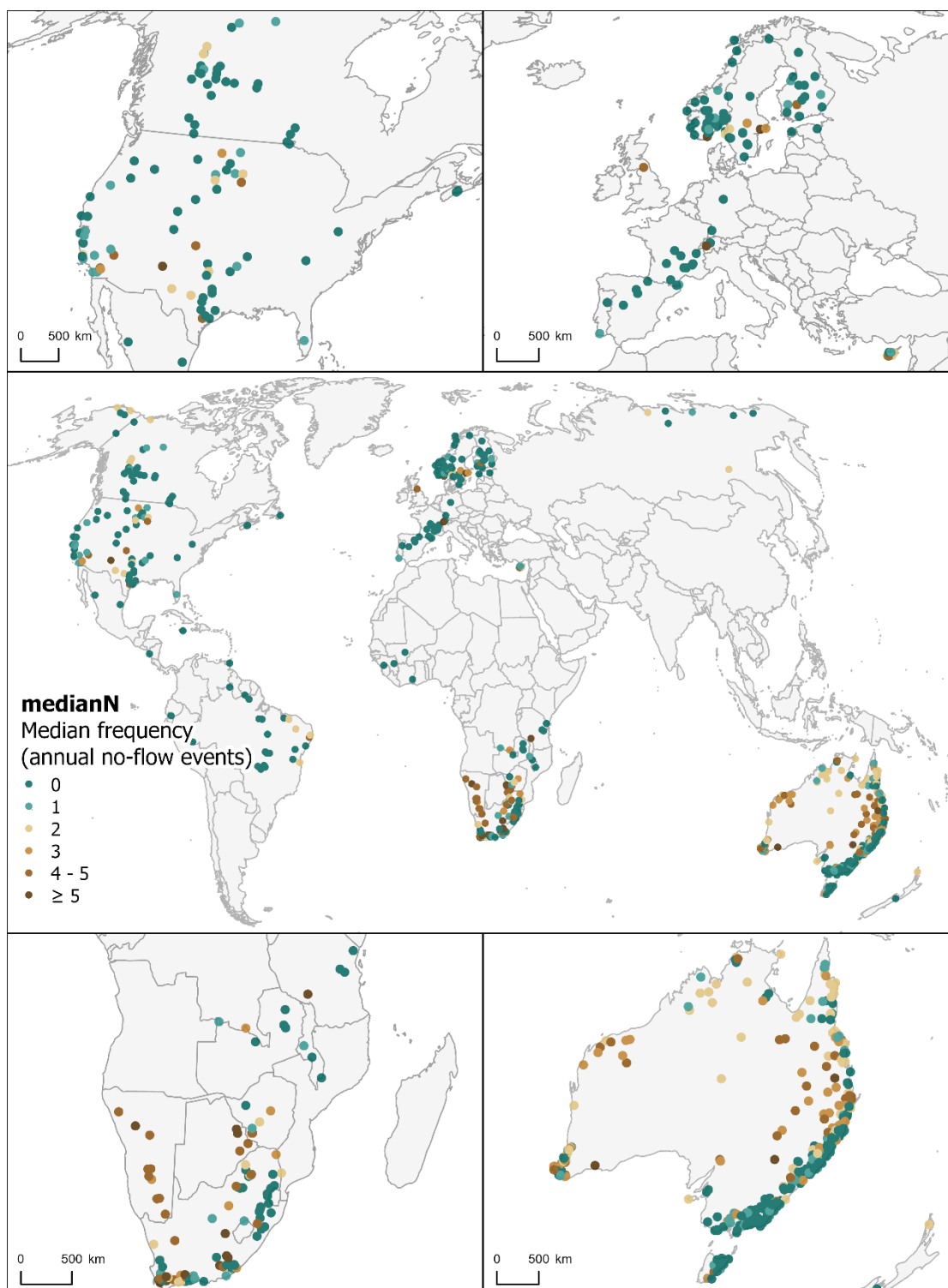


Figure 3.S2. Distribution of median annual frequency of no-flow events (medianN) among gauging stations used in producing the global classification of flow intermittence regimes (n=690).

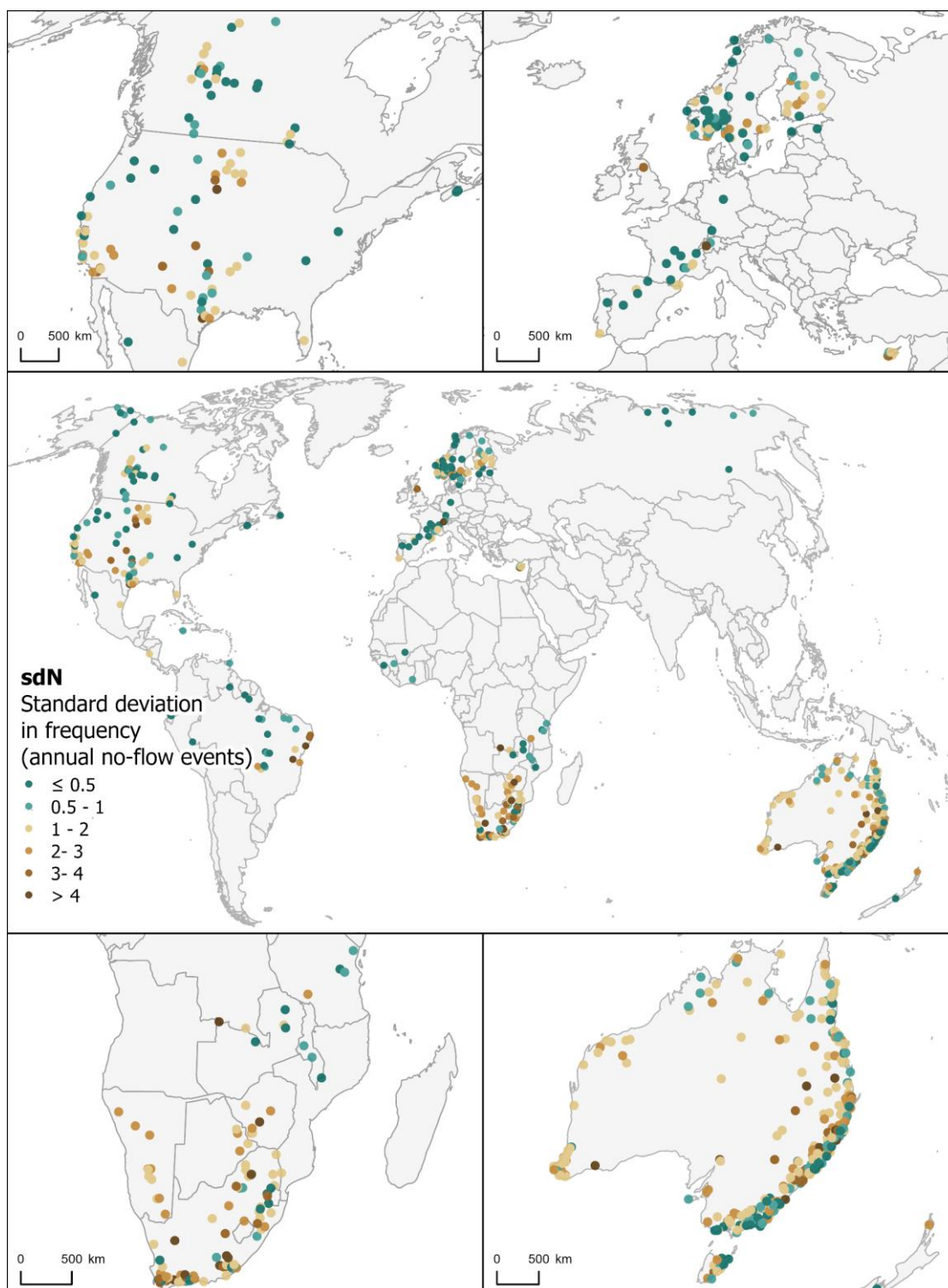


Figure 3.S3. Distribution of standard deviation in annual frequency of no-flow events (sdN) among gauging stations used in producing the global classification of flow intermittence regimes (n=690).

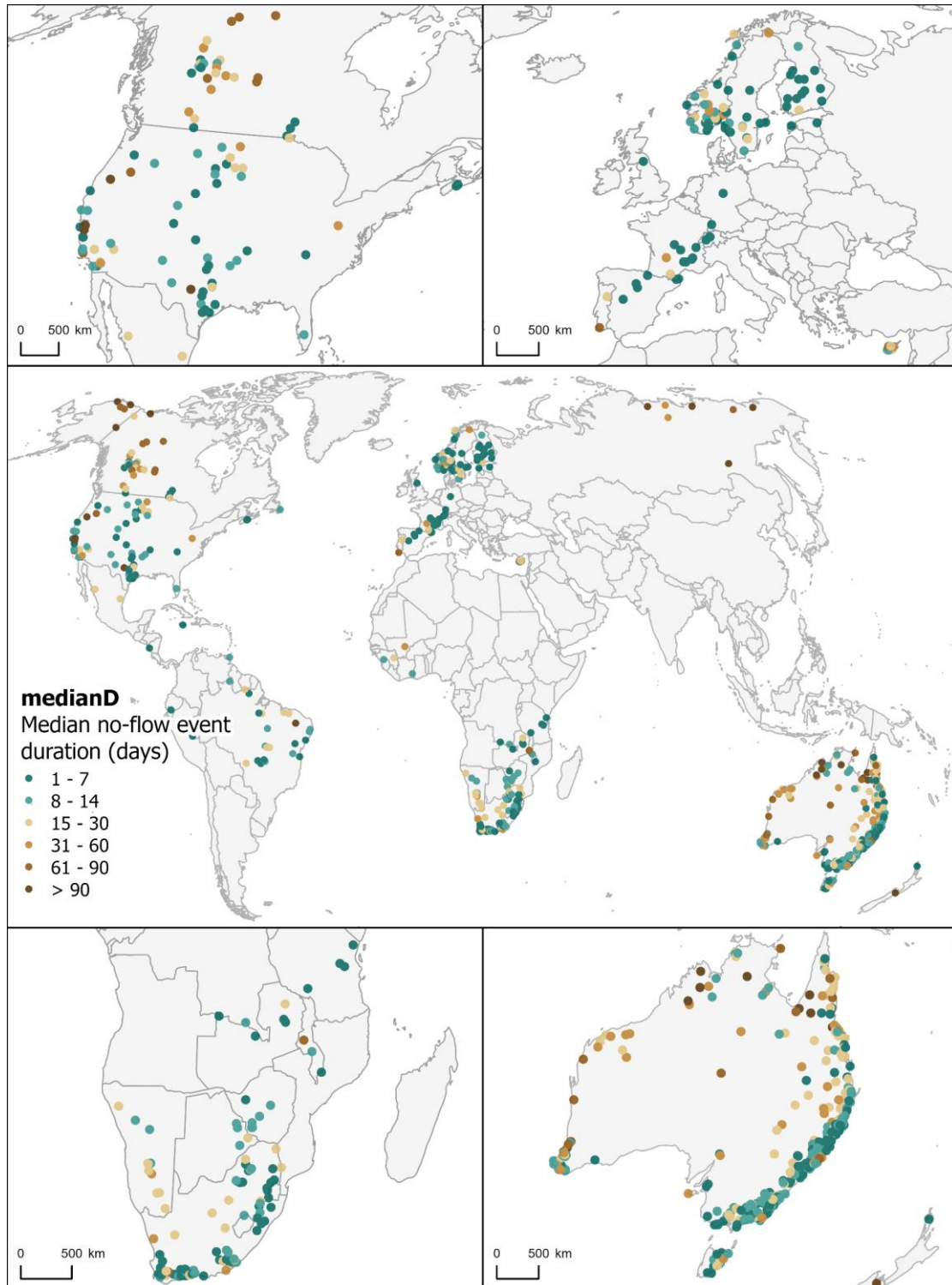


Figure 3.S4. Distribution of the median duration of no-flow events (medianD) among gauging stations used in producing the global classification of flow intermittence regimes (n=690).

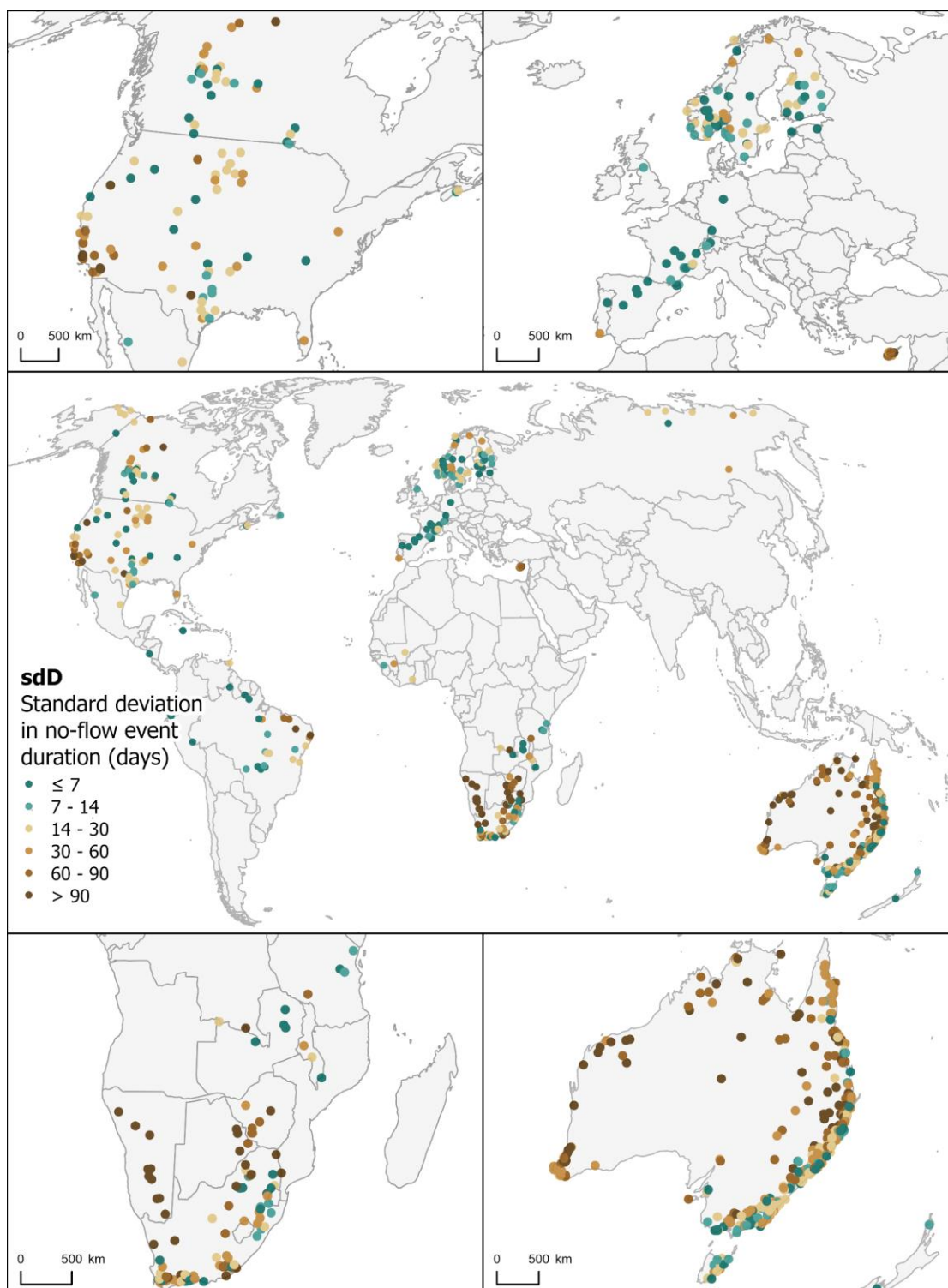


Figure 3.S5. Distribution of the standard deviation in duration of no-flow events (sdD) among gauging stations used in producing the global classification of flow intermittence regimes (n=690).

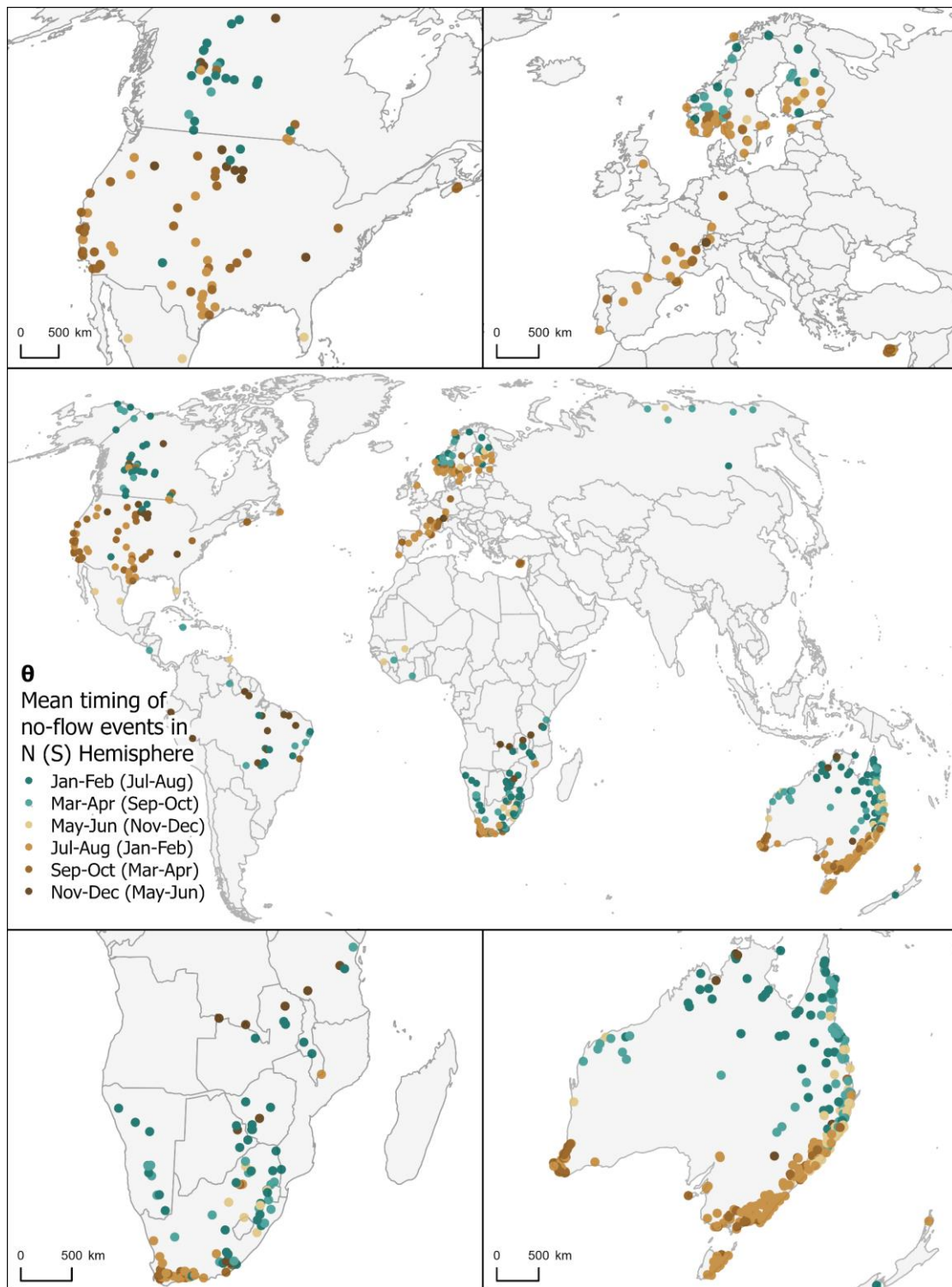


Figure 3.S6. Distribution of the mean timing of no-flow days (θ) among gauging stations used in producing the global classification of flow intermittence regimes ($n=690$).

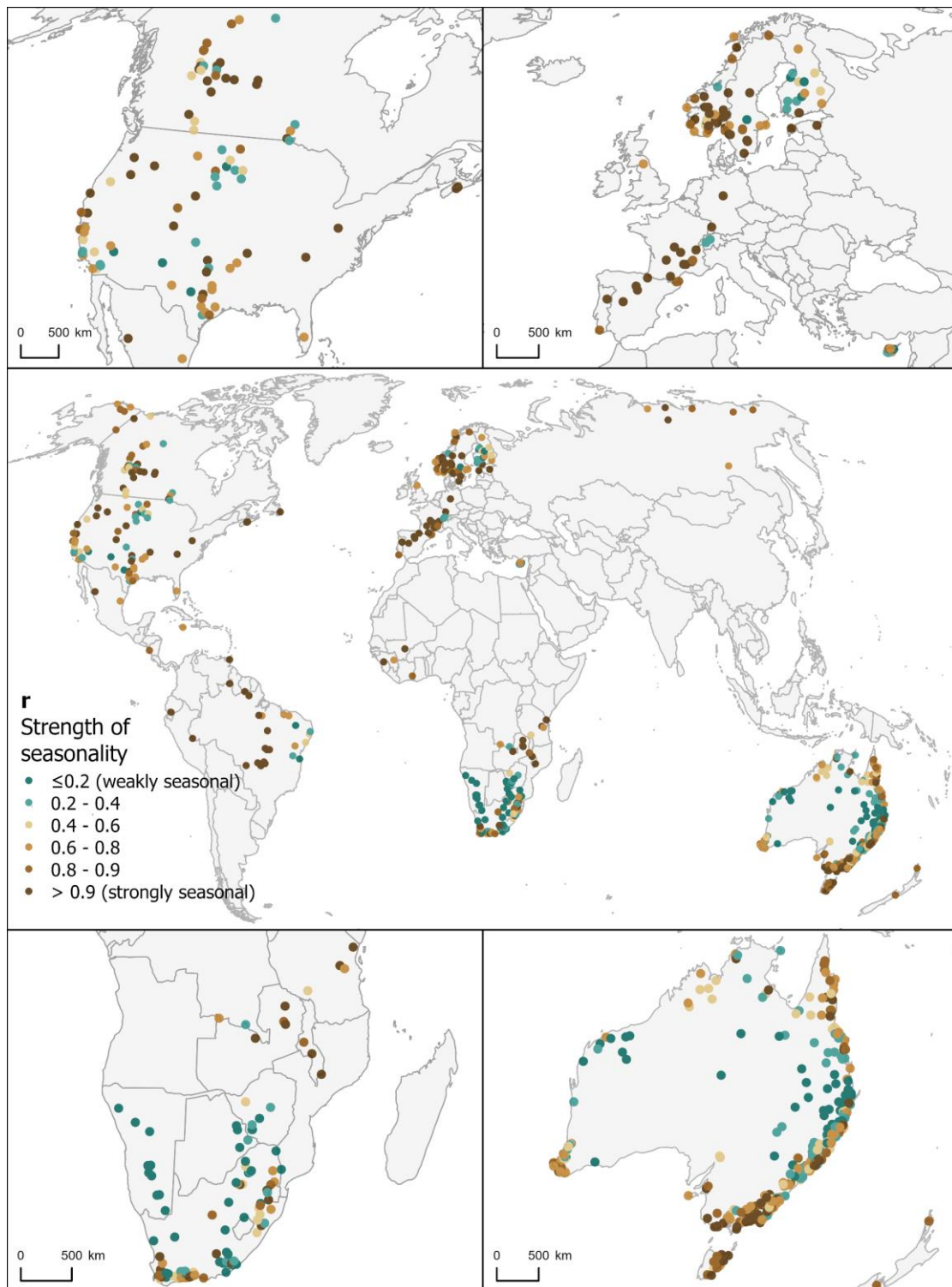


Figure 3.S7. Distribution of the dispersion in the timing of no-flow days (r) among gauging stations used in producing the global classification of flow intermittence regimes ($n=690$).

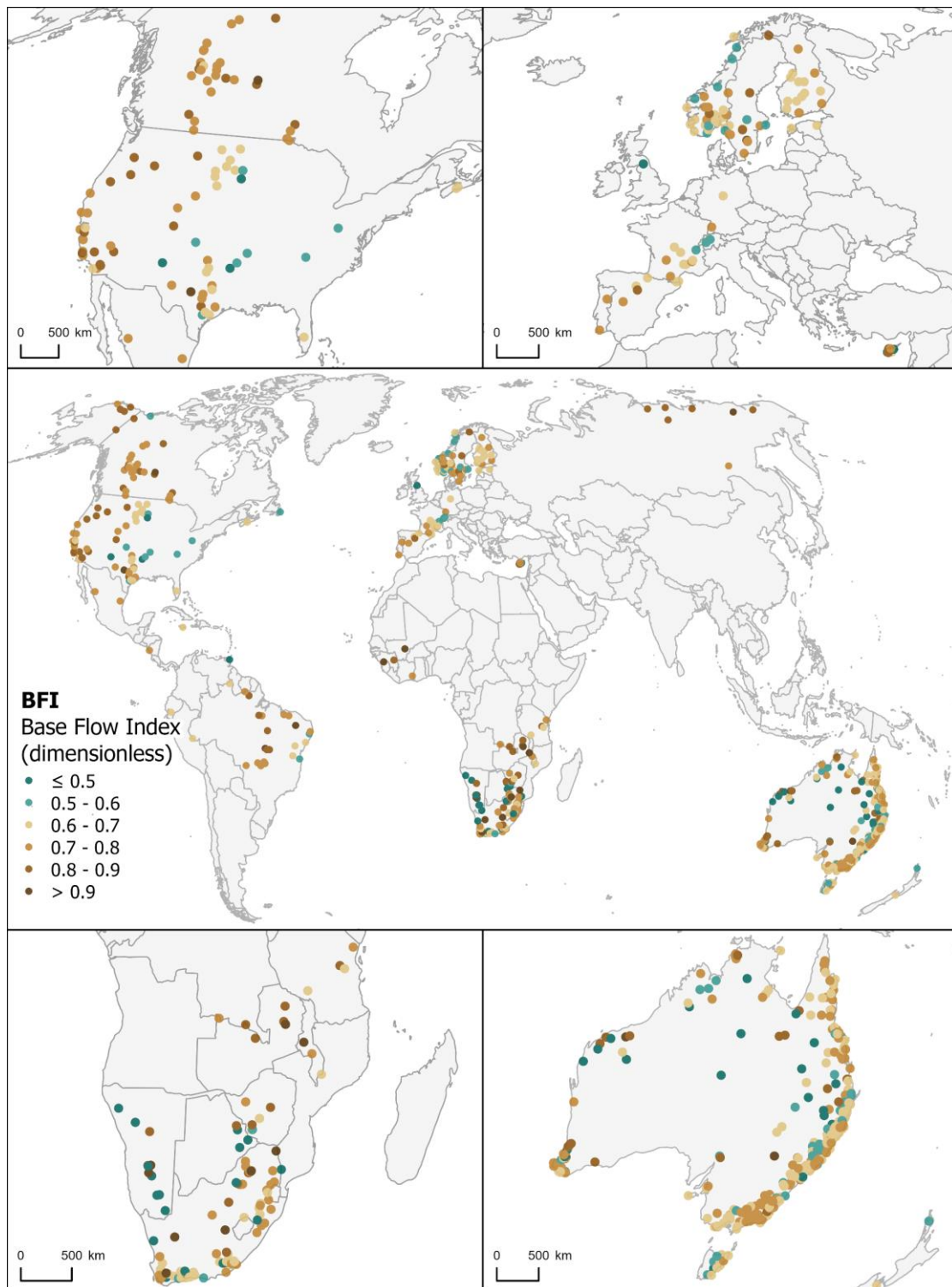


Figure 3.S8. Distribution Base Flow Index (BFI) among gauging stations used in producing the global classification of flow intermittence regimes (n=690).

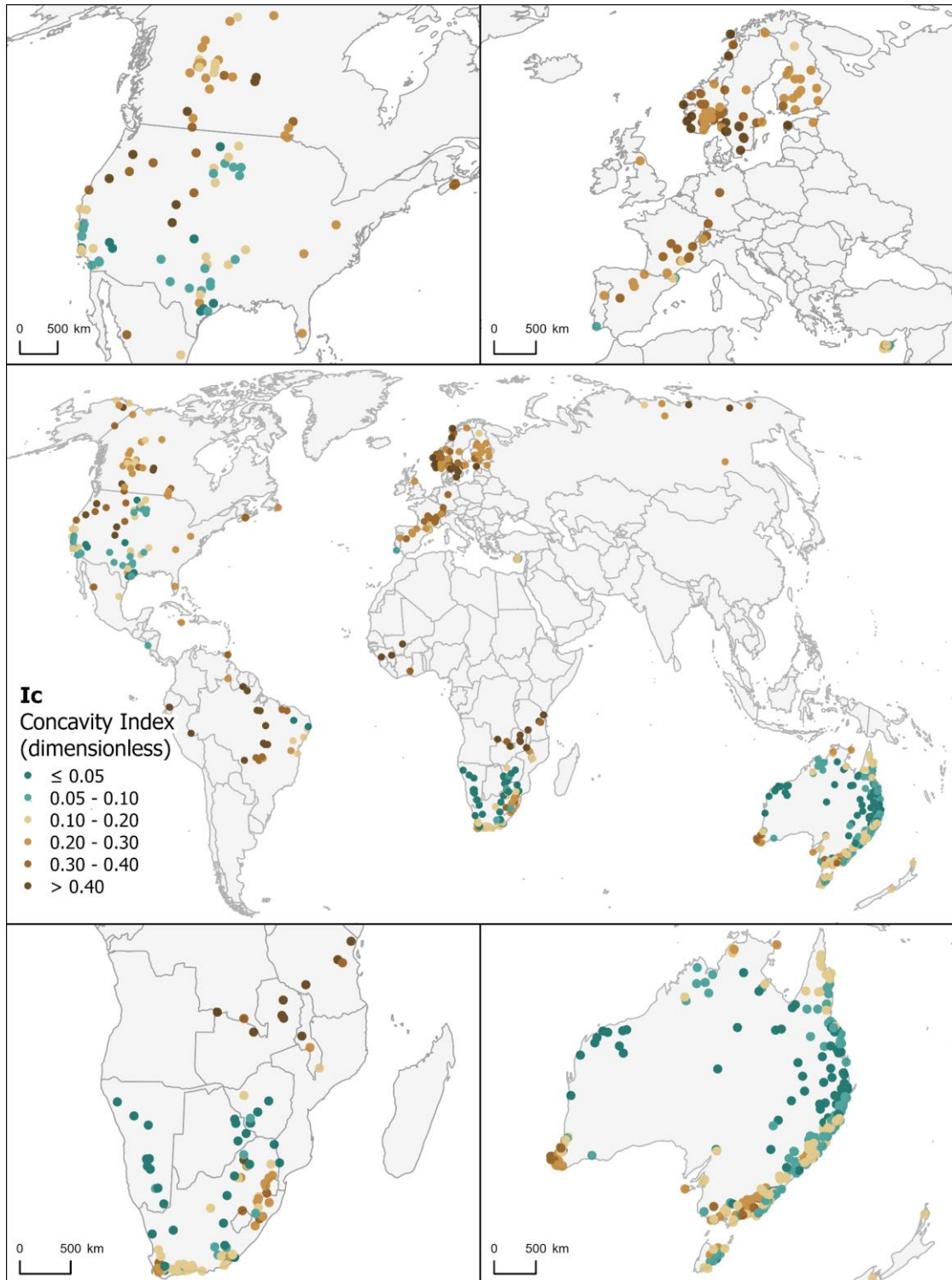


Figure 3.S9. Distribution of the concavity index (I_c) among gauging stations used in producing the global classification of flow intermittence regimes ($n=690$).

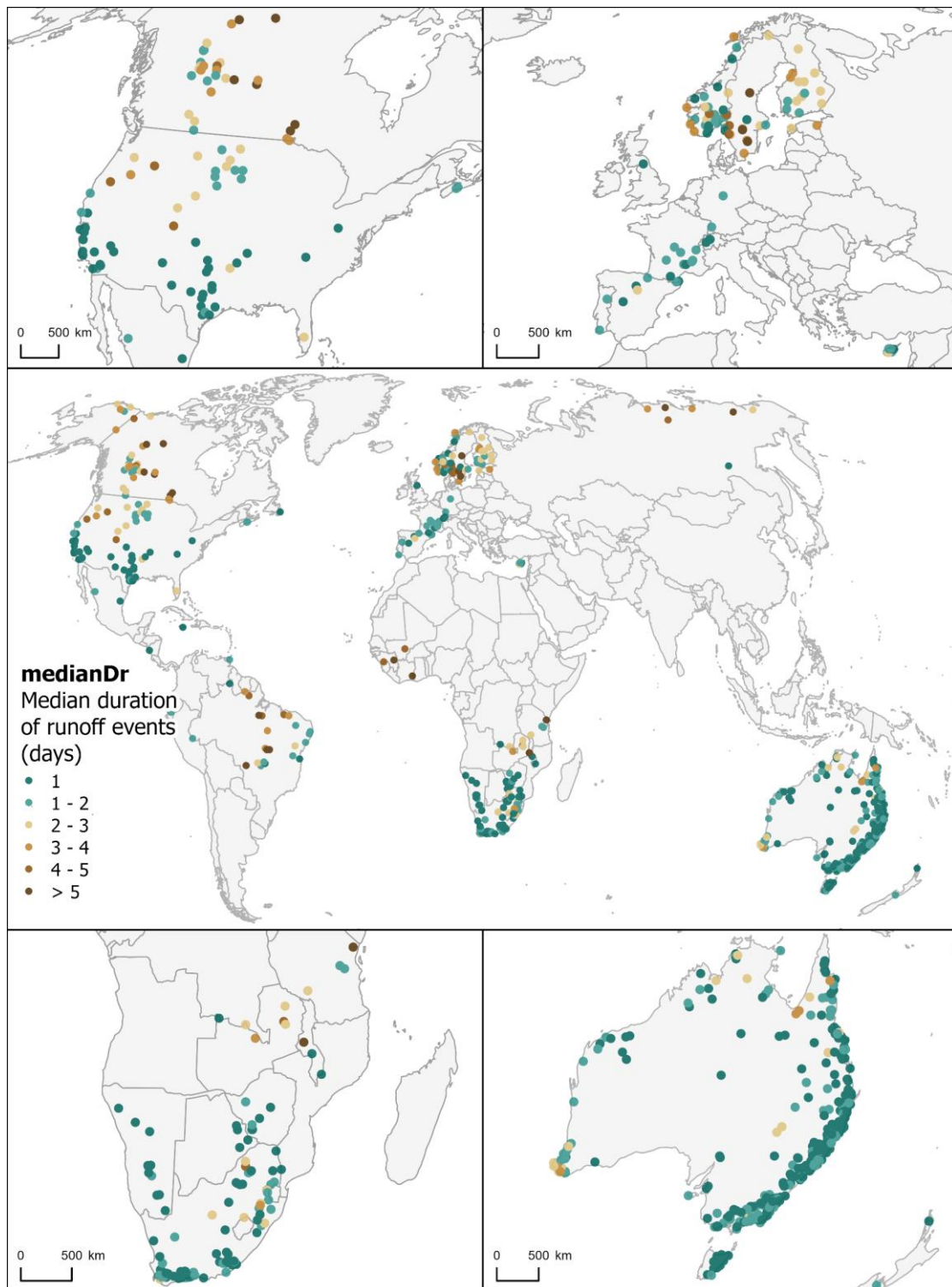


Figure 3.S10. Distribution of the median duration of runoff events (medianDr) among gauging stations used in producing the global classification of flow intermittence regimes (n=690).

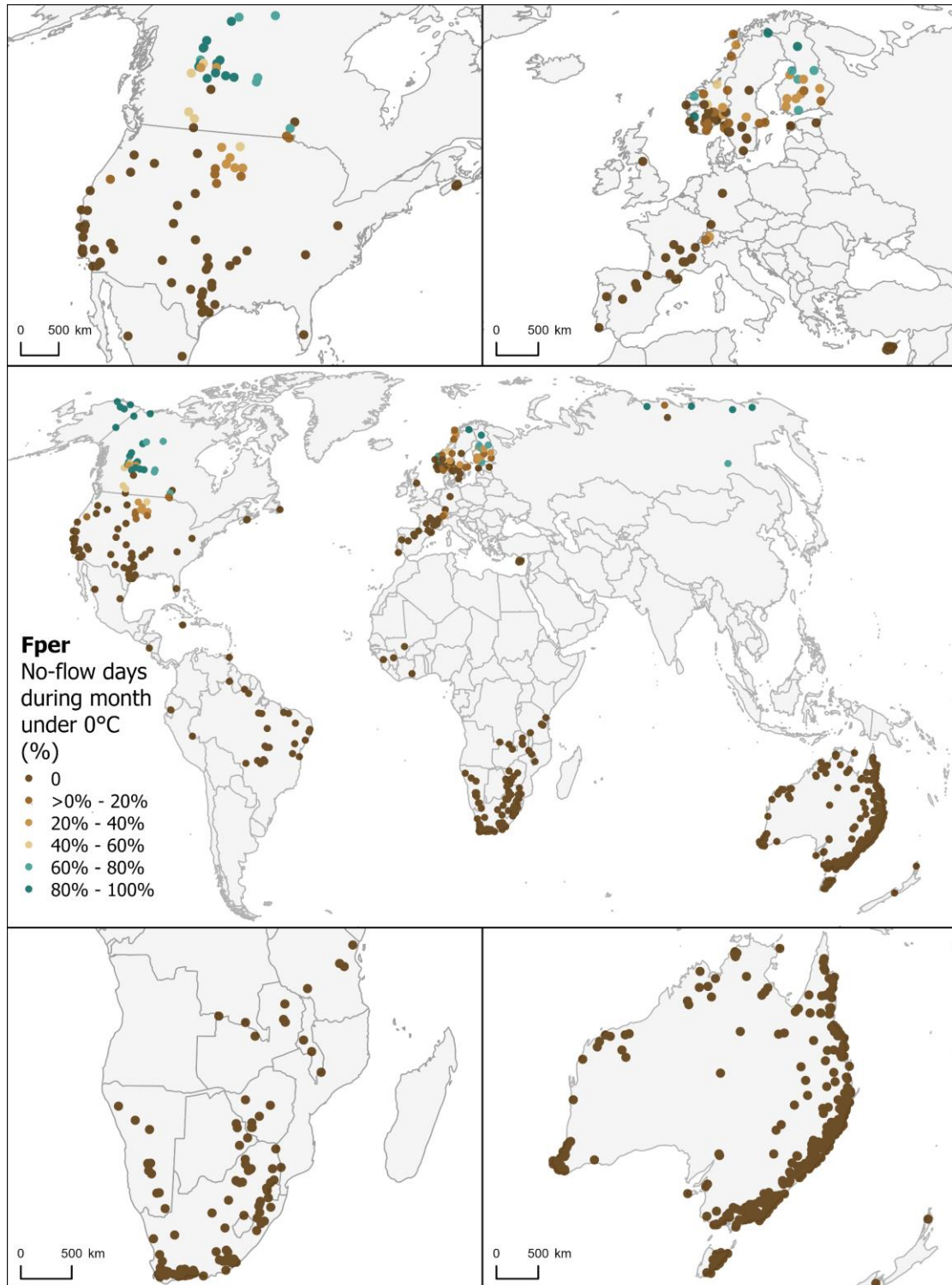


Figure 3.S11. Distribution of the percentage of no-flow days occurring during months when air temperatures do not exceed 0°C (Fper) among gauging stations used in producing the global classification of flow intermittence regimes (n=690).

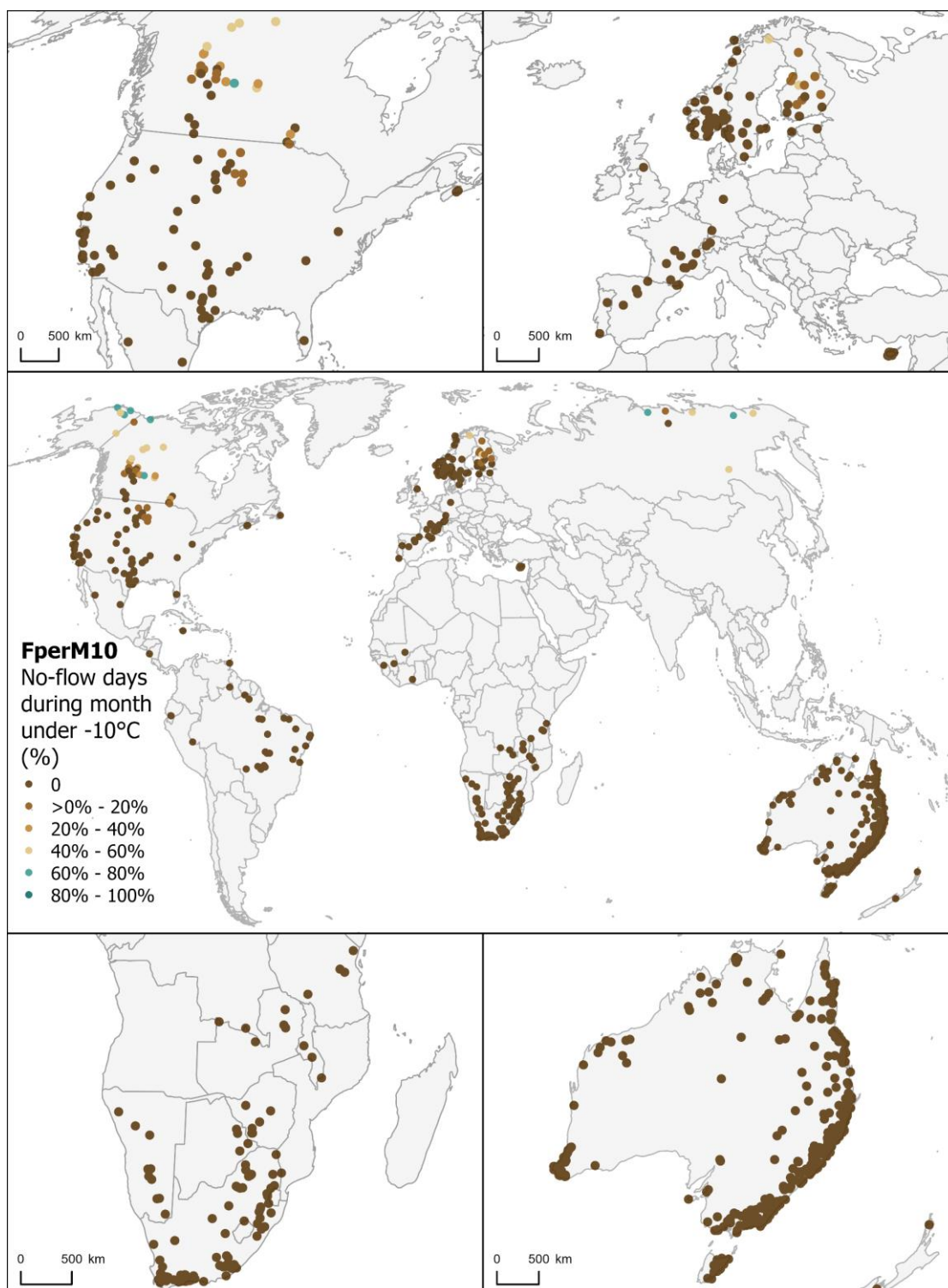


Figure 3.S12. Distribution of the percentage of no-flow days occurring during months when air temperatures do not exceed -10°C (FperM10) among gauging stations used in producing the global classification of flow intermittence regimes ($n=690$).

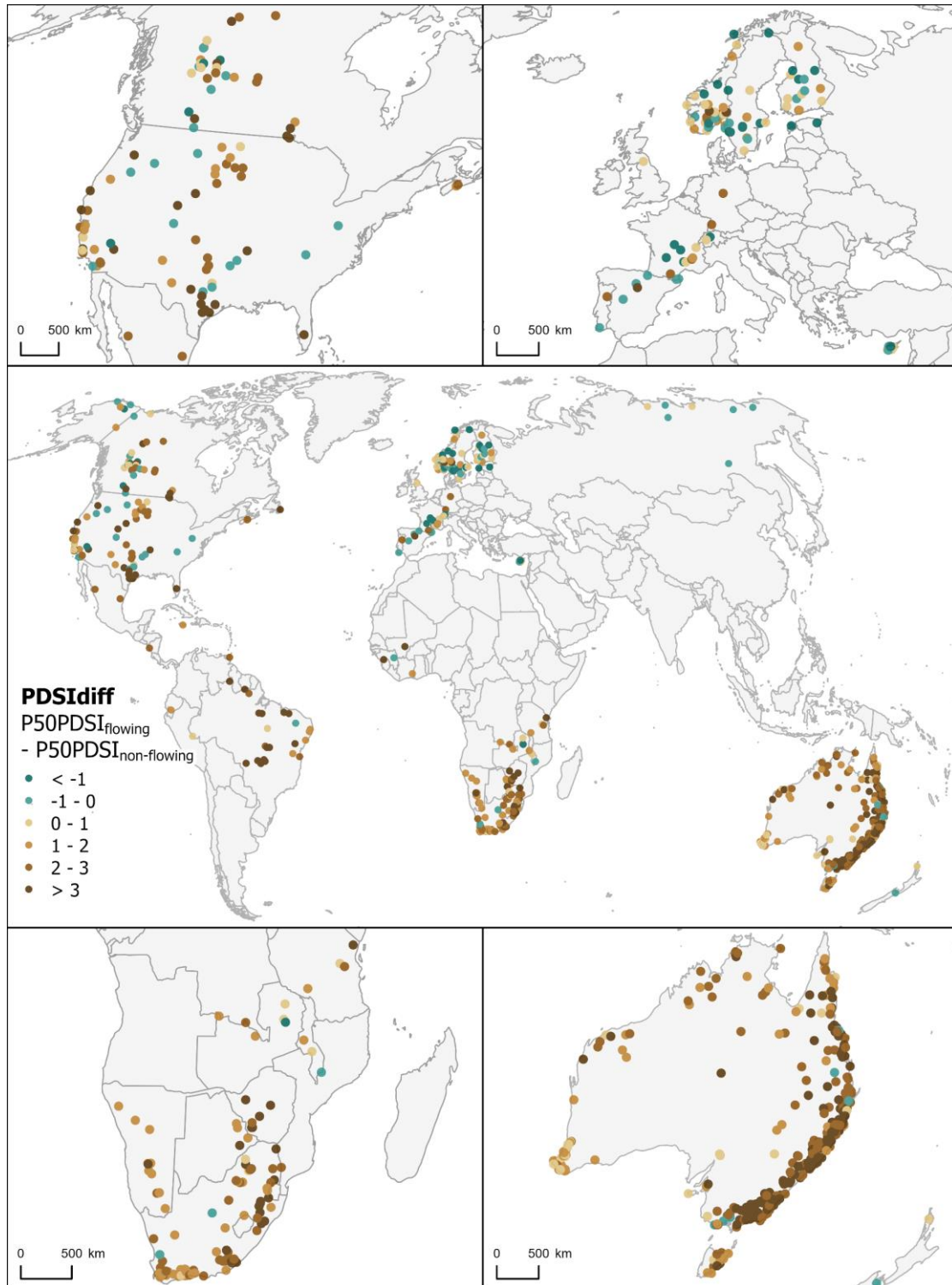


Figure 3.S13. Distribution of the difference in median Palmer Drought Severity Index (PDSI) between flow days and no-flow days among gauging stations used in producing the global classification of flow intermittence regimes (n=690).

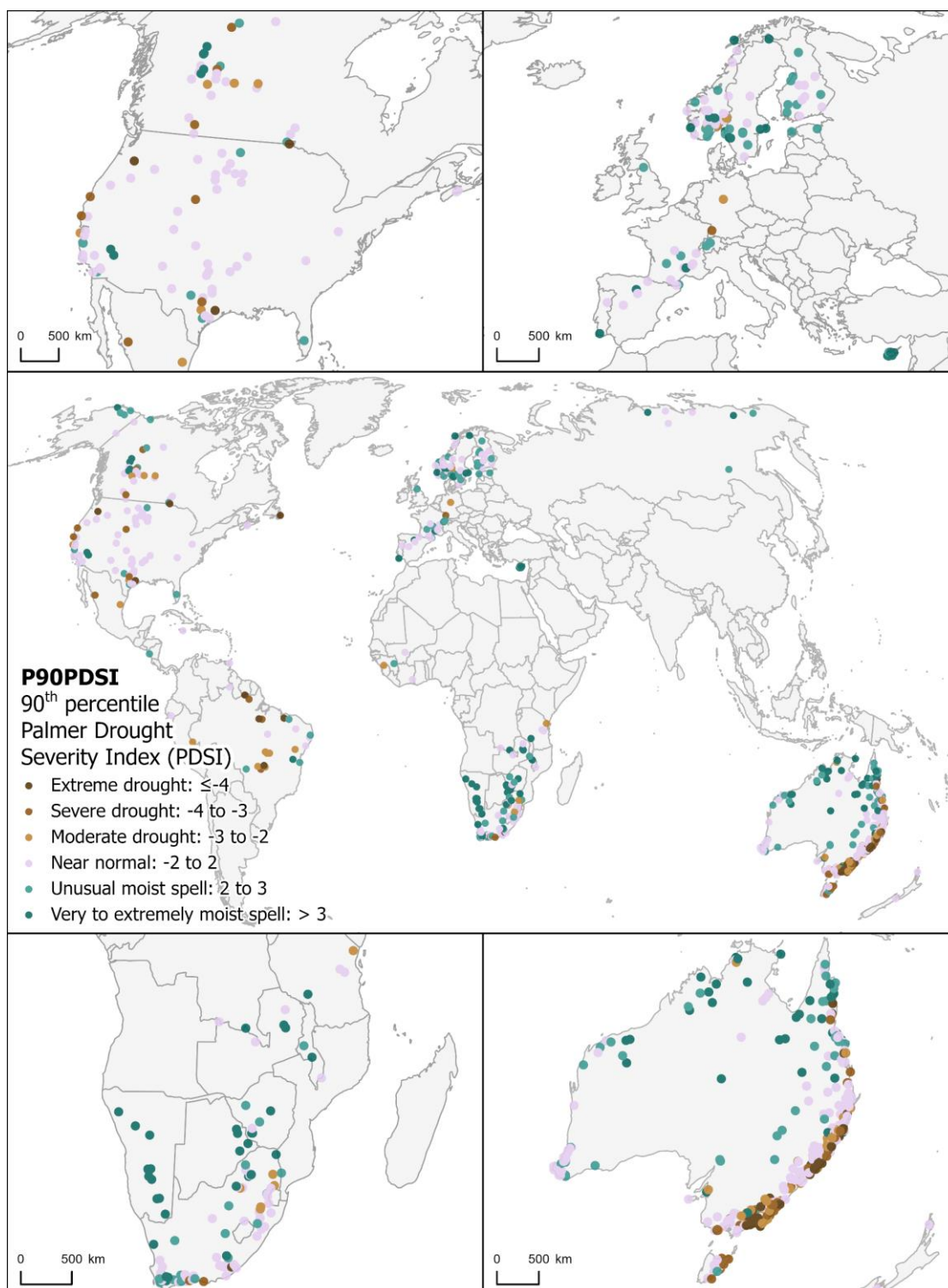


Figure 3.S14. Distribution of the 90th percentile in Palmer Drought Severity Index (PDSI) during no-flow days among gauging stations used in producing the global classification of flow intermittence regimes (n=690).

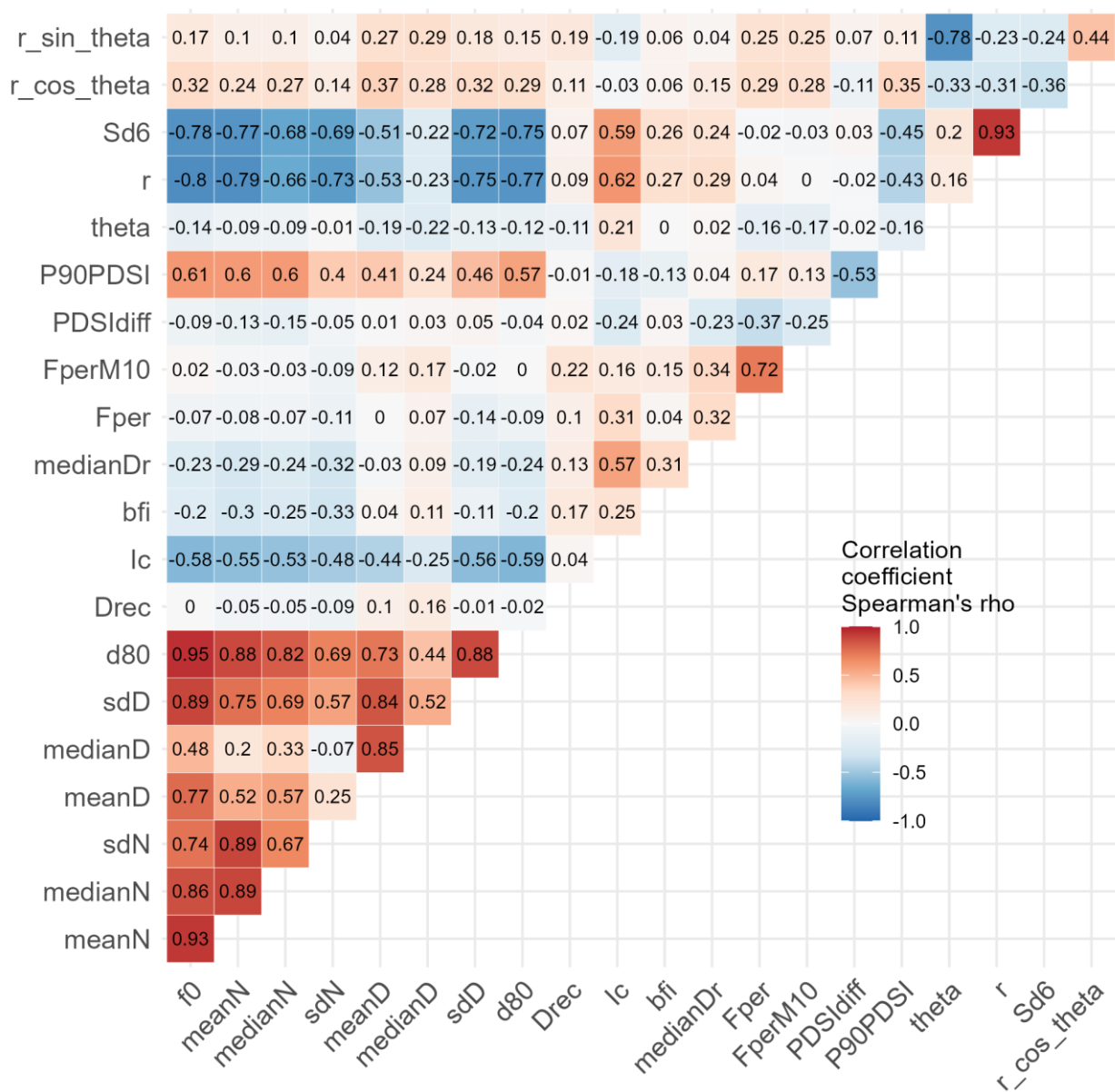


Figure 3.S15. Correlation among candidate hydrological metrics for global gauging stations used in producing the global classification of flow intermittence regimes (n=690).

3.6.3. Availability of global hydrometric data

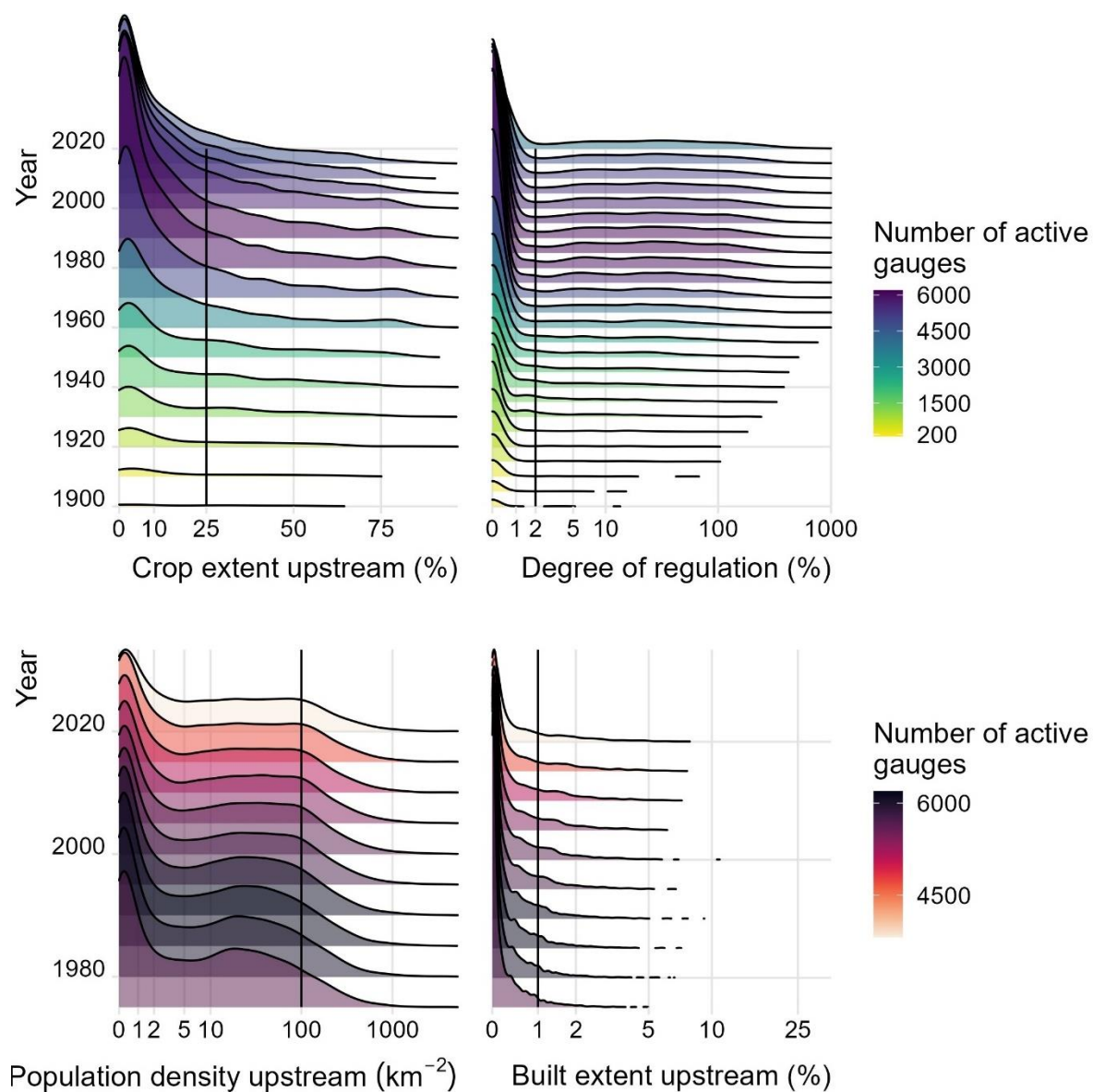


Figure 3.S16. Temporal changes in anthropogenic influences upstream of discharge gauging stations considered for inclusion in this study.

3.6.4. Global flow intermittence regimes: classification and environmental correlates

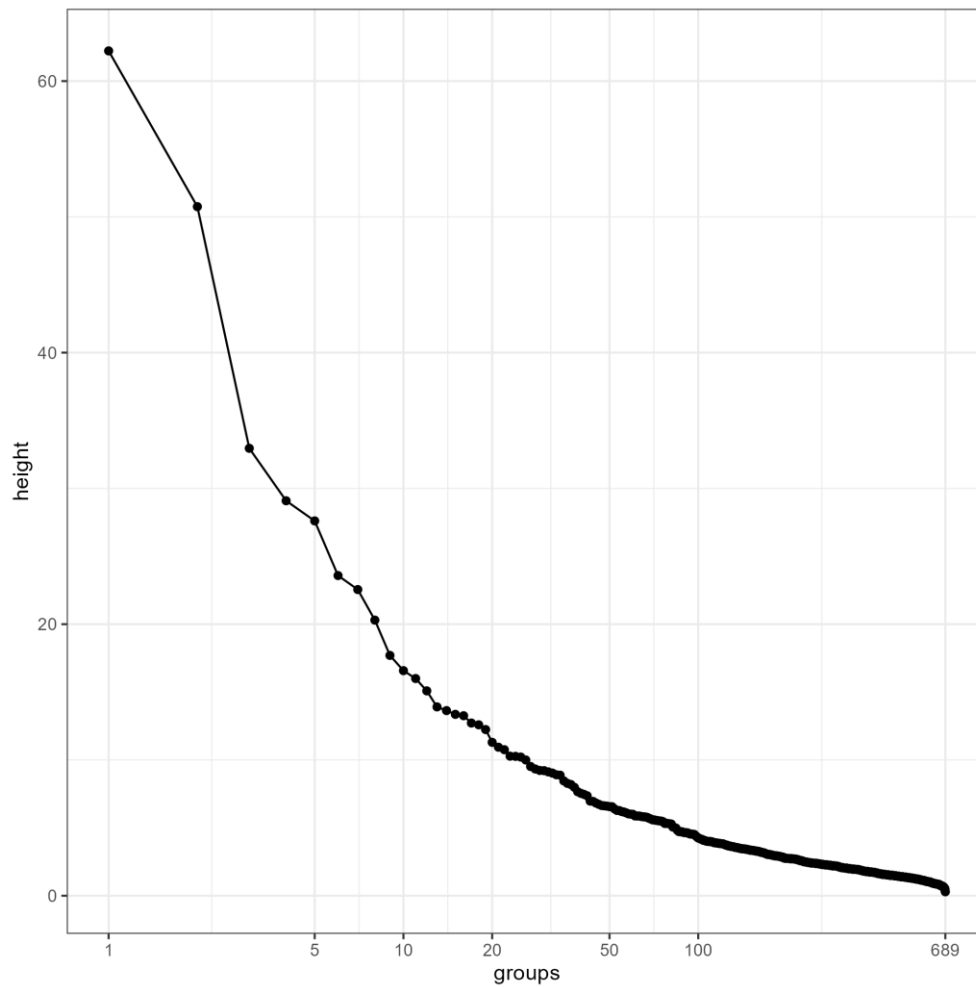


Figure 3.S17. Scree plot depicting the change in the average within-class dissimilarity (y-axis) as a function of the number of clusters (x-axis) for the classification of flow intermittence regimes.

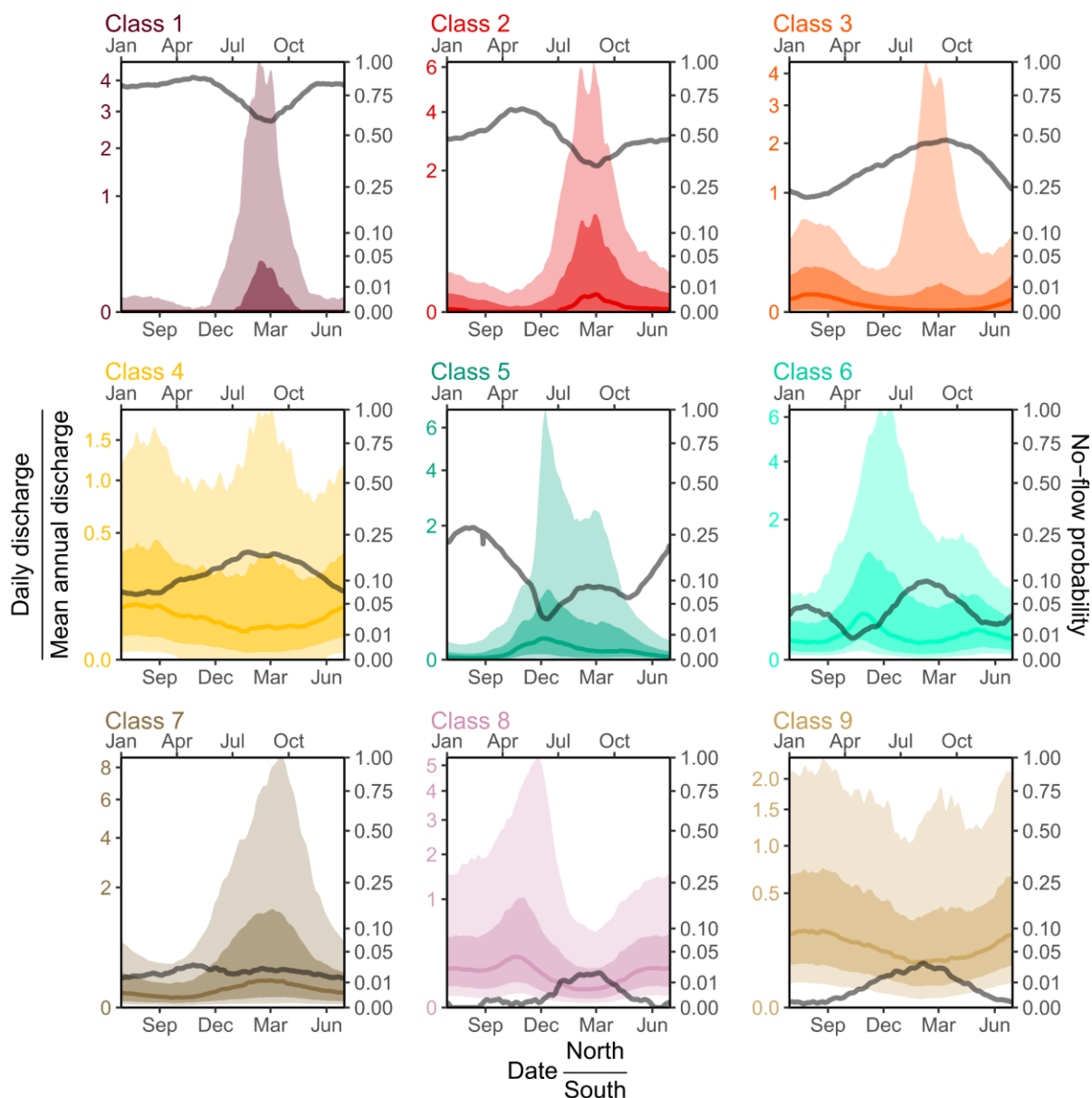


Figure 3.S18. Annual hydrographs and daily probability of flow cessation for each of the nine flow intermittence regime classes.

Standardized daily discharge (left y-axis) was calculated by first dividing each daily discharge record by the mean annual flow. Solid colored lines represent median daily values of standardized daily discharge across all gauging stations and years of data, while the dark (light) shading represents the 25th (10th; lower shading limit) and 75th (90th; upper shading limit) percentiles of standardized daily discharge. The solid black line (right y-axis) represents the daily probability of flow cessation across all gauging stations and years of data. All statistics are represented as 7-day moving averages to remove the influence of individual outliers and differences in the number of gauging stations among classes.

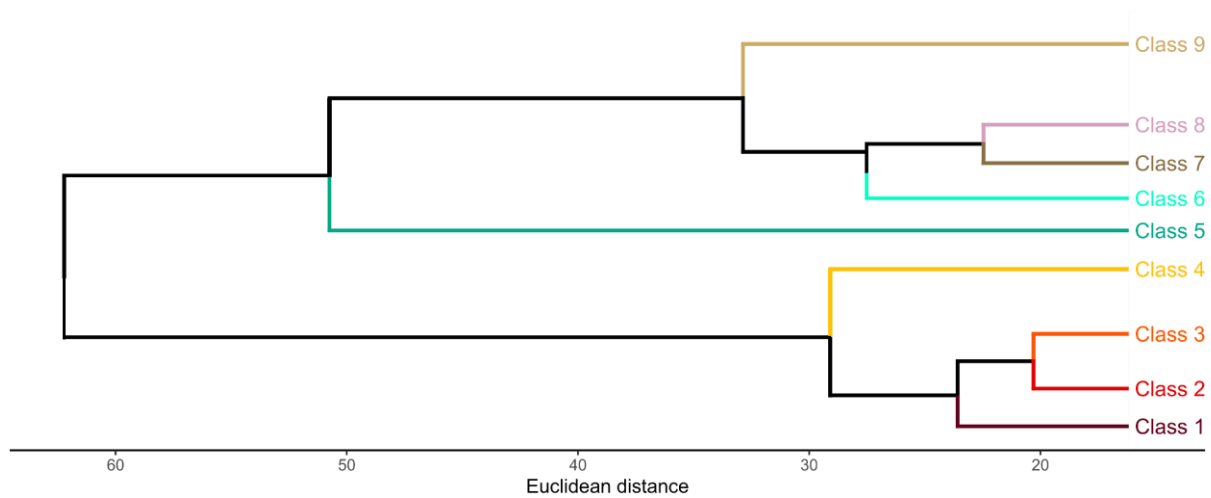


Figure 3.S19. Dendrogram depicting the nine flow intermittence regimes identified by hierarchical clustering of the 690 global gauging stations on non-perennial reaches under limited anthropogenic influence according to 14 selected hydrologic metrics. The horizontal axis of the dendrogram represents the multivariate distance between clusters according to the metrics.

3.6.5. Hydro-environmental correlates of flow intermittence regimes

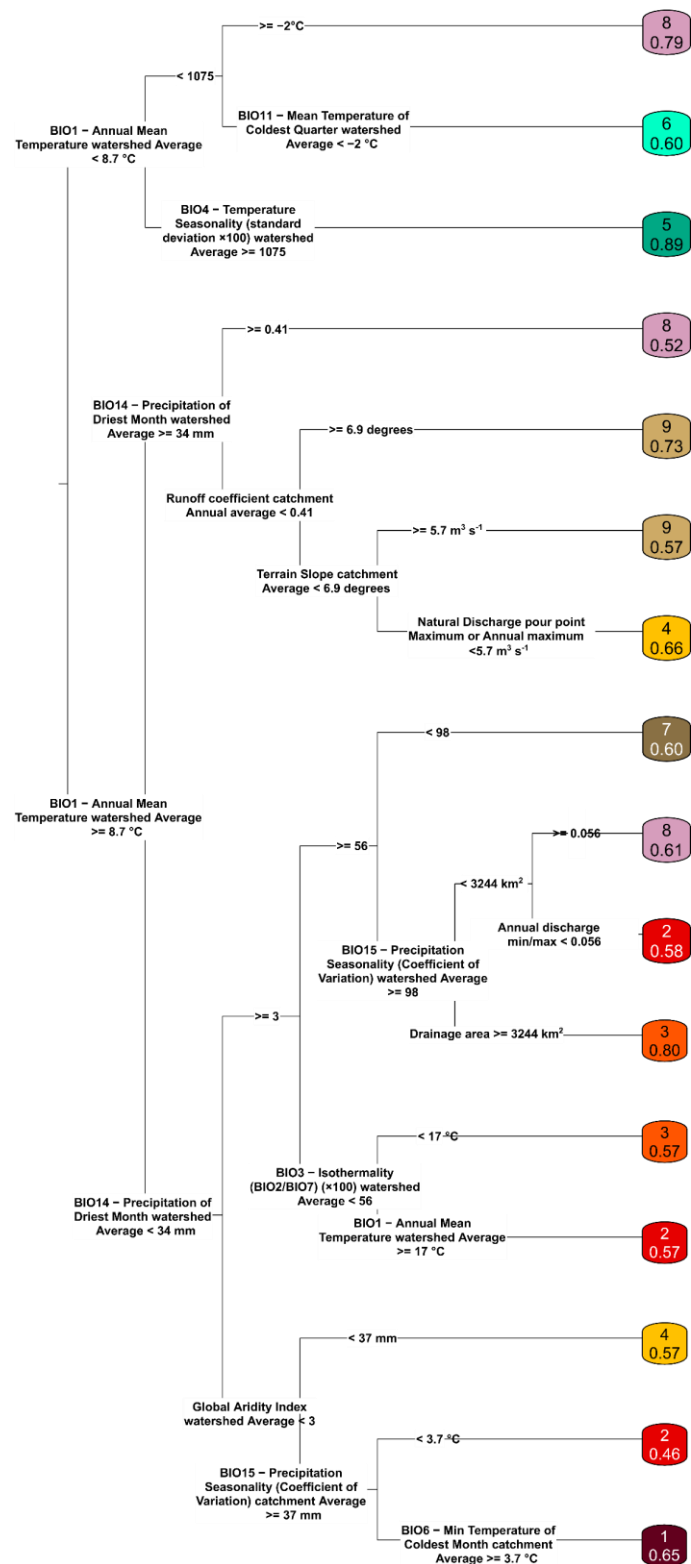


Figure 3.S20. Classification tree illustrating the hydro-environmental correlates of flow-intermittence regimes.

See Table 3.2 for a list of all candidate variables used in building the tree.

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3.8. Connecting statement Chapter 3 to Chapter 4

In the previous two chapters, I contributed to addressing the lack of a global hydrological foundation for the science and management of non-perennial rivers and streams (NPRs). However, even with data and knowledge on NPRs, a major impediment to adequate management and conservation is their uneven representation in regulatory maps defining the scope of environmental protection laws. Therefore, the objective of Chapter 4 is to evaluate the implications of legal definitions of watercourses and their interpretation through jurisdictional mapping on the degree of protection of headwater and non-perennial streams under environmental laws. Chapter 4 does not focus exclusively on NPRs and instead advocates for an integrated view of river networks. See further discussion on this topic in Chapter 6, section 6.3.2.

Chapter 4

Inconsistent regulatory mapping quietly threatens rivers and streams

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4.1. Abstract

Even the most stringent environmental law cannot protect a river if its tributaries remain exposed to pollution and other threats upstream. Excluding a subset of watercourses from legal protection therefore threatens the integrity of entire river networks and the services they provide, like drinking water and flood regulation. Considerable attention has been devoted to defining the scope of environmental laws protecting watercourses. How these legal definitions are implemented, however, has been virtually unexamined, such that an assessment of the extent of protected watercourses is lacking in nearly all countries. Here, we demonstrate the potential consequences of regulatory mapping on the integrity of river networks by assembling and analyzing the first map of France's watercourses protected under the Water Law. We estimate that about a quarter of previously mapped hydrographic segments, by length, were disqualified as non-watercourses, and found stark geographical variations in the extent of protected ecosystems. Vulnerable headwater and non-perennial reaches are overrepresented in non-watercourses by 28% compared to their prevalence (67%) in the overall hydrographic network, with far-reaching implications for biodiversity and people. We expect regulatory frameworks in most countries to be equally susceptible to local interpretation and advocate for transdisciplinary collaboration to support improved governance of watercourses.

4.2. Introduction

Rivers and streams make up the very fabric of human societies, and vice versa. Societal structures evolved from and are still entwined with river networks (Fang et al., 2018; Hein et al., 2021; Wantzen, 2022). To this day, flowing waters are essential to meet basic human needs and enable people's well-being, livelihoods and cultures (Lynch et al., 2023; Martin-Ortega et al., 2015; Wantzen et al., 2016). At the same time, rivers and streams are hybrid features of the landscape, both social and natural (Latour, 1991; Linton, 2021). No watercourse on Earth is free from the effects of climate and land use change, river regulation, channelization, water pollution or nonnative species, among other human impacts (Grill et al., 2019; Reid et al., 2019). And what people perceive as a watercourse is not just the fruit of climate or geology but also reflects local history, culture and politics (Anderson et al., 2019; Linton, 2021; Linton & Budds, 2014).

The ambiguous nature of rivers and streams is well illustrated by the protracted disputes that follow attempts to define them from a legal standpoint. For example, what water bodies are protected by the US Clean Water Act (CWA, 1972), the primary federal instrument for protecting freshwater ecosystems in the country (Walsh & Ward, 2022), still remains intensely debated half a century after its enactment. The CWA is the environmental policy that led to the most US Supreme Court cases (Zellmer, 2013), and successive changes to its jurisdictional scope have figured prominently in the scientific literature (Doyle & Bernhardt, 2011; Greenhill et al., 2024; Sullivan et al., 2020). Similar debates around the legal definition of watercourses take place across the world (Harding, 2015; Taylor & Stokes, 2007), yet the implications of these definitions and their interpretation on the effectiveness of environmental policies have not been examined.

Defining what is a watercourse involves trade-offs and can have far-reaching consequences for the integrity of freshwater ecosystems and the essential services they provide to society, including clean drinking water and flood regulation (Lynch et al., 2023). Once a linear depression legally qualifies as a watercourse, numerous activities in and around it become subject to regulation (e.g., bank modifications requiring authorizations) or banned altogether (e.g., pesticide application within a buffer). Excluding a watercourse from legal protection, on the contrary, exonerates riparian landowners and other users from most regulation. A narrow definition of watercourses hence risks exposing a large swath of river

networks to degradation, threatening the resilience of entire river networks and the people that depend on them (Lane et al., 2023; Leibowitz et al., 2018). In the US, a 2020 White House rule deregulated over a million stream kilometers and 30% of freshwater bodies around drinking-water sources (Greenhill et al., 2024). Subjecting even a limited subset of the river network to degradation can substantially impact water quality and ecosystems elsewhere in the basin. Indeed, nearly all reaches are hydrologically connected, either longitudinally with downstream flow or vertically with groundwater (Datry et al., 2023; Leibowitz et al., 2018). Being too inclusive in the definition of watercourses, on the other hand, can result in a high administrative burden on regulators and the regulated community, as well as a contested reduction in suitable land for conventional agriculture, real estate development and other intensive land uses (Sunding & Zilberman, 2002; Taylor & Stokes, 2007). To alleviate the burden associated with the European Union Water Framework Directive (WFD), for instance, member states were allowed to exclude headwater streams with a catchment area under 10 km² from their River Basin Management Plans (Kristensen & Globevnik, 2014). What legally counts as a watercourse reflects both cultural perceptions (Taylor & Stokes, 2007) and the balancing of multiple, sometimes conflictive, values ascribed to rivers and streams (Pascual et al., 2023).

Regulatory definitions of watercourses have two main elements in common across jurisdictions: the presence of an active channel of natural origin (even if subsequently modified), and flowing water at least part of the year (**Supplementary Table 4.S1**). Accordingly, human-made ditches, pipes, canals, and ephemeral streams that flow only after precipitation events, do not qualify as watercourses in most countries (Doyle & Bernhardt, 2011; Sullivan et al., 2020; Taylor & Stokes, 2007). Whether a depression is an active channel and where its upstream limit is may be debatable (Wohl, 2018), but disagreements more often arise about what “natural” means, and how often water must be present in a channel for it not to be considered ephemeral. Humans have modified water drainage directly (e.g., diversion, channelization, piping, burying, infilling) or indirectly (e.g., land-use and climate change) for hundreds to thousands of years in many regions, re-shaping entire riverscapes (Brown et al., 2018). For example, 100,000 water mills had been built along French rivers by the end of the 18th century (Barraud, 2017); 97.8% of total stream length in Denmark has been channelized (Brookes, 1987). Therefore, maps of the pre-transformation “natural” hydrography of most regions do not exist and, regardless, would give an erroneously static

view of continuously shifting landscapes (Brown et al., 2018). Furthermore, every river network includes intermittent and ephemeral reaches (Datry et al., 2023) that provide valuable ecosystem services, but most are undifferentiated, miscategorized or absent on topographic maps (Drummond, 1974; Fesenmyer et al., 2021; Fritz et al., 2013).

Consequently, ascertaining whether a watercourse is intermittent or ephemeral requires field visits to observe flow multiple days after the last rainfall during a wet period of the year (Ducasse et al., 2017; though proxies of flow duration are commonly used, e.g., Fritz et al., 2008). In short, both criteria — of naturalness and flow permanence — leave room for interpretation and often require a field visit.

In France, jurisdictional mapping of watercourses has taken a new turn that uniquely reveals the socio-political nature of hydrography. What characterizes a watercourse in the eyes of the Water Law was undefined until recently. Only in 2015 did a government directive provide a formal definition (Instruction du Gouvernement du 3 Juin 2015 relative à la cartographie et l'identification des cours d'eau et à leur entretien; translated in **Supplementary Methods 4.6.1**), now legally inscribed in the French Environmental Code. This codification was meant to appease rising tensions between water law enforcement, farmers, municipalities, and environmental organizations that frequently led to court cases and appeals, with overlapping and sometimes contradictory rulings (de La Croix et al., 2020; Ducasse et al., 2017). Beyond defining watercourses, the 2015 directive tasked decentralized government authorities of the second smallest administrative division level in France (departments) to draw comprehensive maps of watercourses across their jurisdiction. Based on the newly minted national definition, each department was to devise and implement a mapping protocol in collaboration with local stakeholders to differentiate watercourses from ditches, canals and ephemeral streams. The objective of this decentralized process was to promote a local “pragmatic” approach ensuring stakeholder buy-in and addressing variations in geography, climate and water uses among. Since then, multiple governmental and journalistic reports have anecdotally mentioned large portions of the river network being disqualified as non-watercourses in some departments (Cinotti & Dufour, 2019; Morenas & Prud'homme, 2018). However, departmental maps of watercourses have never been merged, including by the national government, such that no national map exists and a comprehensive assessment of the implications of this cartography is still lacking.

The aim of this study was to evaluate the implications of the legal definition and decentralized mapping of watercourses in France on the integrity of river networks through cartographic analyses. We present the first map of watercourses that fall under the Water Law and quantitatively show that the associated mapping strategy led to inconsistent mapping of watercourses with potentially deleterious consequences for river network integrity. We then compare our findings to analyses conducted in the US and advocate for research in other countries to examine the implementation of regulatory frameworks for watercourse protection and its implications for ecosystem and human health.

4.3. Materials and Methods

4.3.1. Overview

To assemble a national map of watercourses that fall under the Water Law, we first gathered and harmonized maps from all departments in mainland France except for the Paris region. We then assessed the consistency of the watercourse maps among and within departments by comparing the length of watercourses mapped per unit area (i.e., drainage density) in these maps to the main hydrographic basis used by departments for mapping watercourses. We also evaluated whether this relative drainage density was correlated with various socio-environmental factors, including anthropogenic land covers (e.g., agriculture, impervious area), irrigation, population density, barrier density, soil texture, slope, and aridity (see **Supplementary Table 4.S2** for data sources). Finally, we assessed the potential implications of the maps for the effectiveness of the Water Law in protecting the integrity of river networks across France, with particular emphasis on headwater and non-perennial streams and network connectivity. We provide a detailed description of every step of the analysis in **Supplementary Methods 4.6.2 to 4.6.9**.

The 2015 government directive established general guidelines to frame departments' mapping protocols (see **Supplementary Methods 4.6.1** for a translation). First, departments compiled existing sources of hydrographic data and identified watercourses whose status was either obvious (e.g., major rivers and tributaries) or consensual (e.g., established through other regulations). Then, they determined which remaining uncategorized hydrographic segment qualified as a watercourse — this process is still ongoing in many departments. A body of flowing water legally qualifies as a watercourse if it meets three criteria: 1. having a channel of natural origin (i.e., even if subsequently modified), 2. being

fed by a source other than precipitation alone, and 3. carrying “sufficient flow most of the year” —flow can be intermittent, considering local hydroclimatic conditions (**Supplementary Table 4.S1**). Departments used cartographic methods and field visits to evaluate these criteria, often in collaboration with governmental agencies and stakeholders. Mapping usually progressed in regular consultation with stakeholders to validate and publicize intermediate maps. Legal action cannot be taken against the resulting maps, but requests can be made to verify or edit them.

In this study, we refer to watercourses as those rivers and streams protected under the Water Law (“police de l'eau”), whose scope differs from several other laws regulating flowing waters in France (**Supplementary Table 4.S1**). Nonetheless, this new cartography will eventually replace or complement the maps used to enforce several other laws. Furthermore, we use the term “department” for both the administrative body and the geographic extent of a department.

4.3.2. Assembling the first national map of watercourses under the Water Law

We compiled and harmonized 90 individual watercourse maps in the form of GIS vector layers produced by the cartographic service of each department across mainland France (**Figure 4.1**). As of November 2023, all departments but one provided a map of watercourses online, and 74 (79%) provided online access to underlying data; 20 fully excluded non-watercourses from the maps. Therefore, we individually contacted departments to either request the entire dataset (if it was unavailable online), only excluded segments, or to confirm the currency of the dataset. We then quality-controlled, harmonized, and merged all datasets.

4.3.3. Comparison with other river networks and sources of data

We assessed the consistency of the watercourse maps among and within departments by comparing the length of watercourses mapped per unit area (i.e., drainage density) in these maps to BD TOPO 2015 (version 151; Institut national de l'information géographique et forestière, 2015). BD TOPO was the main hydrographic basis used by departments for mapping watercourses and for our analysis; it is the most detailed vector-based representation (as opposed to scanned topographic maps) of the French hydrographic network. We quantified the difference in drainage density between the departmental

watercourse maps and BD TOPO as the ratio in drainage density between the two. We focused on this drainage density ratio (DDR) because 36 (40%) departments provided either no or partial data on non-watercourses (i.e., some or all hydrographic segments present on source maps deemed not to qualify as watercourses were removed from the resulting jurisdictional map rather than labeled as “non-watercourse”) and because drainage density naturally varies among regions (Luo et al., 2016), so we did not expect constant drainage densities across and within departments. DDR also provides a scale-agnostic metric to compare departments or sub-basins regardless of differences in total network length —thus representing a measure of deviation rather than absolute network length. We conservatively assumed in our main results that uncategorized segments by DDTs would be considered as watercourses. To understand variations in DDR at multiple scales, we analysed DDR both across departments (average area: $6 \times 10^3 \text{ km}^2$) and among consistently sized sub-basins within departments (average area: 67 km^2).

4.3.4. Analyzing socio-environmental correlates of drainage density ratio

We quantified the relationships between DDR and socio-environmental factors with regression models at our two scales of analysis: among departments, and among sub-basins within departments (**Supplementary Methods 4.6.7 and 4.6.8**). Within departments, we first extracted 20 variables for each sub-basin (**Supplementary Table 4.S2**) and computed Spearman’s correlation between DDR and every variable. Departments were then clustered based on their multivariate similarity in terms of Spearman’s coefficients (**Supplementary Figure 4.S1**). Finally, we developed a linear regression model for each cluster to quantify differences in regression coefficients between departments of the same cluster, and in correlated variables among clusters.

4.3.5. Evaluating implications for river network integrity

We analyzed the potential impacts of excluding segments from watercourse maps on the integrity of river networks in two ways. First, we estimated the proportion of headwater and non-perennial reaches excluded from maps. Here, we define headwater reaches as hydrographic segments of Strahler order one (i.e., first-order reaches). Substantial processing was required to conduct these analyses and some uncertainty remains about those results; see **Supplementary Methods 4.6.2 to 4.6.5** for the detailed description of this analysis. Second, we analyzed potential network fragmentation resulting from non-

watercourses and uncategorized segments by identifying individual segments surrounded by other segments of a different category — for example, watercourses surrounded by non-watercourses (i.e., isolated segments), or non-watercourses surrounded by watercourses (i.e., fragmenting segments). Due to the limitations of the geometric networks in terms of missing non-watercourse data and topology (see **Supplementary Methods 4.6.5**), this analysis was possible for only a subset of the segments.

4.4. Results and Discussion

4.4.1. A complete yet inconsistent map of watercourses

The cartography of watercourses in France represents a monumental undertaking by departments. As of 2023, the national map of watercourses covers 93% of mainland France and includes 2.2 million segments totalling 6.8×10^5 kilometres (**Figure 4.1**). As a comparison, the global river network HydroRIVERS (Linke et al., 2019) includes 6.2 million segments. Although most hydrographic segments were classified through cartographic analysis, the amount of field expertise required to follow governmental guidelines was substantial (**Supplementary Methods 4.6.1**)— in one department alone, over 55,000 segments were expertized through field visits.

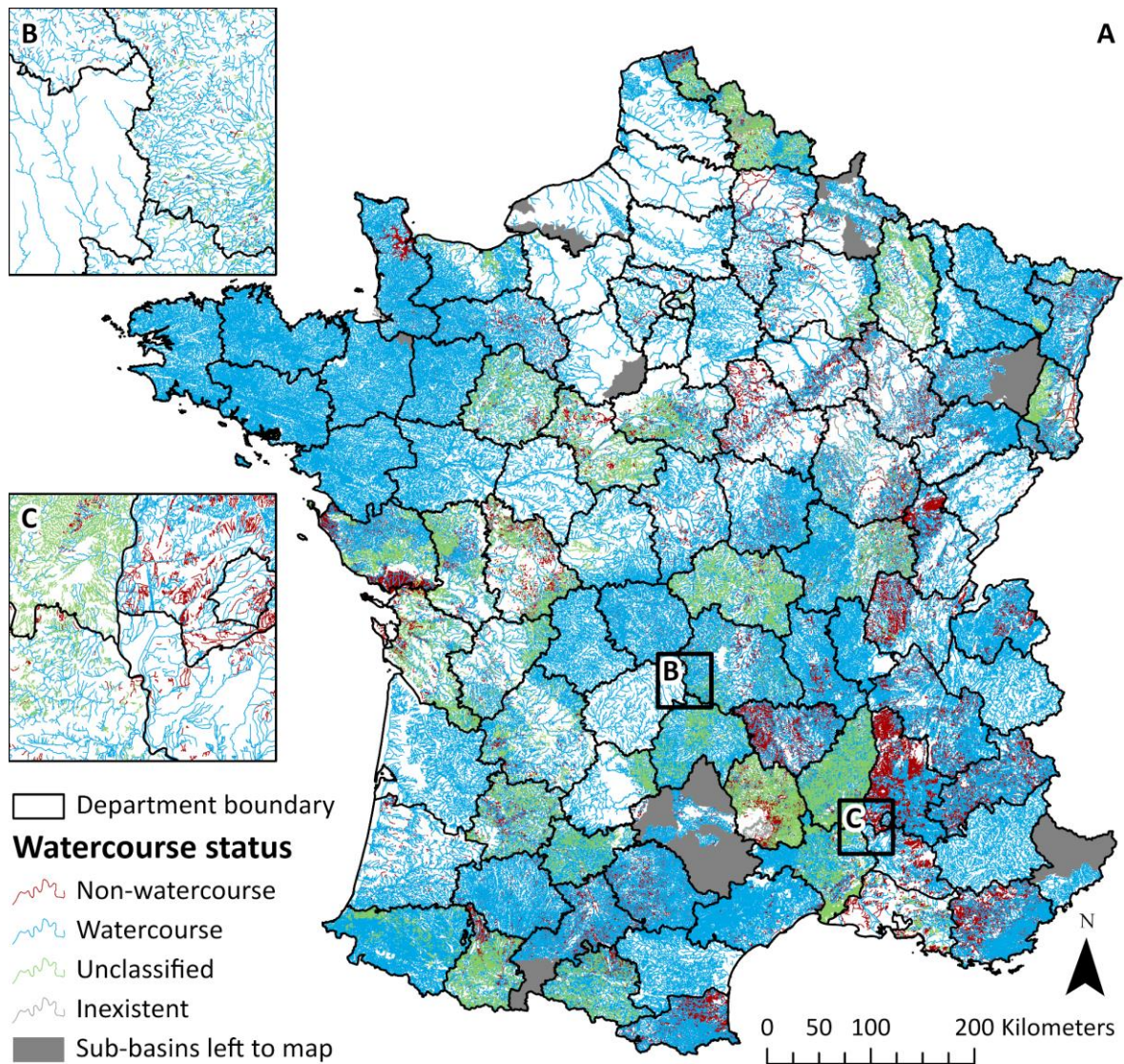


Figure 4.1. National map of watercourses protected under the Water Law in mainland France as of 2023.

The insets (B and C) are illustrative cases of discontinuities in drainage density or watercourse status distribution across neighboring departments. Grey areas show sub-basins where the status of watercourses is either still actively being assessed by departments or individually determined only upon request by a stakeholder.

Despite the apparent comprehensiveness of the map, our assessment reveals diverse and inconsistent interpretations across France of the same definition of watercourses (**Figure 4.2**). We estimate that about a quarter of previously mapped hydrographic segments, by length, were disqualified as non-watercourses (based on an assessment spanning 84% of the country's area; **Table 4.1**; **Supplementary Methods 4.6.9**). DDR varied considerably, both between departments (mean departmental DDR $\pm$ SD = 0.82 ± 0.26) and within a given department (average range in DDR among sub-basins within a department $\pm$ SD range = 1.24 ± 1.54 ; excluding sub-basins under 10 km²; **Figure 4.2**). Neighboring departments could have starkly different drainage densities (**Figure 4.1B-C**). Eighteen departments were particularly

inclusive and complemented BD TOPO with alternative sources of hydrographic data in mapping watercourses, so that their department-wide drainage density exceeded that of BD TOPO. By contrast, 15 departmental maps exhibited a DDR under 0.5, indicating that vast swaths of the hydrographic network were disqualified as non-watercourses.

Table 4.1. Summary statistics of watercourse maps by Strahler stream order (SO) based on a subset of 68 departments with sufficient data (spanning 84% of the country's mapped area).

SO	Length (10 ³ km %)				% length w flow regime	Representativeness among non-watercourses	
	Total analyzed	Non- watercourses	Non- perennial			Stream order	Non-perennial
1	270	83.0 31%	188 80%		87%	1.3	1.1
2	113	21.0 19%	69 65%		94%	0.8	1.3
3	47	4.5 10%	20 43%		97%	0.4	1.8
4	17	0.8 5%	4 25%		98%	0.2	2.3
5	3	0.1 4%	0.5 16%		99%	0.2	3.2
NA	190	38.0 20%	62 35%		94%	0.9	1.5
Total	639	147 23%	344 59%		91%	1.0	1.3

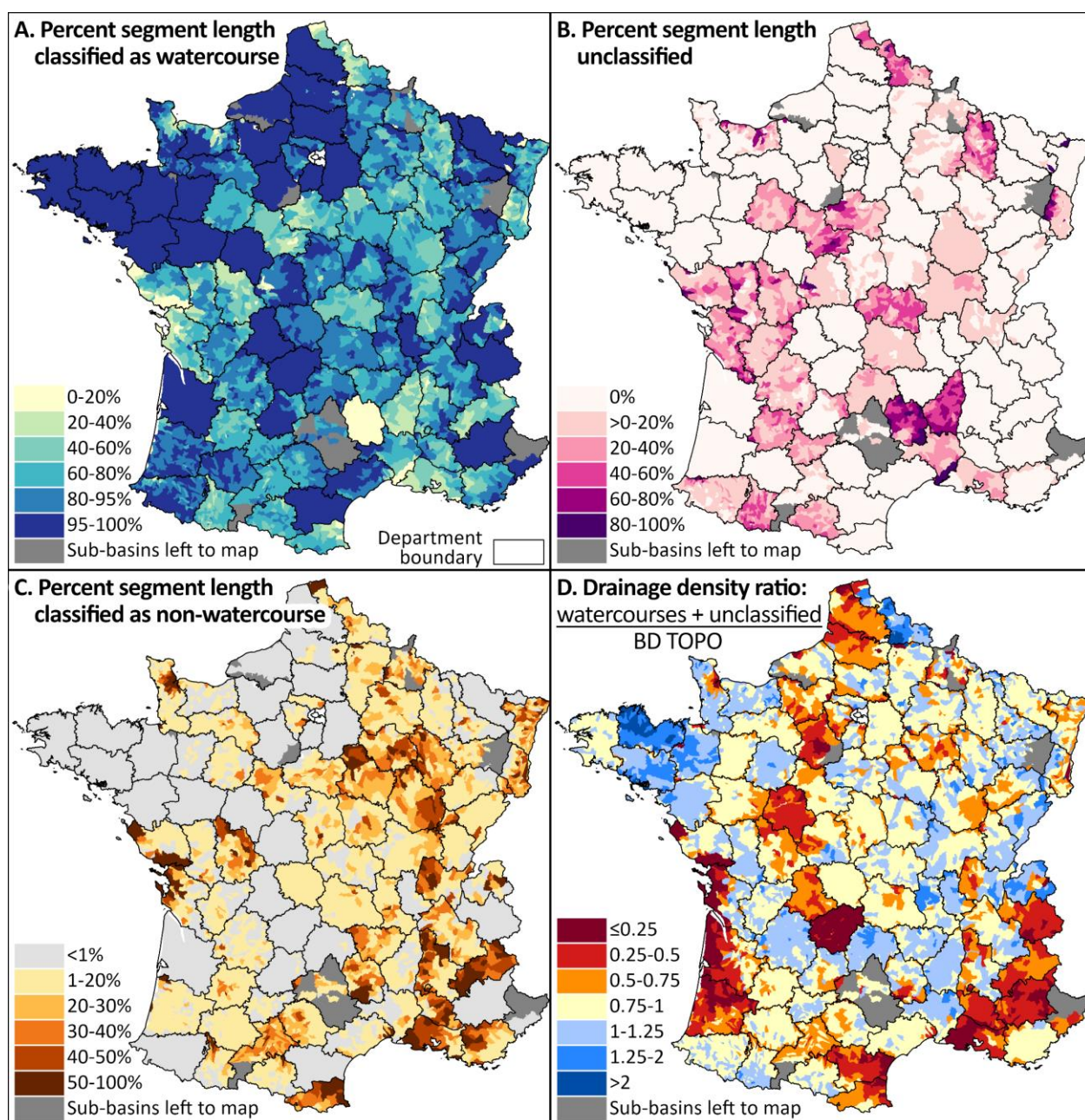


Figure 4.2. Relative prevalence of categories in departmental maps of watercourses under the Water Law in France (A-C) and drainage density ratio (DDR; D) between the watercourse maps and reference hydrographic data from BD TOPO.

Statistics are mapped by sub-basin; the average area of sub-basins (after intersection with departments) is 67 km². DDR was computed assuming that unclassified segments in watercourse maps would by default be considered watercourses unless otherwise expertized.

4.4.2. Correlates of drainage density daylight uneven mapping criteria

Whereas differences in DDR among departments were weakly correlated ($|\text{Spearman's } \rho| \leq 0.4$) to socioenvironmental variables (**Supplementary Table 4.S3**), within-department differences in DDR (i.e., among sub-basins) were moderately to strongly correlated to several socioenvironmental factors (**Supplementary Figure 4.S1**). A common pattern was for DDR to be lower in drier basins with greater cultivated cover (**Supplementary Figures 4.S1-4.S3, Supplementary Table 4.S4**). The extent of winter crops (straw cereal and winter and spring oilseeds), in particular, was commonly associated with lower DDR. Those relationships significantly varied among departments, however, further demonstrating that the official criteria defining watercourses were unevenly implemented across the country. Moreover, there was limited geographic clustering in which factors were associated with DDR variations across France (**Supplementary Figure 4.S2**).

4.4.3. Hydrography is social and political

The mapping of watercourses over the past decade in France is remarkable for being decentralized and consultative, at least in theory. This approach aimed to smooth relationships between government agencies and stakeholders by including local expertise and establishing a common knowledge base of hydrographic features subject to regulation (Instruction du Gouvernement du 3 Juin 2015 relative à la cartographie et l'identification des cours d'eau et à leur entretien, 2015). In many departments, the resulting maps reflect a massive cartographic and consensus-building effort on the part of multiple stakeholders. However, the consultation process has been tense and polarizing in other departments (Cinotti & Dufour, 2019; de La Croix et al., 2020), and the amount of fieldwork required to diligently assess the criteria for identifying watercourses was not equally realistic across departments considering their respective resources. Unfortunately, the national outcome therefore lacks coherence, reflecting stark differences in the implementation of the definition of watercourses with potentially deleterious consequences. Considering the strong documented mobilization of farmers' unions in this mapping process, the tendency for fewer hydrographic features to qualify as watercourses in basins with greater agricultural cover may partly be the outcome of power asymmetries in consultation committees (Cinotti & Dufour, 2019; de La Croix et al., 2020; Morenas & Prud'homme, 2018).

Recent decades have witnessed a growing scholarly recognition of the intricate relations between humans and water (Anderson et al., 2019; Dunham et al., 2018; Hein et al., 2021; Linton, 2021; Linton & Budds, 2014) and, more broadly, an awareness of the hydro-social cycle, the “socio-natural process by which water and society make and remake each other over space and time” (Linton & Budds, 2014). Based on our analysis, we argue that the regulatory definition and mapping of watercourses, in France and elsewhere (**Supplementary Table 4.S1**), is a striking illustration of this cyclicity of human-water relations (**Figure 4.3**). On the one hand, rivers and streams as depicted on hydrographic maps represent a physical reality which results from the historical interaction between climate, geology, biogeography, and the local socio-political and cultural context — forming a hybrid hydrography. A blue line on a topographic map may not correspond to any remarkable feature in the landscape today because the watercourse that used to be there has long been diverted or buried; a historically perennial stream may have become intermittent or ephemeral due to water withdrawals and climate change. On the other hand, watercourse mapping crystallizes a selective perception of the riverscape; this perception is the outcome of specific social relationships and power asymmetries. The resulting maps in turn legitimize this perception (Harley, 1989). They shape the relations between people and the riverscape (e.g., by determining what people can and cannot do), social interactions mediated through these relations, and eventually, the riverscape itself. The erasure of a watercourse on a regulatory map can translate to its actual erasure from the landscape by making it vulnerable to filling, ditching, damming, or water withdrawals.

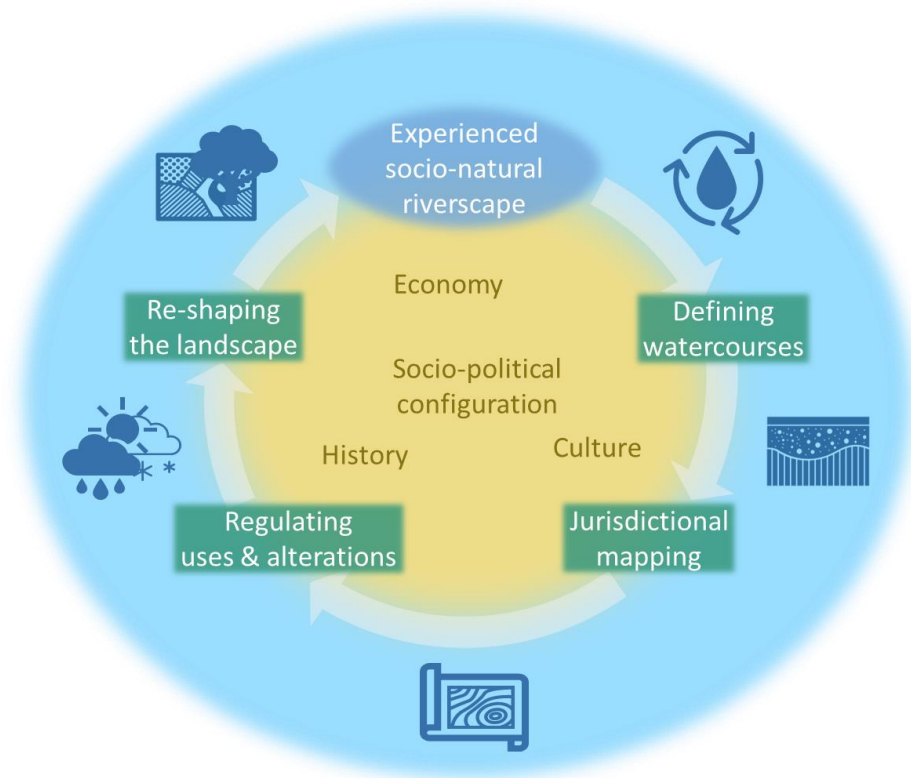


Figure 4.3. Mapping watercourses is part of a broader hydro-social cycle.

Current riverscapes result from the interaction of natural and societal factors. The boundary between these factors is porous -- societies are shaped by and shape their environment. The legal definition of watercourses stems from people's experience of this hybrid riverscape. For example, that ephemeral streams are not watercourses in their own right from a regulatory standpoint in many states of Australia comes from a Eurocentric legal heritage and does not match the reality of local ecosystems (Fritz et al., 2017; Taylor & Stokes, 2007). Once watercourses are defined and criteria are established to differentiate them from non-watercourses, our study demonstrates that the process of applying these criteria during mapping cannot be considered purely technical or abstracted from the local natural and socio-political context either. Jurisdictional maps define what features of the landscape are subject to regulation, which in turn governs humans in shaping or re-shaping the landscape, thus starting the cycle again. Credit for soil/lithology logo: Andy Miranda

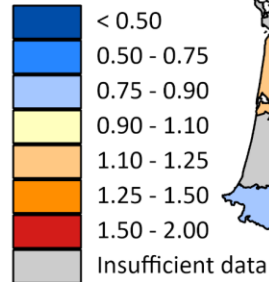
4.4.4. Vague definitions put vulnerable waters at risk

The definition of watercourses under the Water Law disproportionately exposes headwater and non-perennial reaches — already vulnerable ecosystems (Acuña et al., 2014; Meyer & Wallace, 2001) — to human alteration. We estimate that non-perennial reaches comprise nearly 60% of the mapped hydrographic network length but make up about 80% of hydrographic segments which have been disqualified as non-watercourse (**Table 4.1**). Similarly, first-order reaches represent at least 42% of the national hydrographic network length but 56% of disqualified segments in watercourse maps. Taken together, non-perennial and first-order reaches are overrepresented in non-watercourses by 28% compared to their prevalence (67%) in the overall hydrographic network (**Table 4.1, Figure 4.4**).

The apparent dismissal of headwater and non-perennial streams in this cartography is unsurprising considering the ambiguous stipulation in the new definition that a channel must carry “sufficient” flow from a spring most of the year to qualify as a watercourse (**Supplementary Methods 4.6.1**). The definition also specifies that “flow can be intermittent, considering local hydrological and geological conditions”, leaving ample room for interpretation. In a survey of 25 government employees responsible for mapping watercourses in 12 departments of eastern France, respondents considered flow duration to be both the most common criterion for disqualifying segments as non-watercourses, and the most challenging to evaluate (Mars et al., 2020). It is not our goal to evaluate which classified segments we would ourselves deem to be non-watercourses or to critique specific departmental maps. Nonetheless, considering differences among departments in representativeness of vulnerable waters (**Figure 4.4**) and geographic variability in socio-environmental correlates of DDR (**Supplementary Figures 4.S1-3, Supplementary Table 4.S4**), it is probable that numerous ecologically valuable, yet sensitive streams now lack protection under the Water Law.

A. First-order reaches representativeness

$\frac{\% \text{ first-order segments in non-watercourses}}{\% \text{ first-order segments in original network}}$



B. Non-perennial reaches representativeness

$\frac{\% \text{ non-perennial segments in non-watercourses}}{\% \text{ non-perennial segments in original network}}$



Figure 4.4. Representativeness of first-order and non-perennial reaches among non-watercourses in departmental maps.

Positive values indicate departments where headwater and non-perennial reaches are disproportionately classified as non-watercourses (i.e., overrepresented) compared to their prevalence in the original hydrographic network. For A, in a department where first-order reaches make up 60% of network length, a value of 1.5 means that 90% of non-watercourses are first-order streams. Departments where data on non-watercourses were incomplete and where less than 90% of the network could be matched to BD TOPO segments were not analyzed (see **Supplementary Methods 4.6.9** for details on the analytical approach).

The widespread disqualification of headwater and non-perennial reaches as non-watercourses threatens freshwater ecosystems already under pressure. The capillary network of streams at the interface between land and water is both fundamental to the water quality, biodiversity, and ecological integrity of the entire river network, and uniquely vulnerable (Lane et al., 2023; Meyer et al., 2007; Wohl, 2017). Headwater streams are the main point of entry for water, solutes, mineral sediment, and particulate organic matter in the aquatic environment, provide habitat and refuge for diverse riverine and riparian species, and support essential ecosystem services (Ferreira et al., 2023; Wohl, 2017). The spatial and temporal dynamics of drying and rewetting in non-perennial reaches, most but not all of which are small streams, is also a strong driver of local biotic communities, ecosystem processes and ecosystem services (Datry et al., 2023). Because of their abundance and connectivity to the rest of the landscape, headwater and non-perennial reaches are especially vulnerable to degradation (Meyer & Wallace, 2001). And while the functional loss of a single watercourse may have marginal impacts on downstream waters (though not always; Cooke et al., 2024), widespread alteration of these vulnerable waters can cumulatively have network-scale consequences on the hydrology, biogeochemistry, and ecology of aquatic and terrestrial ecosystems (Lane et al., 2023; Leibowitz et al., 2018). Both headwater and non-perennial streams have been historically underappreciated and under-protected across the world, and many are already absent from hydrographic maps, despite comprising the majority of the river network (Acuña et al., 2014; Creed et al., 2017; Datry et al., 2023). As such, their disproportionate exclusion from many of the departmental maps of watercourses in France is only the continuation of a long-standing lack of recognition and protection that risks further deteriorating the ecological quality of entire river networks.

Disqualifying hydrographic segments as non-watercourses in higher-order streams too can threaten the integrity of river networks through fragmentation. If a non-watercourse is surrounded by watercourses or connected to groundwater, this unprotected reach may result in functional or physical disconnection of the network through unregulated water abstraction or physical alteration. Inversely, a watercourse surrounded by non-watercourses is functionally unprotected. We identified over 1500 such cases across France based on a preliminary analysis but expect that many more exist.

4.4.5. Limitations and uncertainties

Our analyses of DDR, socioenvironmental correlates of DDR, and the representativeness of headwater and non-perennial reaches come with several limitations and uncertainties. First, while BD TOPO was the official cartographic basis used by departments in mapping watercourses, it is not uniform nationally, which may partly explain the observed variability in DDR. For example, drainage density in BD TOPO is known to be underestimated in forested areas due to a reliance on aerial imagery (ONEMA & IGN, 2015), and many artificial reaches and headwater streams are missing as the underlying topographic maps were historically drawn for army intelligence (Levavasseur et al., 2015; ONEMA & IGN, 2015). Second, non-watercourses were omitted from nearly a third of departmental watercourse maps, not all segments could be matched between watercourse maps and other hydrographic datasets, and there were numerous geometric artefacts (e.g., erroneously disconnected or looping segments, inaccurate flow direction) and complexities (e.g., multithreaded channels) in the digital river networks. These limitations entail uncertainty in our results (e.g., in the analysis of first-order streams; **Supplementary Methods 4.6.5**), constrained our analysis to the scale of sub-basins rather than individual river segments, and precluded the calculation of network-wide properties like connectivity. Third, the flow regime of many hydrographic segments was undetermined (**Table 4.1**) and is notoriously uncertain in topographic maps (Fritz et al., 2013). Ongoing efforts by national government agencies to quality-check and integrate the departmental maps of watercourses in a new national hydrographic dataset with improved topological integrity and attribute accuracy will enable those analyses in the future. Finally, the precise structure and coefficient values of the regression models presented here were selected through a structured approach, but each represents one of multiple valid alternative models to represent these relationships, owing to collinearity among socio-environmental correlates. Furthermore, the direction of causality between socioenvironmental correlates and DDR cannot be conclusively presumed. For example, lower DDRs in sub-basins with a higher prevalence of winter crops may be simultaneously attributed to two main mechanisms: pressure from agricultural stakeholders to disqualify reaches as artificial non-watercourses in intensively farmed areas, and a stronger imprint by humans on these landscapes manifesting as a higher share of genuinely artificial drainage lines (and thus, a lower share of actual watercourses).

4.4.6. Lessons from France and the US for the world

While we use France as a case study, inconsistent regulatory mapping and the associated exclusion of non-perennial and headwater reaches is likely widespread beyond France — as suggested by our cursory review of legal definitions across continents (**Supplementary Table 4.S1**). In the case of the US Clean Water Act, a critical development in clarifying the definition of the “waters of the United States” came with the 2006 *Rapanos* opinion, which included water resources with a “significant nexus” to navigable waters (implying a biological, chemical, or physical connection; Walsh & Ward, 2022). This ruling was a rare acknowledgement of the connectedness of freshwaters and shifted the definitional focus from the characteristics of individual reaches to their role as part of a whole river network (Creed et al., 2017; Leibowitz et al., 2018). Despite representing a significant advancement, this concept has since been instrumentalized to exclude large swaths of the country’s river networks, however, with inconsistent implementations among administrative units (Fesenmyer et al., 2021; Greenhill et al., 2024). Indeed, predictive models of the jurisdictional status of water bodies trained on approved jurisdictional determinations by the US Army Corps of Engineers performed better when political boundaries were included as a predictor (Greenhill et al., 2024). Accordingly, we argue here that social, cultural and political forces not only influence the definitions of watercourses but also shape the implementation of these definitions in previously underappreciated ways (**Figure 4.3**). A predictive model could similarly be developed to estimate what watercourses fall within the scope of the Water Law in France, but such an approach would not gain buy-in from stakeholders. Instead, we propose that quantitative methods should go hand in hand with political ecology to examine the complex relations at the core of water governance and seek decision-making structures that can transparently support the implementation of legal definitions of watercourses in France and beyond.

Jurisdictional mapping may seem technical and uncontroversial compared to other contentious issues of water governance like water allocation to different uses, barrier removal and restoration (Barraud, 2017; Linton, 2021). However, defining what features of the riverscape are protected by environmental regulations has far-reaching implications for the health of entire watersheds and the people that depend on them (Doyle & Bernhardt, 2011; Lane et al., 2023). Excessive water withdrawals, pollution and direct alterations of river channels compromise drinking water quality, species diversity, nutrient cycling, flood

regulation, and recreational activities, among other services which are essential for human well-being (Lynch et al., 2023). Watercourse mapping in France presented us with a natural experiment to quantitatively evaluate a cartographic expression of the hydro-social cycle playing out in over 90 individual departments. This case study, which echoes similar assessments of the disproportionate impact of changes to the jurisdictional scope of the Clean Water Act on US vulnerable waters (Fesenmyer et al., 2021; Greenhill et al., 2024; Sullivan et al., 2020), has broad and novel relevance. It distinguishes itself from the definitional disputes in the US (Walsh & Ward, 2022) and Australia (Taylor & Stokes, 2007) because the physical criteria to differentiate watercourses from non-watercourses are firmly established at the national level. In France, it is the lack of a consistent framework governing the decentralized implementation of these criteria that resulted in the observed inconsistencies. This lack of governance structure likely enabled local power dynamics among stakeholders to translate into a selective perception of what counts as a watercourse in some departments. Here we took an innovative approach to daylight the implications of this specific process that can inform jurisdictional mapping elsewhere. We expect that regulatory frameworks for watercourse protection are similarly vulnerable to local interpretation yet equally unexamined in most countries, thus putting freshwater ecosystems and their critical contributions to people's well-being at risk.

4.5. Supplementary Figures and Tables

Table 4.S1. Example definitions of watercourses in countries across continents.

	Definition	Domain of application	Associated law or regulation
France	The definition underlying the watercourse maps under study in this article: <i>"A watercourse consists of flowing water in a channel of natural origin, fed by a spring, and carrying sufficient flow for most of the year. Flow may be intermittent, considering local hydrological and geological conditions."</i>	Water Law (<i>Police de l'eau</i>): all installations, structures, works, or activities on watercourses are subject to environmental authorization if they may pose risks to public health and safety, impede the free flow of water, diminish the water resource, markedly increase the risk of flooding, or seriously harm the quality or diversity of the aquatic environment.	Article L.215-7-1 of the Environmental Code (inscribed in 2016).
	Solid blue lines and blue dotted lines named on the most recently published 1/25,000 maps by the National Institute of Geographic and Forest Information (IGN). In some departments, both named and unnamed lines are included. In others, only solid lines are included.	European Union standards of good agricultural and environmental conditions (GAEC): to benefit from EU Common Agricultural Policy (CAP) subsidies, farmers must abstain from applying fertilizers and, except in specific cases, phytosanitary treatments within at least five meters from these watercourses.	Article D615-46 of the Rural and Marine Fishing Code
	All watercourses covered by the Water Law and the GAEC as well as all hydrographic features on most recently published 1/25,000 maps by the National Institute of Geographic and Forest Information (IGN).	No Treatment Zones (ZNT in French): the direct application of phytosanitary products is prohibited within at least 5 m (or more depending on the product) from any element of the hydrographic network, whether mapped or not (permanent or temporary flows, channels, ditches, washhouses, wells, boreholes, rainwater retention basins...).	Governmental Decree of May 4th 2017 , regarding the marketing and use of plant protection products and their adjuvants
United States	The "waters of the United States" include, as of September 2023 (following US Supreme Court's 2023 <i>Sackett</i> decision): - Traditional Navigable Waters: large rivers and lakes that could be used in interstate or foreign commerce; waterbodies affected by tides. - Interstate Waters: streams, lakes, or wetlands that cross or form part of state boundaries. - Impoundments: created in or from "waters of the United States," like reservoirs and beaver ponds. - Tributaries: Branches of creeks, streams, rivers, lakes, ponds, ditches, and impoundments that ultimately flow into the aforementioned waters al., 2017) -- if they meet either the relatively permanent standard or significant nexus standard. - Adjacent Wetlands: next to, abutting, or near other jurisdictional waters or behind certain natural or constructed features -- if they meet either the relatively permanent standard or the significant nexus standard, or where the wetland is adjacent to aforementioned waters. - Additional Waters: lakes, ponds, streams, or wetlands that do not fit into the above categories, if they meet either the relatively permanent standard or the significant nexus standard.	"Waters of the United States" establishes the geographic scope of federal jurisdiction under the Clean Water Act, which is the primary federal mechanism by which the physical, chemical, and biological integrity of streams, lakes, and wetlands are protected. However, the CWA does not define the scope of the waters of the United States, which has caused decades of legal disputes until now. State water quality standards are further differentiated in the degree to which they include non-perennial rivers and streams(Fritz et	Final rule to amend the final "Revised Definition of 'Waters of the United States'" rule under the Federal Water Pollution Control Act, as amended by the Clean Water Act, 33 U.S.C. §§ 1251-1387
Australia	<i>"A watercourse is a river, creek or other stream, including a stream in the form of an anabranch or a tributary, in which water flows permanently or intermittently, regardless of the frequency of flow events (a) in a natural channel, whether artificially modified or not; or (b) in an artificial channel that has changed the course of the stream. A watercourse includes any of the following located in it (a) in-stream islands; (b) benches; (c) bars. However, a watercourse does not include a drainage feature." A drainage feature is "a natural landscape feature, including a gully, drain, drainage depression or other erosion feature that (i) is formed by the concentration of, or operates to confine or concentrate, overland flow water during and immediately after rainfall events; and (ii) flows for only a short duration after a rainfall event, regardless of the frequency of flow events; and (iii) commonly, does not have enough continuing flow to create a riverine environment."</i>	National and federal Acts defining watercourses are diverse. Here we cite as an example the Queensland Water Act, which is similar to legislation in most other states(Fritz et al., 2017). This Act is the main legal tool to govern the sustainable management of Queensland's water resources. Other `	Water Act 2000 (Chapter 1, Part 2, Section 5)
S. Africa	A watercourse is <i>"(a) a river or spring; (b) a natural channel in which water flows regularly or intermittently; (c) a wetland, lake or dam into which, or from which, water flows; and (d) any collection of water which the Minister may, by notice in the Gazette, declare to be a watercourse."</i> What constitutes a natural channel is not defined and is the subject of contradicting interpretations(Harding, 2015).	This Act is the main legal tool to govern the management of the country's water resources and associated ecosystems. Botswana and Namibian definitions are almost identical.	South African National Water Act (NWA; Chapter 1, Article 1)
Colombia	The demarcation of watercourse buffer zones only applies to "natural water bodies with permanent or intermittent flows, provided that the latter show geomorphological evidence associated with the permanent channel". It excludes water bodies with ephemeral flows (i.e., occurring less frequently than intermittent flows and generated only in response to precipitation events, as outlined in technical guidelines).	The main legal tool for "maintaining and restoring the functionality of natural water bodies" in Colombia is through the delineation and protection of watercourse buffer zones ("ronda hidrica") which comprises a "strip parallel to the line of maximum tides or the permanent channel of rivers and lakes, up to thirty meters wide". Similarly to France, the national government leaves it to de-centralised government entities to identify watercourses and their buffer zones following detailed criteria in a common technical guide.	Decree 1076 of 2015, Environmental and Sustainable Development Sector, ARTICLE 2.2.3.2.3A
India	A protected "stream" can include "river, water course (whether flowing or for the time being dry), inland water (whether natural or artificial), sub-terranean waters, sea or tidal waters to such extent or, as the State Government may, by notification in the Official Gazette, specify in this behalf."	The Act is the primary central government legislation for the management of inland water quality in India.	Water Prevention and Control of Pollution Act of 1974

Table 4.S2. Data sources

	Theme	Format	Scale/Resol.	Dataset name	Source (pub. date)
Hydrographic data	Departmental digital networks of watercourses	Vector (lines, some polygons)	Variable scale (mostly 1/25000)	Cartographie des cours d'eau	See Supplementary Methods 4.6.2
	National digital hydrographic network	Vector (lines)	1/25000 (1-m precision)	BD TOPO® version 151 - Hydrographie	National Institute of Geographic and Forest Information - IGN (2015)
	National digital hydrographic network	Vector (lines)	1/50000 (25-m precision)	BD Carthage® version 2014 - Cours d'eau	IGN (2014)
Units of analysis	Administrative boundaries (departments and municipalities)	Vector (polygons)	1/50000 (2.5-m to 30-m precision)	ADMIN-EXPRESS version Octobre 2023	IGN (2023)
	Sub-basin boundaries	Vector (polygons)	1/50000	BD TOPAGE® millésime 2023 – Bassins versant topographiques	IGN (2023)
Socio-environmental correlates	Land cover map	Raster (pixels)	10 m	Theia OSO Land Cover 2019, 2020, 2021	Scientific Expertise Center on Land Cover - CES OSO (2021-2023)
	Aridity	Raster (pixels)	30 arc-sec (~1 km)	Global Aridity Index and Potential Evapo-Transpiration (ET0) Database v3	Zomer et al. (2022)
	Elevation	Raster (pixels)	25 m	BD ALTI® Digital Elevation Model (DEM) version 2.0	IGN (2023)
	Irrigation	Vector (polygons) and tables (time-series)	Municipalities	Recensement agricole 2020	Agreste , Department of Statistics and Foresight Analysis, Ministry of Agriculture (2022)
	Water withdrawals	Vector (points) and tables (time-series)	Individual withdrawal points	Banque Nationale des Prélèvements en Eau (BNPE), Hub'Eau API (2015-2022 withdrawals)	Eaufrance , OFB, BRGM (2023)
	Plant Available Water Capacity (AWC)	Raster (pixels)	90 m	Soil Available Water Capacity in metropolitan France, 0-2 m depth	Scientific Expertise Center on Digital Soil Mapping (2019)
	Predicted flow intermittence	Vector (lines)	50 m	-	Snelder et al. pers. comm. (2013)
	Artificial river barriers	Vector (points)	Individual barrier points	AMBER Barrier Atlas	Adaptive Management of Barriers in European Rivers (AMBER) Consortium
	Population	Vector (polygons)	Variable (min. 200-m)	Dispositif Fichier localisé social et fiscal (Filosofi) ; Income, poverty and standard of living 2019 – grid-based	The National Institute of Statistics and Economic Studies - INSEE
	Building footprints	Vector (polygons)	1/25000 (1-m precision)	BD topo 2019 version 191 - Batiments	IGN (2019)
	Artificial basins not for irrigation	Vector (polygons)	1/25000 (1-m precision)	BD topo 2019 version 191 – Surfaces hydrographiques	IGN (2019)

Table 4.S3. Correlation coefficients and models of the relationships between socio-environmental variables and average drainage density ratios (DDR) among departments

Predictor of DDR	Spearman's ρ
Pasture extent (%)	0.41
Soil available water capacity (mm)	0.15
Agricultural extent (inc. pasture, %)	0.09
Impervious extent (%)	0.08
Slope (degrees)	0.05
Winter crops extent (%)	-0.02
Population density (pop km ⁻¹)	-0.02
Predicted natural intermittency (% river length)	-0.03
Artificial basins not for irrigation extent (%)	-0.11
Vineyard extent (%)	-0.17
Mean annual aridity (PET/P*)	-0.20
Orchard extent (%)	-0.26
Mean summer aridity (PET/P Jul-Sep)	-0.28
Barrier density (barrier km ⁻¹)	-0.29
Irrigated extent (%)	-0.30

*Potential Evapotranspiration/Precipitation

Selected model ($p < 0.001$; adjusted- $R^2 = 0.33$):

$$\widehat{DDR}_d = 0.87 + 1.69(\text{agricultural cover \%})_d - 1.13(\text{irrigated extent \%})_d - 0.14(\text{mean summer aridity})_d - 0.68(\sqrt{\text{barrier density km}^{-1}})_d + 1.05(\text{impervious cover \%})_d + \epsilon_d$$

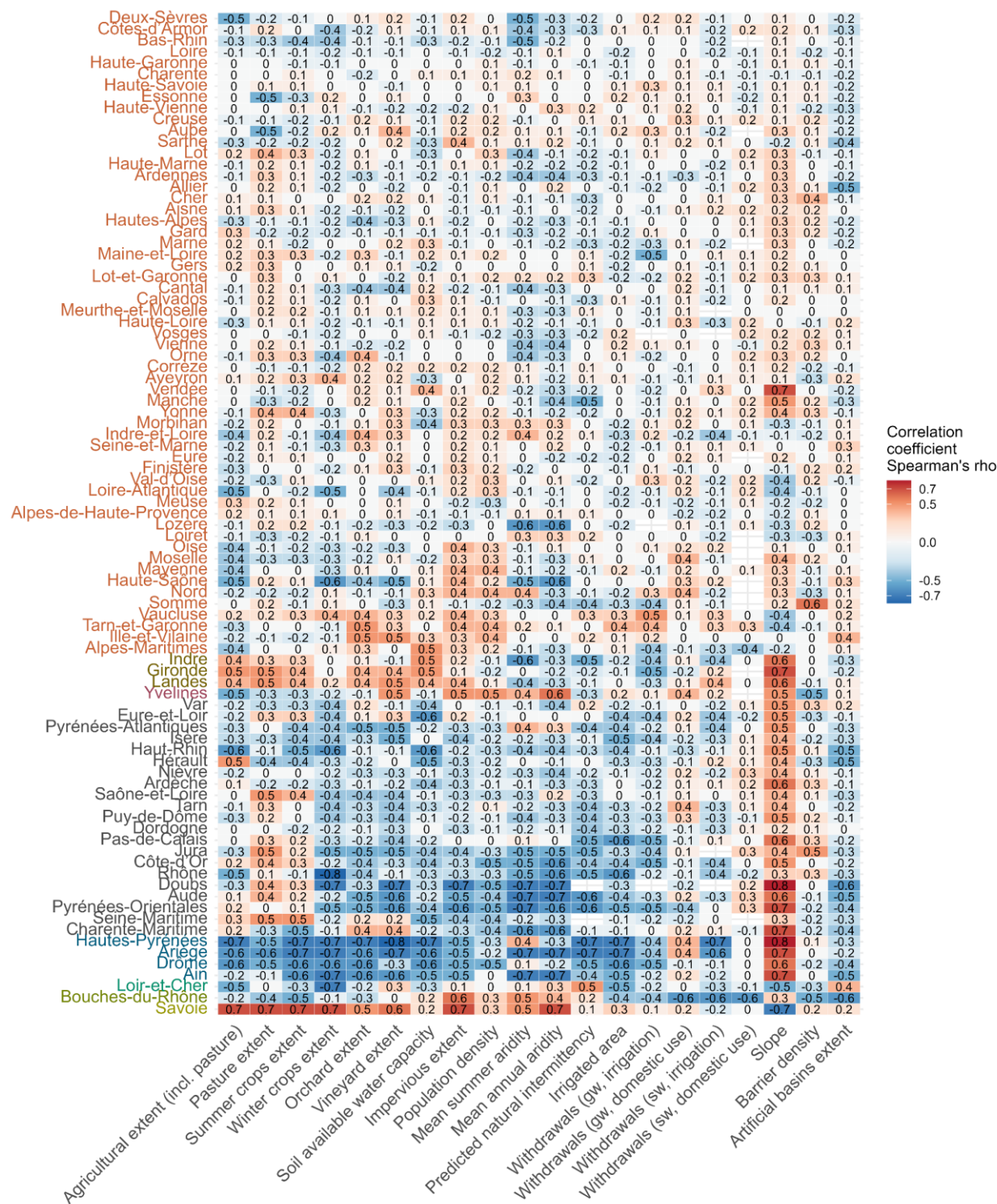


Figure 4.S1. Heatmap of Spearman correlations between socio-environmental variables and within-department variations in drainage density ratio

Table 4.S4. Regression models of the relationships between socio-environmental variables and within-department variations in drainage density ratio (DDR)

Group		n _{dep}	n _{sub-basins}	MAE (null)
1*	$DDR_{grp\ 1,i} = \alpha + \rho \sum_j w_{i,j} DDR_j + \beta_1(\text{agriculture \% extent}_i) + \epsilon_i$	1	47	0.02 (0.14)
2*	$DDR_{grp\ 2,i} = \alpha + \rho \sum_j w_{i,j} DDR_j + \beta_1(\log(\text{artificial basin \% extent}_i) + \beta_2(\% \text{ extent irrigated}_i) + \epsilon_i$	1	27	0.10 (0.18)
3	$DDR_{grp\ 3,d,i} = \alpha + \beta_1(\sqrt{\text{winter crop \% extent}_i}) + \epsilon_i$	1	68	0.08 (0.12)
4	$DDR_{grp\ 4,d,i} = \alpha + \beta_{1,d} + \beta_{2,d}(\sqrt{\text{winter crop \% extent}_i}) + \beta_{3,d}(\% \text{ extent irrigated}_i) + \beta_{4,d}(\text{orchard \% extent}_i) + \beta_{5,d}(\text{vineyard \% extent}_i) + \epsilon_i$	4	332	0.11 (0.17)
5	$DDR_{grp\ 5,d,i} = \alpha + \beta_{1,d} + \beta_{2,d}(\sqrt{\text{winter crop \% extent}_i}) + \beta_3(\text{mean annual aridity}_i) + \epsilon_i$	21	1482	0.13 (0.14)
6	$DDR_{group\ 6,i} = \alpha + \beta_1(\sqrt{\text{barrier density}_i}) + \beta_2(\text{mean slope}_i) + \epsilon_i$	1	25	0.12 (0.19)
7	$DDR_{grp\ 7,d,i} = \alpha + \beta_{1,d} + \beta_{2,d}(\sqrt{\text{pasture \% extent}_i}) + \beta_{3,d}(\text{mean summer aridity}) + \beta_{4,d}(\text{predicted prevalence of intermittence}_i) + \epsilon_i$	3	357	0.14 (0.20)
8	$DDR_{grp\ 8,d,i} = \alpha + \beta_{1,d} + \beta_{2,d}(\sqrt{\text{winter crop \% extent}_i}) + \beta_3(\text{mean summer aridity}_i) + \epsilon_i$	57	4180	0.15 (0.15) [#]

† Departments were first clustered into 8 groups based on their Spearman's correlation coefficients between socio-environmental variables and DDR across sub-basins (**Supplementary Figure 4.S1** for coefficients; see map below for distribution of groups; **Supplementary Methods 4.6.8**). A regression model was then developed for each group, relating DDR in each sub-basin *i* to a set of socio-environmental variables (see **Supplementary Table 4.S3** for units and **Supplementary Table 4.S2** for data sources). A blue coefficient name indicates a significantly negative value, an orange name indicates a positive value, and a green name indicates a value which may be positive or negative or non-significant depending on each department (global intercepts are not colored). The subscripts in $\beta_{1,d}$ indicates that coefficient β_1 varies by department (i.e., there is a fixed-effect interaction between department and that variable). $\epsilon_i \sim N(0, \sigma^2)$

*Spatial lag model (mixed regressive, spatial autoregressive model): incorporates the spatial dependence of DDR in a sub-basin *i* upon the DDR in each k-nearest-neighboring sub-basin *j* (k=4), where ρ is the spatial autoregressive coefficient and $w_{i,j}$ is the globally-standardized inverse distance weight between *i* and each *j*.

[#]The last model afforded nearly no predictive power beyond a variable intercept null model.

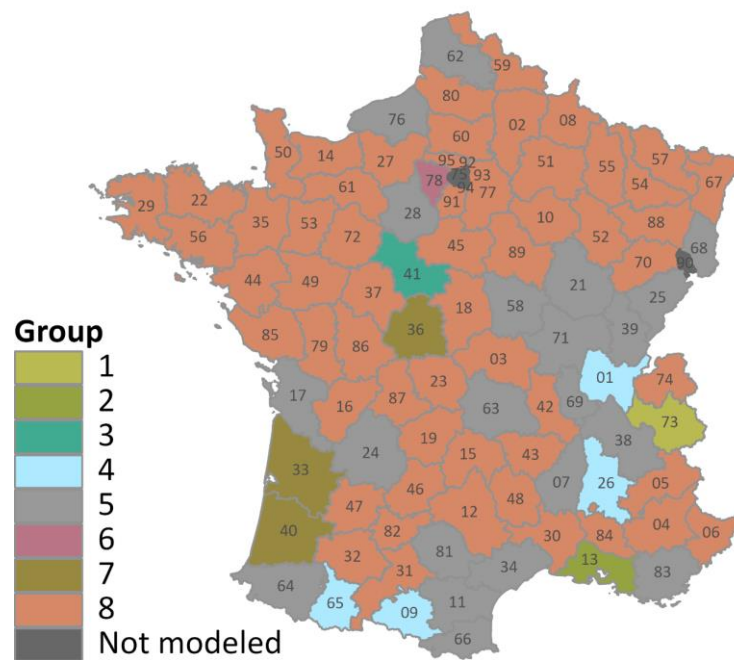


Figure 4.S2. Distribution of departmental groups based on multivariate clustering of correlation coefficients.

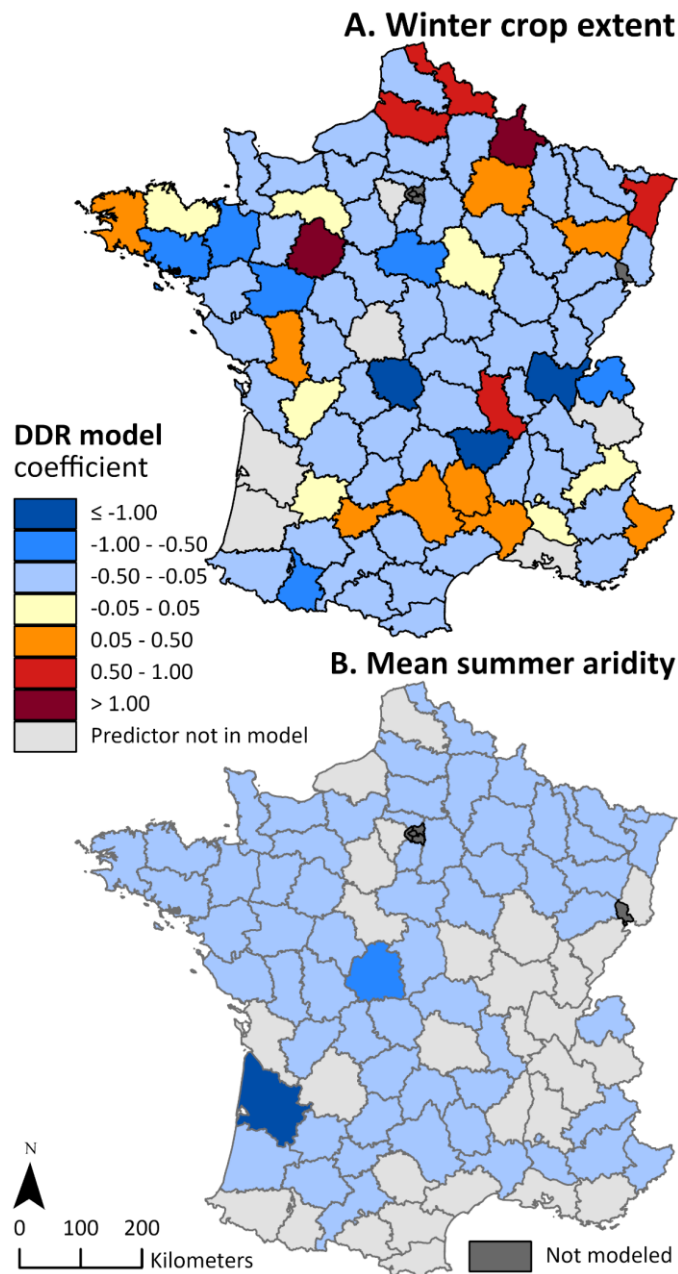


Figure 4.S3. Distribution of coefficients from regression models of drainage density ratio (DDR) across sub-basins within departments for two socio-environmental variables.

Summer aridity was computed as the long-term ratio between potential evapotranspiration and precipitation from June to August. Winter crop extent (as a percentage of sub-basin area) was square-root transformed. For B, a coefficient of -0.5 for a given department means, all things being equal, that a 10% increase in summer aridity from one sub-basin to the next is associated with a mean decrease of 5% in watercourse length compared to BD TOPO (i.e., a 0.05 decrease in DDR). Departments with five sub-basins or less were excluded from the analysis. See **Supplementary Table 4.S2** for data sources, **Supplementary Table 4.S4** for model specifications and **Supplementary Methods 4.6.8** for details on the modeling approach.

4.6. Supplementary methods

4.6.1. Government directive outlining mapping process by departments in France

Below, we provide a direct translation of the directive from June 3rd 2015 by the Ministry of Sustainable Development, Ecology and Energy “on the mapping and identification of watercourses and their maintenance” (Instruction du Gouvernement du 3 Juin 2015 relative à la cartographie et l’identification des cours d’eau et à leur entretien). This directive was addressed to all decentralized government representatives in charge of applying the Water Law at the level of departments and regions in France. We added clarifying annotations in square brackets. Formatting, other than italics (i.e., bold or underlined font, paragraph structure), is included as in the original text.

[Main body of directive]

The concept of watercourse is employed in several legal texts, yet it has been defined neither by law nor by regulation. Its interpretation has been left to the discretion of judges, allowing flexibility to accommodate diverse geographical and climatic conditions.

While there is consensus among users on identifying major watercourses, differentiating between specific watercourses and ditches or canals is sometimes more delicate. However, this distinction has substantial administrative consequences. Indeed, an intervention on a ditch can proceed without any administrative procedure under the water law, whereas an intervention on a watercourse going beyond routine maintenance by the riparian owner (such as altering the longitudinal or cross-sectional profile of the watercourse) requires a “water law” [“loi sur l’eau”] declaration or authorization. This can lead to tensions with certain users, particularly the agricultural sector or communities.

For the application of the provisions of articles L. 214-1 to L. 214-6 of the environmental code, we will rely on the case law of October 21, 2011 of the Council of State [Conseil d’Etat]:

“A watercourse consists of flowing water in a channel of natural origin, fed by a spring, and carrying sufficient flow most of the year.”

Three cumulative criteria must therefore be retained to characterize a watercourse:

- 1. the presence and permanence of a bed, originally natural;
- 2. sufficient flow for most of the year;
- 3. provision of water from a spring.

However, these general criteria, while valid throughout the national territory, must be assessed according to local geographical and climatic conditions. The characteristics of a stream in the Beauce plain, a mountain stream, or a Mediterranean watercourse with dry areas will be very different. Furthermore, these jurisprudential criteria are sometimes difficult to assess at a given moment. In these cases, administrative judges have considered additional clues, such as the presence of aquatic fauna and flora, to characterize whether the flow was a watercourse.

A pragmatic local approach, widely shared and accounting for local uses, is therefore needed for making it known to all whether flowing water features are watercourses or not.

In the departments in which the establishment of a complete map of watercourses is possible without major difficulties, I ask you to do so as soon as possible.

These are cases [those where the establishment of a complete map of watercourses is possible without major difficulties] where the available [hydrographic reference] repositories, and in particular the 1/25,000 maps of the IGN [National Institute of Geographic and Forest Information], are complete enough to serve as a basis for reliable mapping, carried out within a reasonable time, and in any case before the December 15, 2015. These are also the departments where a collaborative approach has made it possible to define a consensual hydrographic foundation for such mapping. If necessary, a collaborative approach should be taken to clarify the situation and finalize the mapping of complex remaining cases. As the State services having knowledge of easy and complex cases, you should firmly commit to this approach. The maps produced should be the subject of a technical exchange with the relevant stakeholders. You should rely on the framework and methodological elements presented in Appendix 1.

However, in certain departments, a [geographically] exhaustive identification [of watercourses] is not possible within an acceptable time frame owing to complexity and cost in particular, for example in the headwaters of basins, where drainage can be both dense and diffuse. In this case, the [State/departmental] services will be allowed to carry out complete maps of watercourses on only part of the department in which the conditions of feasibility specified above have been met, and use another method for identifying watercourses in other areas [of the department where those conditions are not met].

This [other] method should clarify the protocol for identifying watercourses, [which should be] explicit and shared by all users, and reserved for territories where a complete mapping of watercourses cannot be developed. In these cases, based on the framework and methodological elements provided by the water and biodiversity department [“direction de l’eau et de la biodiversité”], I ask you to determine, in conjunction with local partners [i.e., stakeholders], a method for identifying watercourses, based on jurisprudential criteria, and adapted to the contexts mentioned.

This protocol for identifying watercourses, developed locally in territories where it was not possible to produce a complete map of watercourses, should consider geo-climatic specificities and should specify the approach for determining the status of watercourses following a special request. It should [also] specify the methods for making the verdicts already issued [on the status of watercourses] available to the public, in the form of progressive [i.e., partial and evolving] maps.

I request that you communicate by June 29, 2015 the territories where a complete map will be produced [by the end of 2015], and those where the development of a mapping protocol and progressive mapping will be conducted, to the water and biodiversity office via the regional representatives responsible for coordinating and leading water law enforcement. I ask you to transmit, by December 15, 2015, and using the same method, the maps once developed as well as the method for identifying watercourses, where applicable.

I expect that, by December 15, 2015, complete maps of watercourses will cover two thirds of the metropolitan territory and am counting on your commitment and that of your services in this essential clarification process. The long-term objective is to cover the entire metropolitan territory, except for 5 to 10% due to specific field difficulties. A national-level evaluation of the implementation of the approach will be presented to me in the first quarter of 2016.

The regional government services will ensure the overall consistency of the approach, both for the identification of territories where complete mapping will be developed, and for the development of watercourse identification methods developed in the territories where a complete map of the watercourses could not be developed [by 2015]. You should inform the water and biodiversity department of any difficulties you may encounter in the application of

this instruction, and in particular cases in which the approach adopted is not the subject of local consensus.

Furthermore, misunderstandings remain on the ground regarding the routine maintenance of watercourses that riparian owners must carry out, without prior procedure, and about what requires permitting under the water law. Beyond identifying watercourses, I expect [departmental] services to provide a guide for landowners whose property adjoin watercourses on their obligations and on best practices that should be implemented to guarantee the preservation of aquatic environments. To this end, a model guide is available on the intranet site of the general directorate of planning, housing, and nature.

[Departmental] services should ensure that [this guide] is adapted to local conditions and practices in partnership with the relevant stakeholders and that it is widely disseminated. In departments or regions in which such an approach has already been carried out by involving stakeholders of concern, this local version of the guide should be implemented if it provides a useful complement to the documents already developed.

Appendix 1: Framework for identifying watercourses

Several regulations refer to categories of watercourses on which they are applicable.

However, these categories do not include all watercourses under the Water Law. These categories are recalled as an example here:

- *watercourses for good agricultural and environmental conditions (GAEC)*
- *water features for No Treatment Zones (ZNT);*
- *watercourses for the implementation of the Nitrates Directive;*
- *Grenelle watercourses;*
- *watercourses for ecological continuity.*

Action plan for services

1. Mapping of watercourses

Initially (before June 29, 2015), the [departmental] services should identify the areas in which a complete map of watercourses will be established. The mapping carried out by December 15 should cover the zones in which the available repositories, and in particular the maps at a scale of 1/25,000 of the IGN and the georeferenced databases, are complete enough to serve as a basis for exhaustive mapping. Based on these repositories, the decentralized services

*should identify the flowing water features which can be considered as watercourses with regard to jurisprudential criteria (see § 2.20). They should rely on the technical expertise of the departmental offices of ONEMA ["National Water and Aquatic Environments Agency", now part of the National Office of Biodiversity OFB]. The maps must include **at least** the water bodies identified under the water framework directive and the watercourses already identified for other regulations, in particular those establishing categories of watercourses. The maps thus produced should be the subject of a technical exchange with stakeholders (representatives of elected officials, river unions, professional agricultural and forestry organizations, representatives of landowners, environmental organizations, departmental fishing federations, etc.). Where they exist, local water commissions (CLE) should be consulted on the maps produced.*

This mapping will allow any user to know the opinion of State services [on the status of watercourses].

2. Criteria from case law to be adapted to the local context

Case law has recognized three cumulative criteria for identifying watercourses: sufficient flow for most of the year, water supply from a spring and the existence of a bed of natural origin [i.e., that is natural or originally was natural].

Sufficient flow for most of the year

Water flow is often directly dependent on precipitation. A watercourse is characterized by flow that is not exclusively fed by local rainfall events. Thus, we propose that this criterion requires water flow even after a period without significant rainfall. Such a criterion is therefore intended to eliminate ditches that collect runoff water, and where flows temporarily occur after rains, from the inventory.

This flow criterion must be specified according to local geo-climatic characteristics. Thus the length of time without significant precipitation and the amount of precipitation qualifying as significant must be specified. [A] precipitation [event involving at least] 10 mm is generally considered significant.

Furthermore, some watercourses have naturally intermittent flows. These include, among others, mountain streams, Mediterranean rivers, or overseas rivers [in French territories

outside of European mainland]. *Depending on the geographical area, the identification method should specify the observation conditions required to [establish whether the flow criterion is met and] categorize the watercourse.*

Water supply from a spring

A watercourse, even if not flowing year-round, must receive water from at least one source/spring [source and spring are the same word in French] other than precipitation alone. Supply from a spring thus makes it possible to clarify the notion of “sufficient flow for most of the year”. A watercourse is distinguished from a ditch or ravine which only drains runoff from precipitation. [To qualify,] a spring does not necessarily have to be localized. It can be localized, at the place where the water table reaches the surface as an identifiable spring, but it can also be the outlet of a diffuse wetland, particularly at the head of the basin, or a groundwater outcrop.

Regarding the criterion of sufficient flow for most of the year, it must be taken into consideration that certain sources may dry up at certain periods. The conditions of the year in which this criterion must be assessed should therefore be specified.

The existence of a natural bed originally

*Jurisprudence has recognized the existence of a **bed of natural origin** as a criterion. Indeed, heavily anthropogenically altered watercourses (such as canalized or recalibrated watercourses) must be considered as watercourses, even if substantial alteration may have caused it to lose their aquatic life or differentiated substrate.*

This criterion should not make one lose sight of the fact that, depending on local uses, artificial arms (such as diversions towards a canal or mill) left abandoned and in the process of being renatured can be considered as watercourses. Likewise, if an artificial arm carries the majority of discharge, to the detriment of the natural arm (and calling into question the criterion of flow permanence for the natural arm), the artificial arm should be considered a watercourse.

In the remaining cases where the three major criteria set out above do not enable ruling with certainty whether a flowing feature qualifies as a watercourse, a set of ancillary indices previously used in case law may also be considered. This set of clues can help to indirectly characterize the major jurisprudential criteria.

Presence of banks and a bed with differentiated substrate

The repetitive and concentrated flow of water, characteristic of sufficient flow for most of the year, gives rise to an identifiable bed, typical of streams. This bed is characterized by sufficient difference in height with its surroundings that distinguishes it from exclusively erosive drainage features, which can generate gullies and whose location varies from one year to the next. In addition, a watercourse exhibits processes of solid material transport which gives the feature's bottom [i.e., the bed] a characteristic and differentiated substrate compared to soil in the adjacent plot. Phenomena of erosion, deposition, bedload, and suspended sediment transport thus have visible consequences, particularly on the bottom of stream beds.

The chosen indicator [for applying this criterion] should, where applicable, specify the difference in height between the bottom of the drainage feature's bed (at the low point of the talweg) and the average ground level of the [riparian] plot considered to characterize the presence of banks. It is also possible to consider as an indicator whether the substrate of the flowing feature (sand, gravel, organic mud, etc.) is significantly distinct from the soil in the adjacent plot.

Presence of aquatic life

When flow is sufficient for most of the year, it allows the development of specific organisms, characteristic of aquatic environments. Typical flora and fauna communities are therefore regularly present in or around streams. The presence of aquatic life could therefore be an indicator. It may be characterized by the presence of benthic macro-invertebrates (living at the bottom of the bed) having a complete life cycle in an aquatic environment (chironomid larvae, oligochaetes, copepods, etc.), as well as by obvious traces of life: crustaceans and molluscs (shells, empty or not, [or exuviae]), worms (planarians, leeches), beetles, caddisflies (casings, empty or not).

Upstream-downstream continuity

A watercourse is characterized by continuous flow from upstream to downstream. Identifying a watercourse both upstream and downstream can be used as an indicator that the flowing feature [within the segment of interest] is a watercourse. This indicator must, however,

consider the interruptions by bodies of water, certain wetlands or marshes or even losses occurring in karst environments. Likewise, the particular case of artificial arms must be taken into account when using this indicator.

This list may be supplemented by other relevant indices, both technically and with regard to local hydrographic characteristics, and make it possible to indirectly apply the main jurisprudential criteria.

3. Methodology for characterizing watercourses

In addition to contextualizing the jurisprudential criteria and additional indices according to local geographic and climatic conditions, the protocol [developed by departmental services for areas where a complete map cannot already be produced] should indicate how to reach a decision about whether a flowing water feature is a watercourse or not, and when to opt for a more in-depth analysis, in case of indetermination.

The protocol should lay out the different possible options for the three jurisprudential criteria –the criterion is either confirmed, refuted, or a doubt remains – and specify for each option the reasoning to follow and how to arrive at a decision [regarding the status of the feature].

As the jurisprudential criteria are cumulative, a flowing feature will be considered a watercourse if each of the three criteria is confirmed. If at least one of the criteria is invalidated, then the flowing feature will not be considered a watercourse.

If doubt remains on at least one of the criteria, the others being confirmed, then this case is indeterminate. In these undetermined cases, a complementary analysis will be necessary, based on a range of additional indicators taking into account local practices, and if necessary, expertise on the ground. For example, if a judgement cannot be made on the criteria of permanent flow for most of the year and water supply from a spring, the presence of a bank and differentiated substrate on the channel bed, and the traces of aquatic life could constitute a body of conclusive evidence to identify a watercourse.

Upstream-downstream continuity will constitute a complementary element of assessment: if the watercourse has been identified upstream and downstream, and except in special cases (such as a body of water, artificial diversion arm, area wet, loss in a karst area), the flow will be considered as a watercourse.

IMPLEMENTATION OF THE CHARACTERIZATION

The services should make the information necessary to identify watercourses available to the public. They should indicate the areas where comprehensive watercourse maps are available and the address(es) at which they can be viewed.

***For areas where complete mapping of watercourses cannot be implemented,** the services should specify the protocol for deciding on the status of a flowing water feature. In particular, they should indicate how somebody can request [for a flowing water feature to be expertized] by departmental services (responsible for the water law), how departmental services and the public agents whose field expertise can be utilized should communicate, and how verdicts [regarding the status of watercourses] by the administration will be recorded following requests. They will make available to the public in the form of **progressive mapping** the compiled information on flowing features which have already been characterized as watercourses or as non-watercourses.*

1. Coordination of services and [identification request] sheet

To structure requests for characterizing a flowing feature and facilitate exchanges between the services responsible for watercourse characterization, the watercourse identification protocol should include an [identification request] sheet and an intervention flowchart following a request for expertise.

The sheet will outline the information required from the requesting party which should accompany the request for characterization and detail the criteria that the [departmental] services will analyze to characterize the flowing features. The structure of this sheet, which may contain photographs, will facilitate the archival of requests and the associated responses provided by the administration.

Furthermore, based on the method thus defined, the services should establish a model letter to communicate the verdict on the watercourse identification process following a request for expertise.

2. Archival of opinions rendered and progressive mapping

To capitalize on the expertise carried out, the services will record in a geo-referenced database the judgement (and associated justifications) they have made relating to the identification of watercourses, ensuring traceability for all State services.

The services will make progressive maps available to the public which will indicate the sections which have been identified as watercourses, those which have been identified as not being watercourses and those which have not yet been the subject of an expertise on a case-by-case basis.

If a segment should be identified [by a stakeholder] that does not appear on the map, the interested party should request the opinion of the local administration (service in charge of the enforcing the water law) according to the terms defined above.

CONSULTATION, COMMUNICATION AND PROCEDURE IN CASE OF DIVERGENCE

The services are encouraged to involve all stakeholders in the development and implementation of the watercourse identification process. It is indeed essential that the mapping and, where applicable, the protocol for identifying watercourses be discussed early on and be ultimately well known to all stakeholders to facilitate appropriation and therefore good implementation.

The protocol should be published in electronic format and additional communications should be targeted towards the most relevant stakeholders using the most effective means (public meetings, communications during days of technical exchange, brochures, articles in the local specialized press, etc..). Associations of local elected officials, consular chambers and relevant/interested public establishments should be particularly involved in the entire process.

The services should also involve relevant/interested stakeholders in the periodic review of the produced maps, so that they can correct errors which may have been noted in the field [by the stakeholders].

To deal with specific cases of divergence of assessment, which should be very limited to the extent that the mapping and/or the method of identifying watercourses will have

*collaboratively developed and implemented, the services will define an operational **and proportionate procedure**. It will obviously not replace a possible decision of a legal court but will, if necessary, clarify the interpretation of the protocol.*

***For example,** a “watercourse” commission could be established, and bring together qualified people and user/stakeholder representatives. It will include at least a representative of the Chamber of Agriculture, an agent from ONEMA, a representative of the fishing federation and a local elected official. This commission could be consulted on the mapping and identification of watercourses, according to the specific procedures developed on the basis of this present directive. In regions covered by a SAGE [basin-specific water resource development and management plan], this “watercourse commission” may be facilitated by the CLE [local water commission].*

4.6.2. Protocol for producing a national map of watercourses

a. Compiling individual departmental watercourse

To compile watercourse maps, we first inventoried the availability of online data in the form of GIS vector layers for each individual department in mainland France (i.e., excluding Corsica and overseas departments and territories). We inspected the website of each of the 94 corresponding *Directions départementales des Territoires* (the decentralized government entities responsible for mapping watercourses and enforcing the water law at the departmental level) and looked through all layers uploaded by each department on the online interministerial catalogue of geographical data (*catalogue interministériel de données géographiques*, at <http://catalogue.geo-ide.developpement-durable.gouv.fr/catalogue/srv/eng/catalog.search#/home>), the main repository where departments have uploaded cartographic data on watercourses for the public and other agencies to access. We downloaded and examined all available data and associated metadata to customize our request for each department — this also allowed us to compile email and phone contact information for the service in charge of the cartography in each department.

Based on this pre-evaluation, we then contacted each department. The introduction of the email was as follows (originally in French):

“To whom it may concern,

As part of a thesis supported by the French National Institute for Research in Agriculture, Food and the Environment (INRAE) in Lyon, we are quantifying the current state and summarizing the methodology for mapping watercourses under the Water Law across all French departments. We refer specifically to the mapping of watercourses within the meaning of article 118 of the Biodiversity Law of 8 August 2016, and the government directive of June 3rd, 2015. Our priority is to compile geomatic data (usable with GIS software, in shapefile format for example) showing the most recent mapping of watercourses for each department.”

We then made one of three main possible requests (with a few subtle changes depending on the characteristics of the available data):

1. If an online visualization was available:

"To this end, we searched the interministerial catalogue of geographical data and your prefecture's website, but did not find a link to download the map in a format that could be used in a GIS software. We have, however, noted the existence of a platform for viewing the map online, a resource that we appreciate. Could you please provide us with the underlying dataset, which presumably must be the most recent and complete available?"

To carry out our analysis, this dataset should enable us to:

- know which hydrographic features (segments) have been surveyed*
- differentiate between hydrographic those features that have been classified as watercourses and those that were present in the initial hydrographic reference data (e.g. BD Topo, Scan 25, etc.) but which were deemed not to meet the definition of a watercourse."*

2. If online data were available but did not include information on non-watercourses:

"To this end, we have already accessed and evaluated the dataset made available through the interministerial catalogue of geographical data (link) for your department. We would like to thank you for your efforts in developing and sharing this dataset. The most recent file we have access to is dated 24-09-2020. Is this the most recent and complete version of the mapping of watercourses in your department? If not, can you provide us with it?"

We have also noticed that the layer only includes hydrographic features that have been classified as watercourses. In other words, it does not include hydrographic features in the departmental hydrographic reference dataset that have been classified as non-watercourses or that have yet to be assessed. Could you please provide us with this information?"

3. If online data were available and included non-watercourses:

"To this end, we have already accessed and evaluated the dataset made available through the interministerial catalogue of geographical data (link) for your department. We would like to thank you for your efforts in developing and sharing this dataset."

The most recent file to which we have access is dated 04/02/2020. Is this the most recent and complete version of the mapping of watercourses in your department? If not, can you provide us with it?"

The letter then ended with the following:

"Any other information on the classification of hydrographic features may be useful to us, such as the method used to identify the flow (e.g. cartographic analysis, terrain, court decision).

Many thanks in advance for your collaboration - we will then come back to you to distribute the report that will result from this work undertaken on a national scale.

Of course, don't hesitate to forward this e-mail to any contact you think might be relevant to our request. We would like to hear from you by the end of June. If possible, could you let us know that you have received our request? If not, could you tell us when we might expect the geomatic data?"

All initial requests were sent on June 1st, 2023. A follow-up e-mail was then sent to every department that did not respond on June 30th, 2023, except for those with available data on both watercourses and non-watercourses and for which metadata indicated that the dataset had been updated January 1st 2023 or after. One additional follow-up email was sent to departments for which data was available online but non-watercourses were not available. For the other departments for which no online data were available, follow-up emails and phone calls were continued until obtaining data, the last of which was provided in November.

In total, 12 departments did not respond to our request, yet we obtained data on watercourses for all departments — either online, for 68 (72%) departments, or through our direct request for the other 26 departments.

b. Harmonizing and merging watercourse maps

Departmental datasets of watercourses came in widely differing formats, level of detail in metadata, and content. Therefore, the dataset and associated metadata of each department were individually inspected and pre-formatted according to a structured protocol. Datasets which differed in geometric type (some included watercourses as polygons representing buffers around each segment), projected coordinate system, character encoding, file

naming, and file format (e.g., .TAB, .shp) were all converted into a common set of formats. Corrupt and invalid geometric records (single-point lines, records with no associated lines) were identified and removed. Non-standard special characters were removed from all attributes. If two records were fully overlapping geographically, the record with the most amount of attribute information was kept, and the other one was deleted.

The attributes associated with the data (i.e., ancillary information associated with each line in the digital maps) varied as well, with a total of 733 unique attribute names across all datasets. We harmonized attribute names for a limited set of essential attributes for subsequent analysis: the status assigned to the hydrographic segment under the Water Law, the flow permanence status of the segment (i.e., perennial or intermittent), the method of characterization of the segment (e.g., cartography, field expertise), the date of characterization, and the unique identification code associated with reference hydrographic data (e.g., BD TOPO).

Because the different categories within each of these attributes were not consistent across datasets, we also created a harmonized set of possible values for each attribute following formatting guidance provided to the departments by the National Office of Biodiversity (OFB, then called ONEMA) and the National Institute of Geographic and Forest Information (IGN)(ONEMA & IGN, 2015). For the attribute describing the status of the hydrographic segments under water law, for example, a total of 139 unique category names existed across the departmental maps, which we converted to 5 possible categories: watercourse, non-watercourse, uncategorized, inexistant and outside of the department.

After removing all lines located outside of the department to which they were associated, we merged all departmental maps to produce a single national map.

4.6.3. Downloading and formatting reference hydrographic data

Prior to the mapping of watercourses by departments for the purpose of the Water Law, two main hydrographic datasets already existed in France: BD TOPO and BD Carthage. Neither was officially considered to be a legal national reference because they were not exhaustive enough (omitting an estimated 10-30% of the drainage network depending on the area). They also did not enable a complete assessment of the watercourse identification criteria detailed above through cartographic analysis. Notably, no dataset consistently differentiated

watercourses from ditches or canals, or intermittent from ephemeral features (the latter regime being disqualifying). Nevertheless, BD TOPO was used as the starting point for the cartography of watercourses, to be completed by BD Carthage and case-by-case cartographic analysis of other data sources (i.e., scanned topographic maps, current and historical cadastral maps) and field expertise. Therefore, we used BD TOPO as our main source of comparison for the watercourse maps. We also used BD Carthage to impute information on flow regime for watercourse maps with incomplete attribute data. Finally, we used the “topographic catchment” dataset originally associated with BD Carthage as our unit of analysis smaller than departments.

Since 2017, a multi-agency initiative has been working on producing a new official reference hydrographic dataset, aimed to be both exhaustive and uniform. BD TOPAGE®, as it is called, consists of a fusion between BD CARTHAGE® and BD TOPO®, meant to be enriched with cartographic and field expertise from the departmental watercourse mapping in terms of hydronymy, addition, correction or deletion of points or routes, and modification of attributes.

Below, we provide a brief description of BD TOPO and BD Carthage for context. Both BD TOPO and BD Carthage represent all hydrographic features as lines. Therefore, they represent the centerline of flowing water channels, even for wide rivers which would be represented with an areal extent on topographic maps.

a. Description of BD TOPO

We used BD TOPO version 151 from 2015, which was recommended to departments by the guidance document from the National Office of Biodiversity and IGN (ONEMA & IGN, 2015). BD TOPO is a vectorial description (e.g., structured as geographic objects of points, lines, and polygons with attribute data) of the geographic elements of the French territory and its infrastructures, with metric precision. BD TOPO objects are grouped by theme (transport, buildings, etc.), including the hydrographic theme that was used as the cartographic foundation for departmental watercourse maps. In total, this hydrographic theme includes 7.6×10^5 km of flowing water features.

According to the technical documentation (see source in **Supplementary Table 4.S1**):

- All permanent flowing water features, natural or artificial, are included. Large ditches over 2 m wide are included when they flow permanently.
- Non-perennial natural flowing water features are included, except sections less than 200 m long at the upstream end of the network (i.e., first-order stream segments under 200-m long).
- Artificial or anthropogenically altered non-perennial features are selected on the basis of their size and environment (sections running alongside roads are excluded, as are ditches).
- Talwegs not marked by the regular presence of water are excluded.
- Underground or culverted sections longer than 25 m are retained.
- All watercourses over 5 m wide are included as a centerline.

Each hydrographic feature in BD TOPO contains a set of attributes that were supposed to be carried over to the segments in the watercourse maps, including:

- unique identifying code (e.g., TRON_EAU0000000008694588),
- hydronym (when available),
- flow regime (perennial or intermittent),
- artificial (whether the feature is natural or artificial)
- fictive (whether the geometric segment in the dataset was created despite the absence of a defined channel on the ground, either because it is piped underground or represents the centerline of a wide river).

This dataset is limited for the purpose of building watercourse maps in several ways. First, the attribute describing whether a flowing water feature is artificial is notoriously inconsistent: it does not reliably distinguish watercourses from ditches, canals, and other artificial flowing water bodies. Second, as previously mentioned, this dataset differentiates channels that flow perennially from those flowing intermittently, but does not differentiate ephemeral streams. The reliability of this classification is also limited due to inconsistent or outdated field validation. Third, BD TOPO is not exhaustive, exhibits variable precision, and generally omits a particularly large portion of the drainage network in headwater basins and forested areas. The underlying maps were largely drawn from aerial imagery taken in

summer (ONEMA & IGN, 2015) and were historically intended mainly as army intelligence, so the focus was on features of strategic importance (Cinotti & Dufour, 2019). Finally, the network was not built for systematic geospatial analysis requiring topological integrity. Therefore, numerous geometric artefacts (e.g., erroneously disconnected or looping segments, inaccurate flow direction) and complexities (e.g., multithreaded channels) in the digital river networks prevent a direct analysis of flow direction, upstream-downstream relations, or routing along the river network.

b. Description of BD Carthage

We used the 2014 version of BD Carthage, as recommended to departments by the guidance document from the National Office of Biodiversity and IGN (ONEMA & IGN, 2015). BD Carthage is the main “medium-scale” (geometric precision of 35m) vector-based hydrographic reference dataset used in France (as opposed to the large-scale BD TOPO). Although it excludes most low-order streams due to its lower precision and smaller scale, BD Carthage does include certain rivers, streams, and ditches that are not present in BD TOPO. In total, BD Carthage includes 4.7×10^5 km of flowing water features.

According to the technical documentation (accessible at the corresponding link in **Supplementary Table 4.S2**), it includes:

- segments for the main channel of all flowing water features and the centerlines of large rivers, with a minimum length of 20 meters. Exhaustiveness is ensured for features longer than one kilometer.
- In addition to the main channel, secondary channels and those delimiting islands larger than 10 ha are included.

Each hydrographic feature in BD Carthage contains a set of attributes that could complement those of BD TOPO for mapping watercourses when the attribute was missing in BD TOPO. In our analysis, we only used data on the flow regime (perennial or intermittent) of the features.

The limitations of BD Carthage are broadly the same as BD TOPO, including inconsistencies in drainage density, flow regime information, and geometric integrity of the digital river network. However, the distribution of those inconsistencies and errors are not the same as those of BD TOPO and there is no one-to-one match between these two datasets.

c. Linking watercourse maps and reference hydrographic datasets

Departmental datasets of watercourses ideally include the original attributes of each segment sourced from the corresponding hydrographic dataset (i.e., BD TOPO or BD Carthage). In total, 38% of the watercourse segments in the departmental maps included a unique identifying code from BD TOPO or BD Carthage, and 44% included information on flow permanence (from either datasets or from field expertise). Many more segments in the watercourse maps that had no attribute information on their provenance were nevertheless directly taken from one of these two datasets, as evidence by visual comparison. Therefore, we imputed missing attribute information on flow permanence in the departmental watercourse maps by spatially linking the segments from departmental datasets to segments in BD TOPO and BD Carthage. Many watercourse segments that had been directly taken from BD TOPO or BD Carthage did not overlap with their equivalent in the original hydrographic dataset, presumably owing to various geometric modifications and shifts in the departmental watercourse maps, and successive changes in projection and formats (e.g., changes in the number of decimal places in geographic coordinates). Therefore, a custom approach had to be developed to impute data in the watercourse maps, which we briefly describe below:

1. Removed all geometric duplicates from BD TOPO and BD Carthage (hydrographic segments fully overlapping another segment) and used this de-duplicated dataset for the remainder of the study.
2. Created 5-m buffers (spatial polygons uniformly surrounding the input features to a specified distance of 5 m) around every segment in BD TOPO and BD Carthage.
3. Intersected all segments from the departmental watercourse maps with the 5-m buffers and computed the length of the resulting line, denoted $L_{\text{intersection}}$.
4. Identify all pairs of BD TOPO segment and watercourse segment that meet the following conditions:
 - a. The length of the intersection line between the watercourse segment and the BD TOPO buffer must differ by less than 40% from both the length of the watercourse segment and the length of the original BD TOPO segment.
$$\text{maximum}\{|1 - L_{\text{intersection}}/L_{\text{watercourse}}|, |1 - L_{\text{intersection}}/L_{\text{BD TOPO}}|\} < 0.4$$
 - b. The lengths of the watercourse and BD TOPO segments must differ by less than 10%:

$$|1 - L_{\text{watercourse}} / L_{\text{BD TOPO}}| < 0.1$$

- c. The length difference between the watercourse segment and the intersection line, and the length difference between the BD TOPO segment and the intersection line must differ by less than 10%.

$$|(L_{\text{intersection}} / L_{\text{watercourse}}) - (L_{\text{intersection}} / L_{\text{BD TOPO}})| < 0.1$$

5. If multiple BD TOPO segments meet these conditions for a given watercourse segment, keep the BD TOPO segment with the lowest maximum deviation between the watercourse and BD TOPO segments on the one hand and the intersection on the other. That is, the BD TOPO segment that minimizes the following criterion:

$$\text{maximum}\{|1 - L_{\text{intersection}} / L_{\text{watercourse}}|, |1 - L_{\text{intersection}} / L_{\text{BD TOPO}}|\}$$

This matching protocol was developed through visual examination and sensitivity analysis based on the watercourse segments for which the BD TOPO identifying code was already included in the departmental maps. Our aim was to balance precision, the fraction of all watercourse segments linked with this method that were matched to the correct BD TOPO segment, and recall, the fraction of watercourse segments for which we knew that there existed a corresponding BD TOPO segment (because a unique identifying code attribute was available in the department map) that were successfully linked through this method to the correct BD TOPO segment. We estimate that precision is 77% and recall is 85%. We chose thresholds that led to a higher recall than precision because we assumed that if a BD TOPO segment matched all the criteria we established (in terms of position in the catchment and length), then it was likely to have the same flow permanence regime as the original segment that was used to produce the watercourse segment.

The same protocol was implemented to match BD Carthage segments, but allowing only a 20% maximum deviation in length between the watercourse and BD TOPO segments on the one hand and the intersection line on the other.

With this approach, we managed to increase the proportion of watercourse segments with information on flow permanence from 44% to 85% for subsequent analysis.

4.6.4. Computing drainage density ratio

We quantified the difference in drainage density between the departmental watercourse maps and BD TOPO as the ratio in drainage density between the two at the level of departments and sub-basins. To compute the drainage density ratio in sub-basins, we first intersected sub-basins (see **Supplementary Table 4.S2** for the corresponding data source) with the administrative boundaries of departments.

We then identified sub-basins in which watercourse mapping had not been conducted to avoid underestimating the drainage density ratio in departments where mapping is still ongoing. Identifying those incomplete areas is complicated by low or zero drainage density in some sub-basins due to various natural and anthropogenic factors, particularly small ones. In other sub-basins, the lack of segments results from most segments in the original hydrographic datasets having been categorized as non-watercourses and excluded from the final department dataset.

Therefore, we initially identified sub-basins with missing data as those that meet the following conditions:

- The total drainage length in the watercourse map (including segments categorized as watercourses or non-watercourses as well as uncategorized segments) is less than 5% of the total drainage length in BD TOPO.
- The total drainage length in BD TOPO in that sub-basin is more than 1000 m.
- The sub-basin is more than 5 km² or surrounded by other sub-basins with missing data.

These initial criteria were then refined by including additional sub-basins in areas where employees from the cartographic services of a department had warned us that the map was still largely incomplete (e.g., the hilly and forested eastern regions of the Vosges department). In total, these sub-basins represent only 3.4% of the country's area.

After this initial pre-processing, the drainage density ratio (DDR) for a given sub-basin or department (excluding incompletely mapped sub-basins) was simply computed as:

$$DDR = \frac{\sum segment\ length_{watercourse} + \sum segment\ length_{uncategorized}}{\sum segment\ length_{BD\ TOPO}}$$

4.6.5. Stream order assignment to the digital hydrographic networks

Neither the departmental watercourse datasets nor BD TOPO included information on the relative position of segments in the hydrographic network — whether as drainage area, stream order or estimated discharge. In addition, the direction of many hydrographic lines in these datasets did not match the actual direction of flow along the corresponding channels. In other words, there was no consistent, explicit information on whether a given segment was a small headwater rivulet or the outlet of a large river. Consequently, it was necessary to enhance both datasets to examine how the classification of hydrographic features as watercourses or non-watercourses potentially impacted network integrity, with a particular focus on Strahler stream order.

The Strahler stream ordering framework (Strahler, 1957) is a numerical system used to classify the hierarchy of streams within a watershed (**Supplementary Methods Figure 4.S4**). In this system, the smallest headwater streams in a hydrographic network are assigned an order of 1. When two streams of the same order intersect, they form a higher-order stream (2 in this case). The stream order increases by one with each confluence of streams of the same order. This system describes the relative position of individual reaches within hydrographic networks taking in account their branching pattern, and thus provide a proxy for their relative size even in the absence of ancillary topographic or hydrological data.

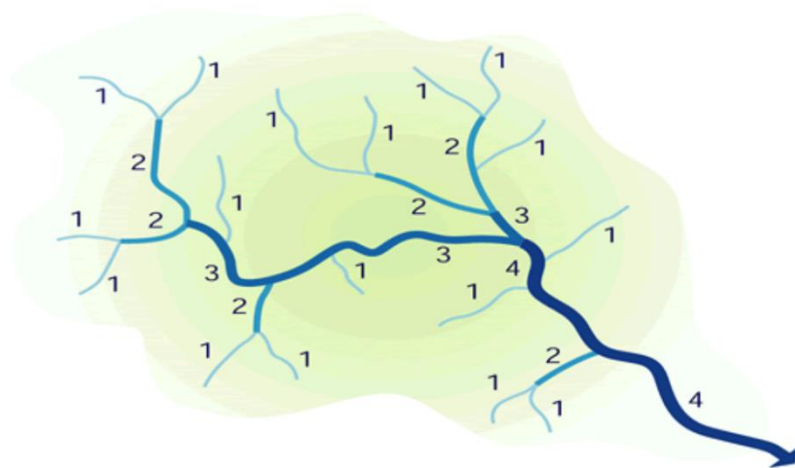


Figure 4.S4. Illustration of the Strahler stream ordering system for a fourth-order catchment.

Reproduced from Federal Interagency Stream Restoration Working Group (1998).

To compute the Strahler order of segments in a digital hydrographic network requires an accurate representation of the spatial (topological) relationship among hydrographic segments. The connectivity between segments should be well-defined, indicating the flow direction from one segment to another. Nodes in the digital hydrographic should be appropriately defined to represent confluences where two or more streams meet. Computation is thus limited when segments are disconnected, flow direction is incorrect, confluences are inaccurately placed, or multiple lines overlap and erroneously intersect each other. Bifurcations and loops in the hydrographic network also complicate this calculation as the Strahler order should not increase by one when the two arms of the watercourse meet downstream. Every departmental watercourse dataset and BD TOPO contained all of these artefacts and difficulties. We thus developed a custom workflow to infer the Strahler stream order of as many segments as possible in the departmental watercourse maps and in BD TOPO up to the fifth order.

Below we provide a technical description of this workflow:

1. Remove segments whose name explicitly mentioned an artificial or estuarian hydrographic feature through pattern matching (i.e., *canal*, *foss[eé]*, *roubine*, *craste*, *d[ée]rivation*, *bief*, *aber*, *hydraulique*), which would confound network analyses (e.g., by crossing across drainage lines, linking naturally disconnected tributaries, etc.).
2. Remove all overlapping segment sections (even if partially).
3. Fuse vertices from adjacent segments within 0.1 m from each other to reconnect segments separated by very small gaps as well as nearly overlapping segments that tend to repeatedly intersect and create artefactual loops.
4. Fuse and re-split the entire hydrographic network to ensure that each segment extends only between two neighbouring confluences (i.e., so that no section between two confluences is split in multiple parts, and no segment extends beyond a confluence).
5. Remove all segments under 10 m in length with at least one end point (start or end point) that are not connected to any other segment. Many of these segments represent drawing inaccuracies (e.g., under- or overshoots at intersections, truncated segments), would artificially increase the stream order of downstream segments if

intersecting with another first-order segment, and their flow direction cannot be reliably inferred from topographic data.

6. Extract elevation every 25 m along the length of every segment based on the BD ALTI® Digital Elevation Model (DEM) version 2.0 (with a 25-m spatial resolution; see **Supplementary Table 4.S2**).
7. Compute the average slope along each segment by fitting an ordinary least-square squares regression to elevation as response variable and distance along the hydrographic segment as predictor. Segments correctly going downstream should have a negative coefficient.
8. Flip the direction of segments with a positive regression coefficient over 0.1, that is, segments whose direction from start to end node is upstream. This threshold was determined through trial and error.
9. Assign a Strahler stream order of 1 to all segments whose starting point (now presumably well identified after correcting flow directions) is not connected to any other segment. This overlap with the starting point is meant to differentiate first-order streams from network outlets whose end point should not be connected to any other hydrographic segment, provided that the direction of the segments (i.e., the relative position of the start and end points of the segment) is correct.
10. Once this initial set of first-order streams are identified, an **iterative stream order assignment approach** which we designed to cope with unreliable flow directions is implemented for each stream order O from 1 to 5:
 - a. Identify all segments that are part of “simple” loops in the hydrographic network. Loops occur in the case of diversion canals (e.g., towards a mill) which flow back into the main channel, or around river islands. Identify loops by excluding segments with an assigned stream order, re-fusing and splitting the rest of the network between confluences, and finding pairs of segments whose start and end points overlap (this fusing and re-splitting of the network is only implemented to identify loops and all their constitutive segments; it is not used in subsequent steps of this iterative workflow).

- b. For loops connected to a single undefined segment (i.e., presumably the downstream segment) and at least one other segment with a defined Strahler order, identify the highest Strahler order connected to the loop (O_{max}).
 - If only one connected segment is of this order, assign this order O_{max} to all segments composing the loop and the connected (downstream) undefined segment.
 - If more than one segment is of this order, assign $O_{max}+1$ to all segments composing the loop and the connected (downstream) undefined segment.
 - c. Assign a stream order of $O+1$ to segments:
 - whose stream order is not yet defined, and
 - that are not part of a loop or connected to segments in a loop (considering only loops whose order was not defined in the previous step), and
 - that are connected to at least two streams of order O , and
 - that are connected by one end point to either one or no other undefined segment, and
 - that are not connected to a segment with stream order $> O+1$.
 - d. For every (source) segment of order $O+1$ that is connected by an end point to a single (target) undefined segment, extend stream order $O+1$ to that target segment if that target segment is not connected by that end point to another undefined segment or to another segment of stream order $\geq O$. Repeat this step (*d, routing stream order $O+1$*) until no remaining pair of segments in the network meets these criteria.
 - e. Go back to step *a* for stream order $O+1$.
11. Assign a stream order of 1 to segments under 500 m length, with no defined stream order, one end point not connected to any other segment, and the other end point connected to at least one other segment with a defined stream order. If multiple segments meet these conditions and are connected to the same segment with a defined stream order, only assign a stream order to one of these previously undefined segments. This measure attempts to correct for first-order streams whose flow direction was not corrected (or erroneously) corrected through the slope calculation.

12. Iteratively route each stream order using the same approach described in step 10.d backward from the highest to the lowest stream order (from 5 to 1).
13. Re-implement the entire iterative stream order assignment approach (steps 10.a through 10.e) for each stream order O from 1 to 5. This continues assigning stream orders downstream of sections that had been blocked by these undefined (first-order) segments.
14. Transfer the assigned stream order from this modified hydrographic network to the original hydrographic network (before deleting partially overlapping lines, fusing, splitting, etc.), assigning to every segment_{original} in the original network the stream order from the segment_{modified} in the modified network that overlaps with that segment_{original} along the longest length.

We applied this approach to the newly produced map of watercourses and to BD TOPO, resulting in 73% and 72% of segments in those hydrographic networks being assigned a stream order, respectively. In total, it took about 10 days to run this workflow for both datasets. We limited it to stream orders 1 through 5 because of the prevalence of complex loops in higher order streams which could not be processed through this approach. Those complex loops (i.e., multiple loops either connected to or nested within one another) result from a combination of intense human alteration (e.g., diversion canals for irrigation or hydroelectric production) and multithreaded planform *involving multiple interconnected channels, often with mid-channel bars and islands*, and many confluences and diffluences in larger lower-gradient rivers.

4.6.6. Assembling a database of socio-environmental correlates

We assembled and processed a suite of datasets to characterize the distribution of potential socio-environmental correlates of drainage density ratio across sub-basins of anthropogenic land covers (i.e., agriculture, impervious area), irrigation, population density, barrier density, soil texture, slope, and aridity. **Supplementary Table 4.S2** details the source of each dataset.

These datasets were selected for two reasons. First, because we hypothesized that the associated variables could influence the proportion of hydrographic features deemed as non-watercourses, and second because of their availability at a sufficient resolution and consistency across France. We used socio-environmental variables rather than all variables

potentially explaining absolute drainage density across the landscape because our focus was on deviations in drainage density from the reference hydrographic dataset BD TOPO. We particularly focused on factors which could affect the criteria used in identifying watercourses: naturalness of the channel bed and flow permanence. Therefore, we selected variables reflecting the degree of alteration of the riverscape (land cover, irrigation, barrier and population density) as well as the relative prevalence of non-perennial rivers and streams (aridity, slope, predicted prevalence of flow intermittence, soil water storage capacity, irrigation and water withdrawals).

Below we briefly present each dataset and how it was pre-formatted to compute summary statistics for each sub-basin.

a. Land cover

We computed the average percentage extent, from 2019 to 2021, of agriculture, pastureland, winter crops, summer crops, orchards, vineyards, and impervious cover in each sub-basin and department based on land cover maps from the Theia Scientific Expertise Center on Land Cover (Inglada et al., 2017). These land cover maps, which span mainland France, were developed at a spatial resolution of 10 meters from Sentinel-2A and Sentinel-2B satellite imagery. They were produced with a supervised classification procedure (i.e., a Random Forest model) calibrated with a dataset combining several national and international sources of vector and raster data (BD TOPO IGN, Corine Land Cover, Urban Atlas, Référentiel Parcellaire Graphique, etc.).

The original maps contain 23 land cover categories with a hierarchical nomenclature (<https://www.theia-land.fr/en/product/land-cover-map/>). We followed this structure to aggregate classes and compute the extent of:

- Agriculture, which includes winter crops, summer crops, pastureland, orchards and vineyards.
- Winter crops includes winter oilseeds, straw cereals, and spring oilseeds.
- Summer crops include soy, sunflower, corn, rice, and tubers and roots.
- Impervious cover includes dense built-up area, diffuse built-up area, industrial and commercial areas, and roads.

We used the data from 2019 to 2021 despite the existence of older land cover maps from this same source for consistency because a change of method and nomenclature took place starting in 2018 (and 2018 files were corrupt).

b. Aridity

We computed long-term (1970–2000) mean annual and mean summer aridity based on the Global Aridity Index and Potential Evapo-Transpiration (ET0) Database v3, which has a resolution of 30 arc-sec (~ 1km at the equator). Aridity in this dataset is expressed as the long-term monthly average ratio of precipitation to Potential Evapo-Transpiration (PET). The underlying climatic variables, including precipitation, were obtained from the WorldClim v 2.1 dataset, and PET is based upon the FAO-56 Penman-Monteith Reference Evapotranspiration equation (Zomer et al., 2022).

The mean summer global aridity index was computed as the average value of July, August and September aridity, and the mean annual index was computed as the average value across all months. For better comprehension in the main text, we inversed the index to express the ratio between PET and precipitation, such that an increase in the index expresses more rather than less aridity. We used this global dataset because long-term climate averages for France at a fine enough resolution to vary across sub-basins within a department were not freely available.

c. Slope

We computed the average slope in sub-basins and departments based on the BD ALTI® Digital Elevation Model (DEM) version 2.0. BD ALTI is an aggregated version at a spatial resolution of 25 m of the 5-m resolution RGE ALTI®. We used a lower-resolution dataset for computing slope and inferring the flow direction of hydrographic segments because it provides a smoother surface, which minimizes the prevalence of outliers and artefacts. BD ALTI is based on airborne altimetric data across mainland France, acquired either with radar or LiDAR technology. After mosaicking all BD ALTI tiles for mainland France, slope in degrees was calculated on the resulting raster in its original projected coordinate system (RGF93 v1 / Lambert-93 + NGF-IGN69 height) using standard methods: slope is measured as the maximum rate of change in elevation value from each cell to its immediate neighbors (i.e., within its 3 by 3 cell neighborhood) using a third-order finite difference estimator.

d. Irrigated extent

We used a national census of irrigated agricultural extent by municipality and department conducted in 2020 as the basis for our estimate of irrigated extent in sub-basins and departments. The census provides the percentage of irrigated “useful agricultural area” for about 25,000 out of 34,500 municipalities in France representing 70% of the country’s surface area and 87% of the irrigated area. No data are available for the rest of municipalities for reasons of anonymity. The useful agricultural area is reported for all municipalities, and the total percentage of irrigated area is also reported for every department.

Therefore, we inferred the area under irrigation in the remaining municipalities with the following approach:

- Compute the irrigated area in each municipality with data (as the product of the percentage of irrigated useful agricultural area and useful agricultural area, which is provided for all municipalities).
- Compute the irrigated area by department as the product of the percentage of irrigated useful agricultural area in the department and useful agricultural area in the department. These statistics are available for all departments.
- Compute for each department the difference between the irrigated area in the department and the sum of declared irrigated area at the level of municipalities. This figure represents the total irrigated area in municipalities of that department where data on percentage irrigated area are not made available.
- Allocate this remaining irrigated area to municipalities without irrigation data proportionally to the useful agricultural area in each municipality. For instance, if 1000 ha of irrigated area were not assigned to any municipality in a department, and a municipality contained 10% of the total useful agricultural area across all municipalities without data on irrigation, then 100 ha of irrigated area would be allocated to that municipality.
- For the handful of municipalities where the reported useful agricultural area exceeds the total area of the municipality (presumably due to data entry errors in the census), leading to the irrigated area exceeding the total area of the municipality, set the irrigated area to 95% of the municipality area.

We then inferred the area under irrigation in each sub-basin with the following approach:

- Intersect sub-basins with municipality boundaries.
- Compute the area of primary irrigated crops and the total agricultural area in 2020 in every sub-basin-municipality intersection based on the previously mentioned land cover maps. We consider primary irrigated crops as those crops for which more than 10% of the surface area was irrigated in France in 2020 according to the national census (Ministère de l'Agriculture et de la Souveraineté alimentaire, 2022): corn, vegetables, orchards, potatoes, beets, soy.
- Compute in every sub-basin-municipality intersection the percentage of potentially irrigated crops in the municipality that is located within the sub-basin. If there are no primary irrigated crops in a municipality, then compute the percentage of total agricultural area among its intersecting sub-basins.
- Compute the irrigated area within each sub-basin by adding up the product across all its intersecting municipalities of the total irrigated area in each municipality and the percentage of potentially irrigated crops within that municipality that falls within the boundaries of the sub-basin.

e. Water withdrawals

Time series of yearly withdrawals amounts, and geographic coordinates of withdrawal structures were downloaded from the French national database of water withdrawals (Banque Nationale des Prélèvements en Eau; BNPE). The database only includes volumes withdrawn, measured, or estimated and reported by users subject to the withdrawal fee to the water agencies and offices. This includes volumes greater than 10,000 m³ (or 7,000 m³ in some cases). Small volumes are therefore not recorded. No information is available on the actual consumption of water and return flows to the environment.

All withdrawal points were first overlayed with sub-basins to allocate each point to a sub-basin. We then computed the average amount of withdrawn water per unit area (m³ km⁻²) from 2015 to 2022 in every sub-basin by water source and usage. Water source categories included surface versus groundwater, and usage categories we considered included irrigation and water for domestic use.

We only considered water withdrawals in building models to examine variations in drainage density within departments rather than across departments because the level of reporting of these withdrawals is still inconsistent across administrative units.

f. Plant available water capacity of the soil

We computed the average soil available water capacity in each sub-basin from a map across mainland France produced by the Theia Scientific Expertise Center on Digital Soil Mapping (Román Dobarco et al., 2019). This map was produced at 90-m resolution by applying pedo-transfer functions to predicted soil properties estimated through spatial modelling (regression-kriging and quantile regression forest) calibrated with empirical data (Román Dobarco et al., 2019). Plant available water capacity (AWC) refers to the maximum amount of water in millimeters that a soil can store in its pores and provide to plant roots. We used this property as an available, high-resolution integrative measure of the hydrologic properties and overall depth of the soil profile, which influences both drainage density and the suitability of soils to agriculture. We computed the average AWC from 0-2 m depth across each sub-basin with simple weighted mean of the AWC across soil horizons (0-5, 5-15, 15-30, 30-60, 60-100, 100-200 cm).

g. Flow intermittence

We calculated the estimated prevalence of non-perennial rivers and streams in each sub-basin based on model predictions of natural intermittence by Snelder et al. (2013). These estimates by Snelder and colleagues were produced at the scale of river reaches in a theoretical hydrographic network (Pella et al., 2012) derived from a digital elevation model with 50 m resolution (i.e., neither BD TOPO nor BD Carthage). The underlying Random Forest modelling approach used climatic, topographic and geological data as predictors and was calibrated with daily flow records from 628 gauging stations on rivers with minimally modified flows distributed throughout France. Because the digital hydrographic network used in that study did not correspond to any of the ones we used in our analysis, we computed for each sub-basin the percentage length of rivers and streams in the theoretical network that was predicted to stop to flow at least once from 1978-2009. We included this variable as a relative measure of natural intermittence among sub-basins and departments rather than as an absolute measure of intermittence.

h. Artificial barrier density

We calculated the density of artificial longitudinal barriers (barriers km⁻¹) on hydrographic features in each sub-basin as the ratio between the number of barriers recorded in the Adaptive Management of Barriers in European Rivers barrier atlas (AMBER Consortium, 2020) and the total length of uncategorized and watercourse segments. In France, the AMBER Barrier Atlas contains geographic information on over 60,000 barriers, which were mostly but not exclusively sourced from the government-curated national repository of obstacles to water flow. The AMBER Barrier atlas has the advantage of having undergone an additional data-quality checking process to remove duplicates (Belletti et al., 2020). In our computation, we included all types of barriers: dams, weirs, sluices, culverts, fords, ramps, and other or undefined types. The aim of including this variable was to examine the relative degree of human alteration of the longitudinal connectivity of flowing waters across sub-basins and departments.

i. Population density

We calculated the average population density in each sub-basin based on 2019 census data from the National Institute of Statistics and Economic Studies (INSEE). Census data on the number of people and tax households across the country is provided either as a regularly sized grid composed of 200-m square tiles but with no data in low-density areas due to anonymization, or as a grid composed of tiles of variable sizes. The variable-size grid is produced by iteratively aggregating the 200-m tiles to progressively larger sizes until no tile contains fewer than 11 tax households. After 200 m, the size increments are 1 km, 2 km, 4 km, 8 km, 16 km, 32 km, or 64 km. We used this variably sized grid and ancillary data to estimate the population in each 200-m tile in the regularly sized grid for which no data were available.

Our approach consisted of downscaling population data from the scale of tiles of variable size to the scale of individual buildings, and to then infer the population in each 200-m tile with missing data by adding up the population across all buildings within it. This approach, called dasymetric mapping, has been shown to be successful in previous studies (Messenger et al., 2021).

We used a dataset of building footprints and associated attributes from the 2019 version (191) of BD TOPO. It contains a polygon for each individual building, defined as any

construction above ground used to shelter humans, animals, objects, for producing economic goods or for the provision of services. It contains information, for most buildings, of their architectural form (e.g., church, monument, industrial, undifferentiated), primary and secondary purpose (e.g., residential, agricultural, commercial and services, religious, sports, and undifferentiated), number of floors and height, number of housing units, whether it is a light structure (without foundations, or with part of the building open on at least one side) and whether it is still in use or abandoned. No building footprints are available for the departments of Ain and Sarthe, so we were unable to apply this approach there.

Our downscaling workflow consisted of the following steps:

- Subset buildings to only keep those in use, with foundations, whose primary or secondary purpose is residential or undifferentiated, whose architecture is either undifferentiated or a castle, whose height is either over 2 m or undefined, and whose footprint's surface area is at least 20 m² (the minimum legal size of a new house in France is 30 m²).
- Assign each building to the variably sized tile that overlaps with over half of its footprint.
- Similarly assign each building to a 200 m tile (in the constantly sized grid).
- Compute the volume of each building as the product of its height and surface area. If no height information is available, compute its volume based on the standard minimum height of a single floor house in France, which is four meters.
- In every tile, make sure that the number of housing units assigned to buildings matches the number of tax households according to the census in that tile:
 - If the total number of building-based housing units is inferior to the number of households according to the census, and there are buildings without a registered number of household units in that tile (mainly due to inconsistencies in reporting in the buildings database), allocate the unaccounted housing units to those buildings proportionally to their volume.
 - If the total number of building-based housing units is inferior to the number of households according to the census (e.g., by 15%), and all buildings in the tile have a

registered number of household units, then uniformly decrease the number of housing units in all buildings (i.e., by 15%).

- Similarly, if the total number of building-based housing units exceeds the number of households according to the census, and all buildings in the tile have a registered number of household units, then uniformly increase the number of housing units in all buildings.
- Compute the number of individuals in each building as the estimated number of household units in the building multiplied by the average number of individuals per housing unit in that tile according to the census.
- Compute the population in each 200-m tile with no data as the sum of the number of individuals across all buildings in the tile.

We then estimated the average population density in each sub-basin and department as the mean population across all tiles whose center falls within the sub-basin.

j. Artificial non-irrigation basins

Visual examination of DDR maps revealed areas of very low DDR along coastlines characterized by high densities of managed marshland, often meant for sea salt production (in Charentes-Maritimes and Bouches-du-Rhône, for example). These areas are characterized by high densities of small hydraulic works, ditches meant to control the ebb and flow of seawater into the managed salt marshes. We computed the relative extent of those artificial non-irrigation basins by intersecting standing water bodies from the 2019 version of BD TOPO (**Supplementary Table 4.S2**) that were classified as artificial or altered marsh/swamp or non-irrigation basin. We used the 2019 version of BD TOPO because these categories were inconsistent in the 2015 version.

4.6.7. Analysis of interdepartmental correlates of drainage density ratio

We developed multiple linear regression models to quantify the relationships between drainage density ratio (DDR) and socio-environmental factors across departments. The objective of this model development was explanatory rather than predictive. Our goal was to understand potential mechanisms driving the observed differences in drainage density ratio among departments. Therefore, we chose to use simple linear regression models for their simplicity and interpretability, provided that the underlying assumptions were met.

These regression models were developed through manual forward model selection and standard diagnostics (Faraway, 2004; Kuhn & Johnson, 2013). Model diagnostics were primarily performed through extensive graphical examination of the data, model predictions and residuals, rather than through formal tests. The full model selection workflow is reproduceable by code in R: https://github.com/messamat/cartographie_cours_deau_R.

Prior to model development, we visualized the distribution of all variables. We also examined the degree of correlation between each predictor variable and DDR by computing Spearman's rank correlation coefficient (**Supplementary Table 4.S3**) and inspecting scatter plots of each variable against DDR. We also assessed correlation among predictor variables through a Spearman's correlation matrix.

After this initial assessment, we iteratively built regression models of increasing complexity by progressively adding predictors with the following workflow, starting from a "null" model with only an intercept:

1. Build a regression model, adding the predictor variable with the strongest correlation to DDR (based on Spearman's correlation and the scatter plots).
2. Assess whether the model is significant, the regression coefficients are significant (both in terms of p-value and effect size) and sensible, and whether the residuals suggest that model errors are independent and identically distributed (i.i.d.) with mean 0 and variance σ^2 . To this end, we examined a histogram of residuals, a Q-Q plot, as well as scatter plots of residuals against observed DDR, predictor variables, the fitted values, and leverage.
3. In the case of heteroscedasticity or non-linearity in residuals, consider transformation in a relevant predictor.
4. Diagnose multicollinearity in predictors by looking for large changes in regression coefficients between this model and the previous one, and by computing variance inflation factors (VIF). We aimed for VIF values as low as possible and under 5.
5. Determine whether the adjusted R^2 and Mean Absolute Error of the model improved enough compared to the previous model to justify the variable addition.
6. If the model does not improve compared to the previous one, remove the added predictor variable and use the previous model as the final model. Otherwise, examine

scatterplots of the model residuals against all other predictor variables. If relevant, select the predictor variable with the stronger correlation to the residuals and to DDR, and add it to the next model for diagnostics (going back to step 1).

Although presented linearly and mechanically for simplicity, this model involves multiple back and forth as well as the comparison of multiple competing models for every addition of a variable. Variable selection here is meant to find the least number of variables that provide the most explanatory power, while making sense. Variables that are not included in the final model are not unrelated to the response, they only provide either less or no additional explanatory power to the model without unnecessary complexity. The original correlation coefficients can be used as an indicator of those variables which could likely be substituted with those in the final model. Inspection of the residuals did not call for transformation of the response variable or the use of generalized linear models.

Once a final model was chosen, we evaluated whether model residuals were spatially autocorrelated through cartographic visualization of the residuals and Moran scatterplots. Moran scatterplots in this case showed the relationship between the residuals in a department and the weighted average value of the residuals of neighbouring departments. We modeled the relative strength of autocorrelation between a department and its six nearest neighboring department as a pairwise matrix of Inverse Distance Weights (IDW, of power 2). We tested for spatial error dependence or for a missing spatially lagged dependent variable with Lagrange multiplier diagnostic tests (both simple and robust to account for outliers; Anselin & Rey, 1991). In this model across departments, no significant spatial autocorrelation was detected in residuals.

4.6.8. Analysis of intradepartmental correlates of drainage density ratio

We developed multiple linear regression models to quantify the relationships between drainage density ratio (DDR) and socio-environmental factors across sub-basins within departments. Our goal with this analysis was to use these relationships as indicators of the different ways that the watercourse jurisprudential criteria were applied across departments. For example, a strong negative relationship between aridity and drainage density ratio among sub-basins of a department would suggest a particular emphasis in that department on the flow permanence criterion in differentiating watercourses from non-watercourses (and likely a pronounced gradient in aridity across the department). Strongly

contrasting coefficients among departments in this relationship suggests a potential difference in the application of that criterion.

For this analysis, we only focused on sub-basins with a surface area of at least 10 km² and a hydrographic network length of at least 500 m in BD TOPO. This subset comprised 98.7% of the country's area and was meant to avoid biasing the models with outlying values due to locally varying drainage density and watercourse mapping, and greater uncertainty in summary statistics of predictors in small areas.

Before developing regression models, we examined the Spearman's rank correlation coefficients between each socio-environmental variable and drainage density ratios across sub-basins in each of the 90 departments (**Supplementary Figure 4.S1**). We then statistically identified groups of departments that displayed similar correlation coefficient values across all predictor variables and developed a regression model for each of those groups. This grouping was meant for us to get a general understanding of the different sets of relationships present in the dataset, considering the large number of departments (90), sub-basins (6523) and variables (20), and to look for possible geographic patterns in those relationships. It also enabled us to neither develop 90 tailored models for individual departments nor build a single model for all departments. Building dozens of models would be onerous but more importantly would fail to leverage the large sample sizes and greater precision afforded by pooling sub-basins across departments, and to formally test for differences in regression coefficients among departments. A single large model, by contrast, even if including interactions, assumes that the relationships between predictors and DDR are somewhat homogeneous across all departments. If some departments display a strong relationship between DDR and a specific predictor while the others do not show any relationship for this predictor, adding this predictor will add noise for the latter departments. Even with the use of interaction terms, pooling all departments tends to produce an average model, making it more difficult to detect unique patterns present in individual groups of departments. Therefore, developing models for groups of departments that we preliminarily identified to display similar relationships was a tractable compromise between those two approaches.

We grouped departments through agglomerative hierarchical clustering according to multivariate similarity based on the Spearman correlation coefficient between DDR and the

20 socio-environmental predictors (**Supplementary Figure 4.S1**). Multivariate similarity was measured as the weighted pairwise Gower's distance calculated among departments. Because all variables (correlation coefficients) were continuous and on the same scale (0-1), the Gower's distance is equivalent to the multivariate Euclidean distance with weights assigned to each variable to avoid the dominance of collinear variables in driving the clustering (**Supplementary Methods Table 4.S5**). The precise value of these weights did not strongly influence the cluster memberships.

Table 4.S5. Candidate predictor variables and associated clustering weights for multiple linear regression models of drainage density ratio at the scale of sub-basins

Variable	Weight
Agricultural extent (% area)	0.25
Pasture extent (% area)	0.25
Summer crop extent (% area)	0.25
Winter crop extent (% area)	0.25
Orchard extent (% area)	0.25
Vineyard extent (% area)	0.25
Impervious extent (% area)	0.50
Population density (people km ⁻²)	0.50
Mean summer aridity (-)	0.25
Mean annual aridity (-)	0.25
Predicted prevalence of intermittence (% length)	0.50
Irrigated extent (% area)	1.00
Withdrawals from groundwater for irrigation (m ³ km ⁻²)	0.25
Withdrawals from surface water for irrigation (m ³ km ⁻²)	0.25
Withdrawals from groundwater for domestic use (m ³ km ⁻²)	0.25
Withdrawals from surface water for domestic use (m ³ km ⁻²)	0.25
Plant available water capacity (mm)	0.50
Slope (°)	1.00
Barrier density (barrier km ⁻¹)	0.50
Artificial basins extent (% area)	0.50

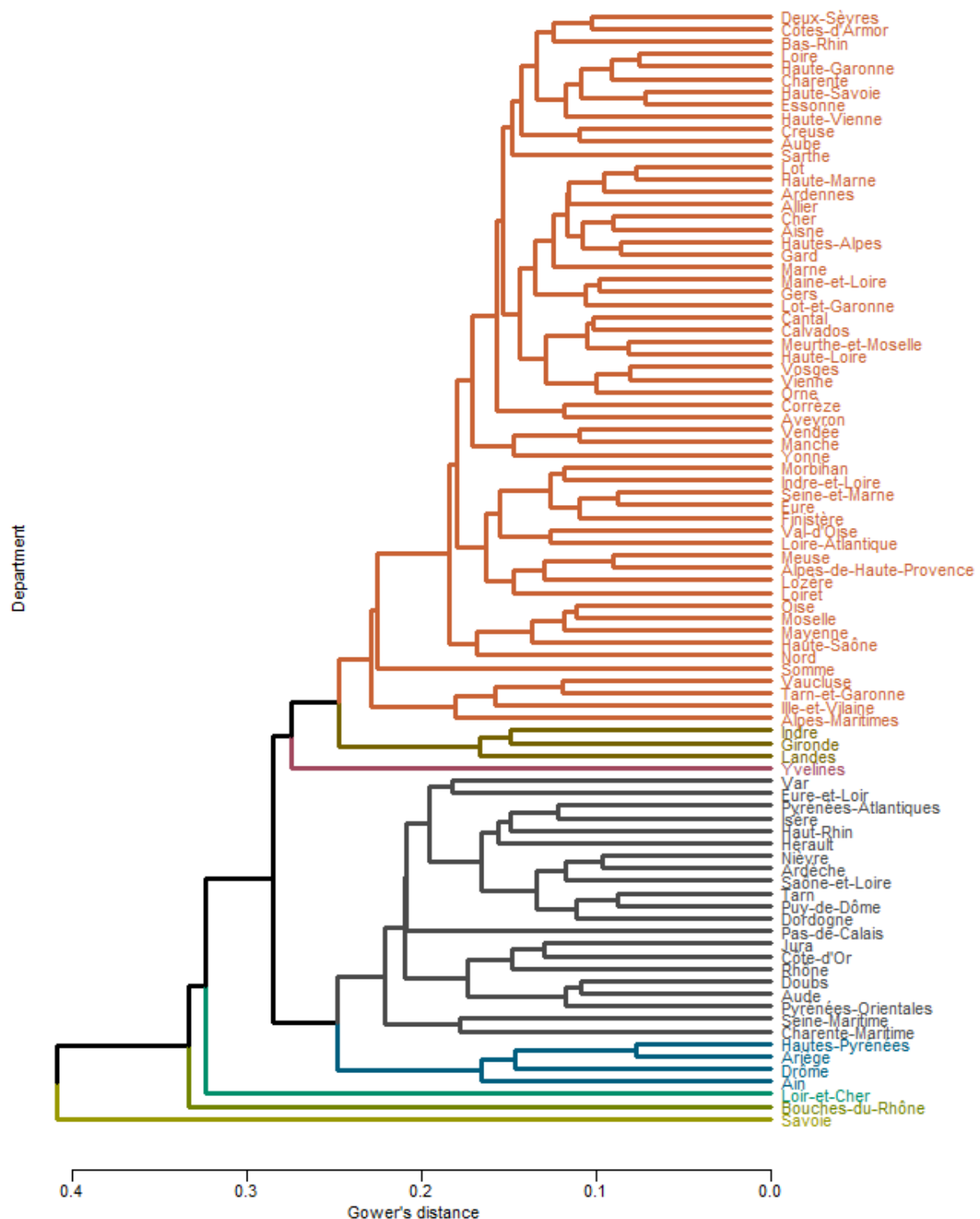


Figure 4.S5. Dendrogram depicting the eight groups resulting from the hierarchical clustering of the 90 departments in France according to the correlation coefficients between drainage density ratio and 20 socio-environmental variables.

The horizontal axis of the dendrogram represents the multivariate distance between departments and between clusters according to the correlation coefficients.

We compared the results from two clustering algorithms, Ward's Minimum Variance algorithm and Unweighted Pair Group Method with Arithmetic Mean (UPGMA), both known to be space-conserving (i.e., they are not biased with respect to artificially forcing the formation of clusters) and to maximize clustering performance. We selected UPGMA as the method with the highest cophenetic correlation coefficient (0.70 vs 0.58 for Ward's), the linear correlation between the distances among departments according to dendrogram branches (**Supplementary Figure 4.S1 for UPGMA**) and the original pairwise Gower's distances among departments. The scree plot of the resultant dendrogram was examined to identify a tractable yet discriminating number of clusters.

Once departments were clustered into relatively homogeneous groups, the development workflow implemented for the single interdepartmental model was applied to develop a model for each group of departments. The main differences in this model are that:

- we square-root transformed population density, barrier density and winter crops extent for all departments and log-transformed artificial basin extent to ensure comparability of the associated regression coefficients across models.
- We inspected pairwise correlation heatmaps across predictor variables for each separate group of departments.
- For almost all models including multiple departments, we included department-specific intercepts and tested fixed-effect interactions between departments and predictors to allow for department-specific coefficients. Interactions were introduced if visual analysis of color-coded scatterplots (by department) between the predictor and DDR, or between residuals and the predictor suggested differing relationships among departments.

Spatial collinearity was detected among the residuals of two models with Lagrange multiplier diagnostic tests. Therefore, we built a spatial lag model (mixed regressive, spatial autoregressive model) for two departments (clusters 1 and 2). This spatial lag model incorporates the spatial dependence of DDR in a sub-basin i upon the DDR in each k -nearest-neighboring sub-basin j ($k=4$), where ρ is the spatial autoregressive coefficient and $w_{i,j}$ is the globally-standardized inverse distance weight between i and each j , such that:

$$DDR_{grp,i} = \alpha + \rho \sum_j w_{i,j} DDR_j + \beta_1(socioenv.correlate) + \dots + \epsilon_i,$$

where $\epsilon_i \sim N(0, \sigma^2)$.

Supplementary Figure 4.S2 and **Supplementary Table 4.S4** show the distribution of clusters and final models selected through this process.

4.6.9. Representativeness analysis of vulnerable waters in subset of departments

We analyzed the potential impacts of excluding segments from watercourse maps on the integrity of river networks by estimating the proportion of headwater and non-perennial reaches categorized as non-watercourses nationally and for each department. Following previous publications in the US (Creed et al., 2017; Lane et al., 2023), we collectively refer to first-order and non-perennial reaches as vulnerable waters. This analysis was based on a joint analysis of both departmental watercourse maps and the BD TOPO hydrographic dataset.

This analysis required information on which hydrographic segments had been categorized as non-watercourses as well as the flow permanence status (perennial or intermittent) and Strahler stream order of each hydrographic segment. We managed to determine the Strahler stream order of most segment length and for nearly all first-order reaches (**Supplementary Methods 4.6.5**). We were thus primarily limited in this analysis in departments where data on non-watercourses was not or partially available (i.e., those that included some non-watercourse segments in the final database but omitted others which were present in BD TOPO or BD Carthage) and where a small proportion of segments had information of flow permanence (either provided in the original departmental watercourse map or inferred through spatial linkage to BD TOPO).

We coped with limited data on non-watercourses by analyzing the subset of departmental datasets with partial or no data on non-watercourses for which more than 90% of segments could be matched to a BD TOPO segment. In those departments, we considered that all BD TOPO segments that could not be matched to an uncategorized or watercourse segment in the departmental map had been deemed to be non-watercourses, and analyzed the representativeness of headwater and non-perennial reaches based on the BD TOPO hydrographic network. With this procedure, we could also obtain a secondary estimate of the percentage length of non-watercourses.

We considered that sufficient data were available on non-watercourse segments to conduct the representativeness analysis directly on the departmental dataset if at least 1% of the segment length in the departmental network was categorized as non-watercourse and the ratio in total hydrographic network length between the departmental dataset and BD TOPO (including watercourses, non-watercourses, and uncategorized segments) was at least 0.8. We considered that if this ratio was lower, then a substantial proportion of watercourses that were originally present in BD TOPO had not been included in the departmental map. In departments with very small percentages of non-watercourses (over 0% but under 1 %), we considered that the map was exhaustive enough in including non-watercourse data to be directly analyzed (and genuinely categorized only a small portion of hydrographic segments as non-watercourses) if the BD TOPO-derived percentage of non-watercourses (mentioned in the previous paragraph) was also under 1%.

We found that the BD TOPO derived percentage of non-watercourses provided a reasonable equivalent to that computed from the departmental maps in departments that were considered to provide sufficient data on non-watercourses (**Supplementary Table 4.S4**).

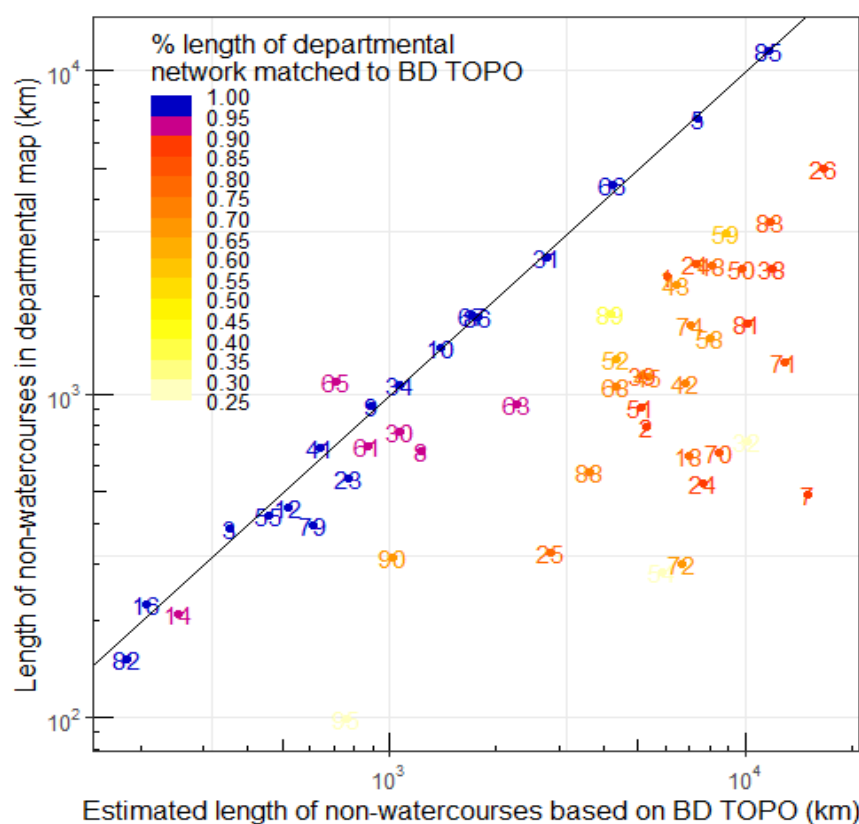


Figure 4.S6. Increasing agreement between estimated length of non-watercourses based on BD TOPO and the length of non-watercourses in departmental maps with greater proportions of matching segments.

Numbers show official codes for departments that provided data on non-watercourses.

In total, we therefore conducted the representativeness analysis directly on data from departmental maps for 56 (61%) departments and extended this analysis with estimates from BD TOPO for another 12 (13%) departments in which 90% of departmental map segments could be matched to a BD TOPO segment and non-watercourse data were not or partially available. As a result, this analysis includes departments covering 84% of the country's area included in the broader study.

We then computed representativeness as a measure of the over- or under-representation of certain types of segments in non-watercourses:

- The representativeness of first-order reaches (i.e., with a Strahler stream order of one) among non-watercourses for these departments was then calculated as the ratio between the percentage of non-watercourse length that is of first order and the percentage of the total network length that is of first order.
- The representativeness of non-perennial reaches among non-watercourses was calculated as the ratio between the percentage of non-watercourse length with a defined flow permanence status that is intermittent over the total percentage of network length with a defined flow permanence status that is intermittent.
- The representativeness of vulnerable waters among non-watercourses was calculated as the ratio between the percentage of non-watercourse length that is either intermittent or of first order (or both) over the total percentage of network length that is either intermittent or of first order (or both).

4.6.10. Identifying isolated and fragmenting segments

We analyzed potential network fragmentation resulting from non-watercourses and uncategorized segments by identifying individual segments surrounded by other segments of a different category. This analysis was restricted to departments that provided at least some data on non-watercourses. Additionally, we focused on segments that were connected to at least two other segments (i.e., excluding first-order reaches and segments that may be isolated due to the full erasure of surrounding segments) but intersected with other segments in no more than three points. Finally, we excluded all isolated or fragmenting segments that were within 10 m of a standing water body. Indeed, many departmental maps assigned the same category to all segments going through or leaving a standing waterbody (some departments classified them all as uncategorized or all as watercourses, etc.) regardless of the surrounding segments, and these hydrographic segments are likely not to correspond to an actual channel on the ground.

4.7. Bibliography

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4.8. Connecting statement Chapter 4 to Chapter 5

In the first two chapters, I addressed the gap in the lack of global hydrological information on global non-perennial rivers and streams (NPRs), a pre-requisite for their study and management. In this last chapter, I shed light on the inadequate protection of NPRs under current regulatory frameworks. Such protective legislation is a primary enabling factor for designing and implementing successful environmental flows (e-flows) programs which I discuss in Chapter 5. Chapter 5 moves from policy to management and aims to address the inadequacy of conceptual and operational frameworks for the design and implementation of e-flows in river networks with a high prevalence of non-perennial reaches. It takes like Chapter 4 an inclusive perspective and proposes improvements to e-flows programs in all river networks. See further discussion on this topic in Chapter 6, section 6.3.2.

Chapter 5

A metasystem approach to designing environmental flows

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5.1. Abstract

Accelerating the design and implementation of environmental flows (e-flows) is essential to curb the rapid, ongoing loss of freshwater biodiversity and the benefits it provides to people. However, the effectiveness of e-flow programs may be limited by a singular focus on ensuring adequate flow conditions at local sites, which overlooks the role of other ecological processes. Recent advances in metascystem ecology have shown that biodiversity patterns and ecosystem functions across river networks result from the interplay of local (environmental filtering and biotic interactions) and regional (dispersal) ecological processes. No guidelines currently exist to account for these processes in designing e-flows. We address this gap by providing a step-by-step operational framework that outlines how e-flows can be designed to conserve or restore metascystem dynamics. Our recommendations are relevant to diverse regulatory contexts and can improve e-flow outcomes even in basins with limited in situ data.

5.2. Introduction

Rivers and streams contribute significantly to global biodiversity, biogeochemical cycles, and human well-being and are concurrently among the most threatened ecosystems on Earth (Tickner et al., 2020). To curb the decline of freshwater biodiversity and the loss of benefits to people, environmental flows (e-flows) have emerged globally as a central water resource management tool (Arthington et al., 2018). E-flows are broadly defined as “the quantity, timing, and quality of freshwater flows and levels necessary to sustain aquatic ecosystems which, in turn, support human cultures, economies, sustainable livelihoods, and well-being” (Arthington et al., 2018). Accelerating the design and implementation of e-flows is recognized as a management and policy priority to ensure ecologically sustainable water management both now and into the future (Arthington et al., 2018; Tickner et al., 2020). E-flow assessments have historically relied on ensuring minimum instream flows for individual rivers below dams, but recent decades have witnessed a shift to e-flow standards encompassing multiple aspects of the flow regime and developed at the regional scale rather than on a river-by-river basis (Poff et al., 2017). Nonetheless, regional e-flow planning remains focused on species’ responses to the local flow regime, overlooking mounting evidence that biodiversity and ecosystem functioning in river networks result from the interaction between ecological processes at local to regional scales (Cid et al., 2020, 2022; Gounand et al., 2018; Poff, 2018). Standard e-flow prescriptions may therefore be less effective, for example, when the population and community dynamics within a river are strongly driven by regional processes such as species dispersal. Local communities may not recover following e-flow implementation if dispersal limitation due to river fragmentation limits recolonization from source populations elsewhere in the river network (Brooks et al., 2011; Chester et al., 2014). In such cases, adopting a metasystem perspective (see **Box 5.1** for background) that considers links between river flows and diverse ecological processes across local and regional scales could enhance the success of e-flow practices. The potential for the metasystem perspective to strengthen the management, conservation, and restoration of river networks is increasingly recognized (Chase et al., 2020; Cid et al., 2020, 2022; Patrick et al., 2021), and greater integration of advances in ecology, including metacommunity ecology, into e-flow science has been widely called for (Auerbach & Poff, 2011; Poff, 2018). However, a framework to guide e-flow design from a metasystem perspective and bridge the current gap between theory and practice remains elusive. In this

article, we discuss how metasytem concepts and tools can be incorporated into the science and implementation of e-flows. We first demonstrate how riverine metasytem processes mediate ecological responses to flow alteration. We then provide an operational framework for designing e-flows to conserve or restore metasytem dynamics. Recognizing that the effectiveness of e-flow programs can be limited by unexamined ecological processes, our aim is to provide a conceptual basis and empirical examples, and to discuss available tools with which researchers and managers can broaden the set of ecological processes integrated into the design, implementation, and monitoring of e-flow programs and, therefore, enhance the likelihood of positive outcomes. We focus predominantly on the metapopulation and metacommunity scales for the next generation of e-flow design (see **Box 5.1** for definitions) but stress the need for future developments in e-flow science to assess and protect metaecosystem dynamics (Gounand et al., 2018) in river networks. In addition, we focus strictly on the ecological benefits of e-flows but recognize the importance of integrating sociocultural objectives into these efforts (Anderson et al., 2019). Throughout, we illustrate the relevance of adopting a metasytem perspective for e-flow programs using examples from freshwater conservation and restoration programs, with a particular focus on the basin-wide e-flow program of the Murray–Darling Basin (MDB; **Box 5.2**).

Box 5.1. Basics of metasytem theory

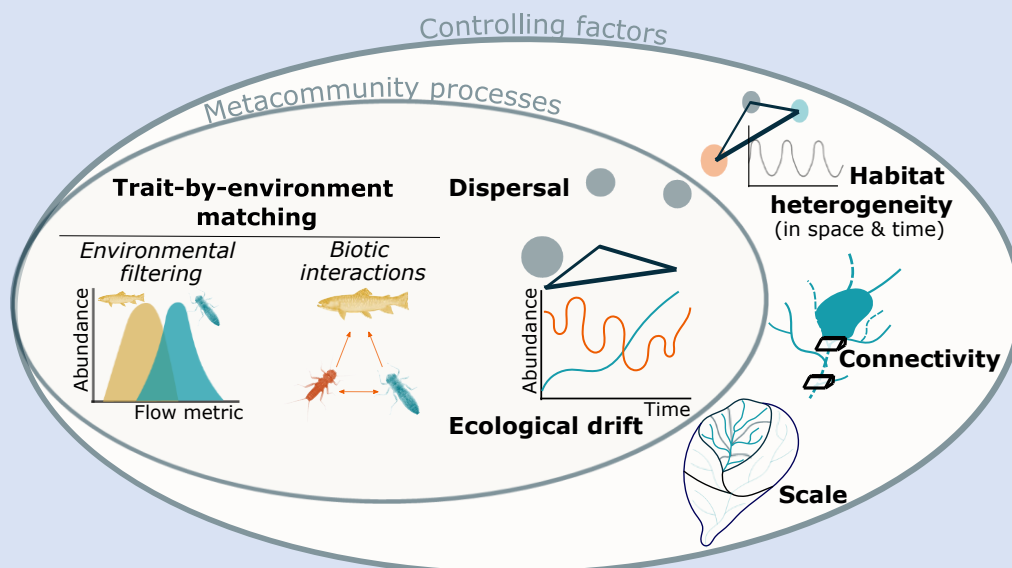


Figure 5.1. Processes and factors driving the distribution and abundance of species in metacommunities (on the basis of Leibold and Chase 2017).

Rates of dispersal (arrow thickness) vary among habitat patches (circle size represents species or community abundance). Metacommunity processes are modulated by heterogeneity in space and time (the circle colors represent habitat heterogeneity among sites linked by dispersal); connectivity among sites, driven by habitat (e.g., continuous and dashed lines represent perennial and nonperennial river segments, respectively) and instream barriers (e.g., dams, represented by triangular prisms, creating reservoirs); and scale.

The *metasystem* concept posits that landscape-scale variability in biodiversity and ecosystem functioning results from the interaction of regional and local-scale processes (Cid et al., 2022; Gounand et al., 2018). The regional structure of the physical landscape regulates flows of materials, energy, and organisms among the subcomponents (e.g., sites, habitat patches) of a metasystem. Each subcomponent is in turn characterized by local dynamics driven by abiotic conditions and biotic interactions. Local-scale ecological processes (e.g., within a river reach) are influenced by ecological processes operating at the regional scale (e.g., across multiple reaches in a river network or multiple basins) and vice versa, such that both scales require concurrent consideration to understand metasystems. Metasystem dynamics exist across levels of biological organization from populations to ecosystems. A *metapopulation* consists of multiple populations of a single species connected by dispersal (Hanski, 1998). Such spatially structured populations may form *metacommunities*, whereby a set of local communities are connected by the dispersal of multiple potentially interacting species (Leibold et al., 2004). Finally, energy and materials, such as inorganic and organic matter or nutrients, also move through *metaecosystems* in which patches exhibit heterogeneous ecosystem functions (Gounand et al., 2018). From a metacommunity perspective, the distribution and abundance of species across the landscape are driven by three mechanisms: trait-by-environment matching, dispersal, and stochastic ecological drift (Leibold & Chase, 2017). These processes are in turn influenced by three factors: habitat heterogeneity, connectivity, and scale (Leibold & Chase, 2017). *Trait-by-environment matching* operates when organisms differ in their fitness (e.g., growth rate) across gradients of abiotic and biotic conditions (Leibold & Chase, 2017). This is related to the concept of a species' niche, incorporating both *environmental filtering* (whereby the abiotic environment prevents the establishment or persistence of certain species) and the effects of *biotic interactions* such as competition and predation. *Dispersal* refers to the movement of individuals from one site (emigration) to another (immigration), which connects populations and communities (Leibold et al., 2004). *Ecological drift* describes the stochastic dynamics of events such as births, deaths, immigration and emigration that lead to random changes in population sizes and, therefore, species' relative abundances (Vellend, 2010). All three processes structure metacommunities simultaneously. Their interactions and relative strength shape the diversity of species in space and time. Variability within and among metacommunities is influenced by habitat heterogeneity and species identity. The relative strength of trait-by-

environment matching, dispersal, and ecological drift in driving the abundance and distribution of species varies across patches, through time and among species (Leibold et al., 2022). System *connectivity* alters dispersal and ecological drift; low connectivity can have similar effects to poor dispersal ability, limiting community diversity and ecosystem functioning (Leibold & Chase, 2017). Finally, the relative importance of metasytem processes and drivers varies across temporal and spatial *scales*. For example, spatial scale influences the environmental gradients organisms experience and the patchiness of the environment, whereas the connectivity of a metasytem, the dispersal ability of organisms, and ecological drift vary across both spatial and temporal scales (Leibold & Chase, 2017).

5.3. Metasytem processes mediate ecological responses to flow alteration and influence environmental flow outcomes

E-flow design currently relies on the premise that local habitat conditions, governed primarily by the flow regime, define the distribution and abundance of species through environmental filtering. Environmental filtering (see **Box 5.1, Figure 5.1**) implies that resident species that are adapted to a local flow regime become less abundant and less likely to persist at a site as flows increasingly differ from the original flow regime (Poff et al., 1997). To evaluate environmental filtering, e-flow assessments often rely on flow–ecology relationships which relate ecological responses (e.g., abundance of a species, taxonomic richness, recruitment) across sites or through time to various facets of the flow regime (e.g., **Figure 5.2**; Freeman et al., 2022; Poff et al., 2010).

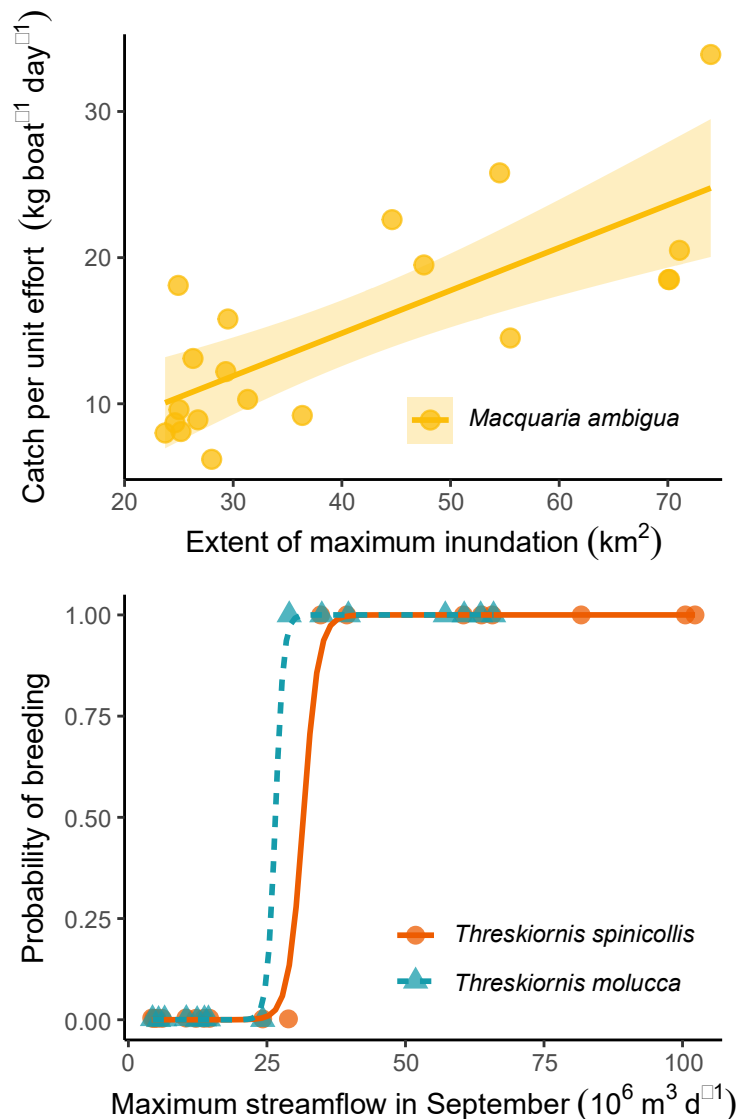


Figure 5.2. Standard examples of empirical flow–ecology relationships derived from monitoring data in the Murray–Darling Basin.

Source: The data are from Colloff and colleagues (2018). (a) For the native fish golden perch (*Macquaria ambigua*), relationship between catch per unit effort and extent of maximum inundation in each year from 1984 to 2003, River Murray (South Australia), with line of best fit from linear regression ($R^2 = 0.571$, $p < 0.05$); (b) for waterbirds, attempted breeding by ibis (*Threskiornis* spp.) from 1978 to 2005, Lake Merreti (South Australia). The lines show logistic model fits predicting breeding success from maximum flow in the month of September.

However, metasystem dynamics other than environmental filtering, such as biotic interactions (as part of trait-by-environment matching; see **Box 5.1**), dispersal, and ecological drift can cause ecological responses to altered flow regimes to deviate from those expected in isolated populations or communities. The influence of habitat heterogeneity, scale, and connectivity on these metasystem processes can also strongly mediate the observed response of species to flow alteration (**Box 5.1**). Flow–ecology relationships and the resulting e-flow prescriptions are always uncertain because of the inherent complexity and stochasticity of ecosystems, but deviations resulting from overlooked metasystem

processes and influencing factors can further blur or bias standard assessments and compromise the effectiveness of subsequent flow management. Few programs monitor the outcomes of e-flow implementation and even fewer investigate the processes behind these outcomes (Souchon et al., 2008). In addition, e-flow recommendations and post-implementation evaluations are rarely published in accessible databases (Tonkin, Jähnig, et al., 2014). However, a few cases are documented in which metacommunity factors, such as limited dispersal strength and connectivity (Brooks et al., 2011; Chester et al., 2014; Growns, 2016; Reinfelds et al., 2010), may have limited the effectiveness of e-flow implementations. For example, Reinfelds and colleagues (2010) found that historical e-flow releases provided insufficient water depths for riffle passage by Australian bass (*Macquaria novemaculeata*), a migratory fish, but that small increases in flow releases could increase water depths and effectively promote connectivity. By contrast, targeted e-flows have enabled fish movement in the MDB (Beesley et al., 2014; Koster et al., 2017). Spring–summer freshes resulting from e-flow releases, for example, supported spawning-related movements by golden perch (*Macquaria ambigua*; Koster et al., 2017). Several instances also exist in which biotic interactions altered species’ responses to flow alteration (Gido & Propst, 2012; Stefferud et al., 2011) or to e-flow implementation (Marks et al., 2010) or where e-flow implementations have proved more beneficial to nonnative than to native species (Conallin et al., 2012). In Fossil Creek (Arizona, United States), native fish abundance did not respond to e-flows where nonnative fish were present, whereas a 50-fold increase in abundance was observed where e-flows were combined with nonnative fish removal (Marks et al., 2010). Leveraging multi-objective optimization models to design dam operation releases in the San Juan River (United States; Chen & Olden, 2017) concluded that novel e-flow regimes could more efficiently benefit native species while controlling nonnative species when compared with e-flows designed to resemble historical flow conditions. Below, we summarize how metacommunity processes, modulated by habitat heterogeneity, connectivity, and scale, may influence e-flow outcomes, and we propose a set of solutions (**Table 5.1**) that we embed in an operational framework in the following section. We focus on flow–ecology relationships, but these considerations apply equally to hydraulic-habitat models, which also emphasize local conditions (Lamouroux et al., 2017).

5.3.1. Trait-by-environment matching: Biotic interactions

E-flow designs seldom explicitly account for biotic interactions, but competitive, trophic, and host–commensal interactions can modulate species’ responses to flow alteration at local and regional scales (**Figure 5.3**; Bogan & Lytle, 2011; Dewson et al., 2007). Flow alterations can directly or indirectly shift the outcomes of competitive interactions, altering species’ abundance and distribution. For example, the local extinction of competitors following a shift from a perennial to an intermittent flow regime was the likely cause of an 11-fold increase in the abundance of two diving beetles in a desert stream (Bogan & Lytle, 2011). The widespread occurrence of nonnative species in freshwater systems can also interact with flow alterations and fundamentally change the abundance and spatial distribution of native species (Ruhí et al., 2019), confounding flow–ecology relationships. In some cases, flow alteration can facilitate the invasion and dominance of nonnative species, which can be mitigated by e-flows. For example, nonnative riparian *Tamarix* sp. shrubs have become most dominant over native *Populus deltoides* in flow-regulated river reaches of the southwestern United States (Merritt & Poff, 2010), but targeted e-flows could help to reverse this trend (Lytle et al., 2017). Equally, e-flow implementations that disregard the flow preferences of nonnative species may have a net negative effect on the ecological targets of conservation actions. For example, e-flows designed to reduce the incidence of low-flow periods in southern Victorian streams (Australia) benefitted nonnative trout at the expense of the native fish roundhead galaxias (*Galaxias anomalus*; Leprieur et al., 2006). Finally, when flow alterations cause aquatic habitats to shrink, biotic interactions tend to intensify, especially if partial streambed drying occurs. During drying, organisms become confined to pools, amplifying predation and competition for declining food resources (Magoulick & Kobza, 2003).

Table 5.1. Possible implications of metacommunity processes and influencing factors other than environmental filtering for environmental flow (e-flow) design and proposed solutions. Note: see Box 5.1 for a description of the processes and factors.

Metasystem process or factors	Possible implications for flow–ecology relationship and e-flow outcomes compared to standard expectations	Example for native fish in the Murray-Darling Basin	Proposed measures that may improve the e-flow program outcomes
<i>Dispersal (enabled by network connectivity)</i>	High or low dispersal can blur flow–ecology relationships and limit effectiveness of standard e-flow design. Different ecological targets of e-flow design (e.g., species, guilds) may have different dispersal needs.	Stocks et al. (2021): Difficulty relating hydrological conditions to recruitment because of dispersal of golden perch juveniles. Thiem et al. (2021): Contrasting dispersal patterns among fish species calls for diverse management actions to promote population recovery and persistence.	Quantify relative strength of dispersal in structuring a metacommunity. Account for dispersal among sites when modeling species’ responses to flow. Design e-flows to maintain, restore, or limit dispersal for ecological targets. Select multiple ecological targets with varied dispersal traits.
<i>Biotic interactions</i>	Competitive or trophic interactions (e.g., from nonnative species) modulate species’ response to flow.	Stoffels et al. (2015): Immigration of competitor following flow pulse reduces floodplain population of eel-tailed catfish despite favorable local conditions. Rolls et al. (2013): Boost in golden perch recruitment is probably mediated by flow-induced increase in prey production.	Account for biotic interactions when modeling species’ responses to flow. Design flow regime to benefit native species at the detriment of invasive species (or balance these two objectives if trade-offs exist). If possible, design e-flow to limit dispersal of invasive species. Complement e-flow programs with nonnative population reduction.
<i>Ecological drift</i>	Small, isolated populations and communities are vulnerable to stochastic processes. Isolated populations may have developed divergent flow–ecology relationships.	Pavlova et al. (2017): Macquarie perch populations are small and vulnerable to stochasticity. Despite flow restoration, recolonization is impeded by insufficient physical connectivity. Zampatti et al. (2021): Substantial variability in age structure, recruitment source and movement patterns of golden perch across the basin is potentially related to reduced connectivity.	Design e-flows to restore dispersal if populations and communities were naturally more connected. Complement e-flow programs with population augmentation programs or restoration of instream connectivity. Develop separate flow–ecology relationships with time-series analysis rather than through comparison across sites. Limit e-flows that promote dispersal among naturally isolated populations and could jeopardize metapopulation resilience.
<i>Scale and heterogeneity</i>	Flow–ecology relationships developed at too small a spatial scale and in hydrologically homogeneous areas may not capture species’ response to a range of flow conditions. Flow–ecology relationships developed at too large a spatial scale may span separate regional species pools and be blurred by divergent adaptations of individual species to flow regimes. Metacommunity processes can vary in time and among different areas of a river network.	Colloff et al. (2018): Of 11 flow–ecology relationships for phytoplankton, invertebrates, fishes, waterbirds, and vegetation, those developed at small spatiotemporal scales are weaker than at larger scales. Huey et al. (2011): Golden perch populations are usually highly connected by dispersal, but drying of normally perennial refuges can cause strong spatial genetic structure via genetic drift.	Collect hydrological and ecological data in heterogeneous flow conditions, across river networks (both in mainstem and headwater reaches), and throughout the year. Assess spatial autocorrelation in flow–ecology relationships.

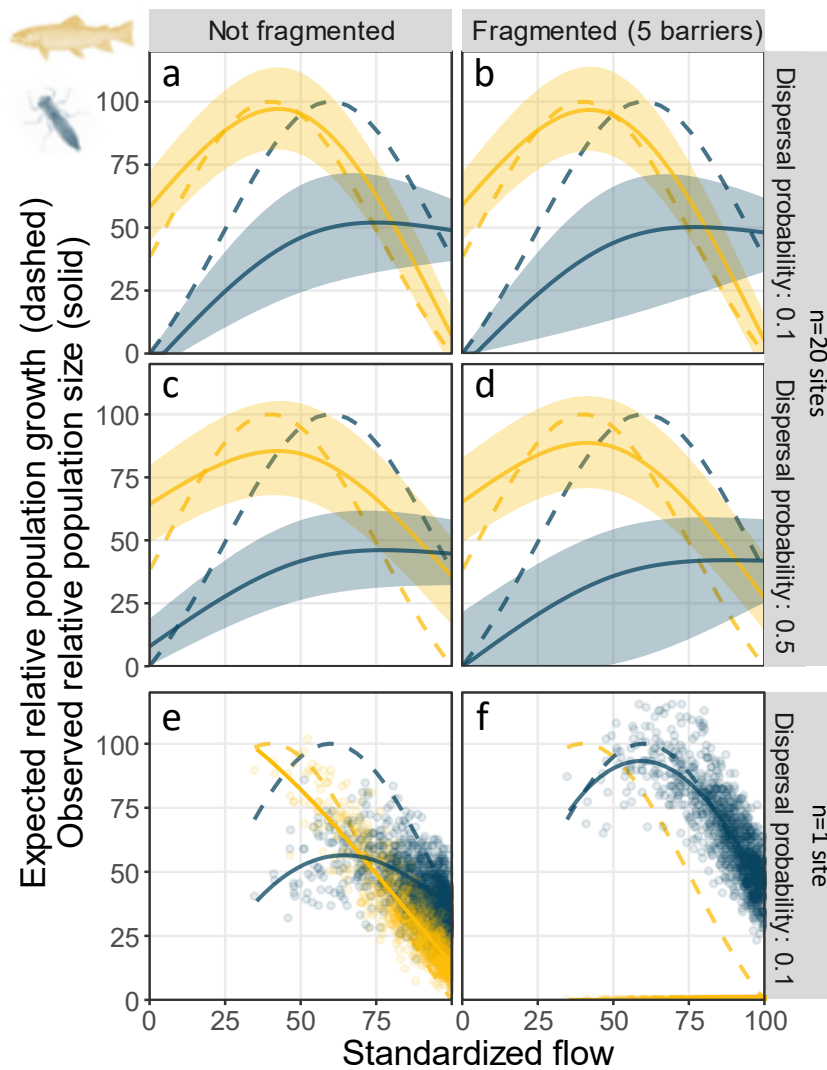


Figure 5.3. Metacommunity processes can cause empirical flow–ecology relationships to differ from relationships expected from only environmental filtering.

A general metacommunity model (Thompson et al., 2020) was developed to simulate the population dynamics of two interacting species across 100 river sites in a synthetic river network (Carraro, Bertuzzo, et al., 2020) with spatiotemporally autocorrelated flow conditions. This model shows how the presence of a predator (light yellow) may decrease, shift, and blur the observed flow–abundance relationship (the solid line) of a prey species (dark blue) compared with its expected flow–population growth relationship (the dashed line). The effect of biotic interaction is stronger with decreased dispersal ability (modeled as decreased dispersal probability; panel (a) compared with panel (c)) and greater fragmentation (panel (b) compared with panel (a)). With high dispersal ability, mass effect may lead a species to be abundant in sites where it is maladapted (the solid yellow line extending beyond the dashed line in panels (c)–(d)). Flow–ecology relationships derived from monitoring at a single site (e–f) may provide a biased view of the flow preferences of species compared with relationships from multiple sites ($n = 20$) (a)–(d). In a fragmented context, stochasticity may even lead to the local extirpation of a species without possible recolonization despite moderately favorable conditions (f). Individual points in panels (e) and (f) represent the species' relative population abundance at different monthly time steps. The solid lines, lower and upper uncertainty bounds show fits from quantile general additive models (GAM) of population size for the 0.5, 0.1, and 0.9 quantiles, respectively. The expected population growth as a function of flow (the dashed line) was standardized from 0–5 to 0–100. The population size (the solid line) was standardized separately for $n = 20$ sites and $n = 1$ site by the maximum value across scenarios of the fitted median GAM.

5.3.2. Dispersal

The relative strength of dispersal and local processes of environmental filtering and biotic interactions influences the predictive power of flow–ecology relationships. Both dispersal surplus and dispersal deficit can decrease the precision of standard flow–ecology relationships established through correlative studies (**Figure 5.3**). If dispersal among sites is high, source–sink or mass effects may override local-scale processes (Leibold et al., 2004). In cases of mass effects, species may occupy sites in which they are inferior competitors or maladapted to local habitat conditions if they can continuously immigrate from nearby source sites where conditions are more favorable (Mouquet & Loreau, 2003). If dispersal is limited, species may be unable to track their preferred abiotic conditions to access sites in which they would exhibit high fitness or be superior competitors (Leibold et al., 2004). Similar to situations of high dispersal, some species may persist in suboptimal sites, in this case because superior competitors are unable to colonize and outcompete them owing to dispersal limitation. For instance, an analysis of the relationships between flow magnitude and fish species richness for large-river specialists in the tributaries of the Missouri and Mississippi rivers showed that flow magnitude alone underrepresented richness in lower-flow sites accessible to dispersers and overrepresented richness in isolated sites (Dunn & Paukert, 2021). Low dispersal is often thought to limit the success of local efforts to restore physical habitat (Stoll et al., 2013; Tonkin, Stoll, et al., 2014), water quality (McManamay et al., 2016), and e-flows (Brooks et al., 2011). The greatest ability to predict ecological responses to flow may manifest in metacommunities with intermediate levels of dispersal and strong environmental filtering (i.e., species sorting; Leibold et al., 2004). In such networks, species can disperse across the landscape into habitats in which environmental conditions maximize their fitness but where the local communities are not swamped by colonists from the regional species pool. Beyond accounting for dispersal in flow–ecology relationships, the effectiveness of e-flow programs could be improved by considering dispersal in their overall design (see the framework in the next section). Flow alteration can also affect dispersal. Changes in flow regimes can either increase or decrease dispersal rates, depending on species traits and instream physical barriers with flow-dependent passability (e.g., low-head dams, natural knickpoints). Increases in discharge can boost dispersal by promoting instream drift (Naman et al., 2016), inducing nonmigratory and upstream migratory movement by fish (Taylor & Cooke, 2012), increasing the passability of instream

barriers by drowning them out (Marshall et al., 2021), enhancing the connectivity among river reaches during low-flow periods (Rolls et al., 2012), or providing access to side channels and floodplain habitats if overbank flows occur (Stoffels et al., 2016). If increases in discharge are accompanied by high flow velocities, downstream hydraulic forces can reduce upstream dispersal or create velocity barriers, particularly in road culverts (Warren & Pardew, 1998). Lower discharge generally decreases connectivity and, therefore dispersal, particularly when surface water is lost and the river network becomes fragmented, although flow decline may also trigger dispersal away from shrinking aquatic habitat (Naman et al., 2016; Rolls et al., 2012). Beyond flow magnitude, the timing, duration, frequency, and rate of change in flow events also affect dispersal. Fish migration (Jonsson, 1991), plant seed transport (Kehr et al., 2014), and insect emergence and adult dispersal (Lytle, 2003) may be synchronized to coincide with (or avoid) flow events at specific times. An earlier onset of drying, for instance, may prevent access to refuges (Hwan & Carlson, 2016), dispersal to spawning grounds (Scoppettone et al., 2015), and emergence of the terrestrial adults of insects with aquatic life stages (Drummond et al., 2015).

5.3.3. Ecological drift

Small and dispersal-limited populations and communities are often more susceptible to demographic stochasticity, genetic drift, and inbreeding, potentially reducing the effectiveness of standard e-flow implementation to below what would be expected (Gido et al., 2016). In isolated communities composed of few individuals, ecological drift may override environmental filtering or alter the outcome of competitive interactions driving community composition (Ron et al., 2018; Siqueira et al., 2020). Flow–ecology relationships may therefore be particularly uncertain when ecological drift is dominant. In turn, flow alterations that isolate or shrink populations put them at a greater risk of stochastic decline and local extinction. Providing adequate local flow conditions may be insufficient to sustain small, isolated populations (e.g., in the MDB; Pavlova et al., 2017), such that a species may be driven to local extinction unless flow management increases its dispersal rates or is complemented with population augmentation (Ryman & Laikre, 1991) or barrier removal. Alternatively, naturally isolated populations may have adapted to local habitat conditions, resulting in population viability despite small numbers and limited dispersal potential (Phillipsen & Lytle, 2013). Even in such situations, particularly when selection pressures are strong and divergent across populations, the transferability of standard flow–ecology

relationships and the effectiveness of the resulting e-flow management program may be limited by independent evolution among local populations.

5.3.4. Controlling factors: Scale and heterogeneity

The effects of scale and spatiotemporal variation in the relative strength of trait-by-environment matching, dispersal, and ecological drift are important to recognize in e-flow assessments. Flow–ecology relationships developed from data at small spatial scales and in metacommunities from networks in which habitat heterogeneity is low may be more uncertain than those developed with sites spanning a greater extent and flow gradient (**Figure 5.3**; Colloff et al., 2018; Viana & Chase, 2019). At large scales that span river basins with separate regional species pools, the transferability of relationships between species and environmental factors may also be limited by biogeographic barriers and recent speciation events (Heino et al., 2015). For example, whereas flow–ecology relationships developed for fish species exhibit as much transferability within as among river basins in the southwestern United States (Chen & Olden, 2018), ecoregions are more effective than river classifications derived from hydrology alone for explaining the variation in fish traits across the United States (McManamay et al., 2015). The mechanisms that shape riverine metacommunities vary over time (**Box 5.1, Figure 5.1**; Datry et al., 2016; Perkin et al., 2021; Sarremejane, Cañedo-Argüelles, et al., 2017), so e-flows designed from snapshot or seasonal ecological data may overlook important metacommunity dynamics. For example, snapshot studies may not capture the temporal synchronization of species and trait composition across sites by flow alterations such as hydropeaking, which increases the risk of population and community collapse (e.g., across the Colorado River Basin; Ruhí et al., 2018). Flow–ecology relationships are often derived from data collected during only one or two specific seasons rather than year-round—during summer or fall in temperate regions when rivers are more easily wadable (Harper et al., 2022; Morgan et al., 2022). Low-flow statistics are often strong predictors of taxonomic community composition and species’ abundances during these periods of strong environmental filtering (Arthington et al., 2014; Rolls et al., 2012). However, the roles of other flow events that promote connectivity (e.g., with floodplains), flood disturbances, and community composition following recolonization in intermittent reaches are often overlooked. Temporal variability particularly influences flow–ecology relationships in dynamic river systems, including those with extensive nonperennial river reaches (Ruhí et al., 2017; Sarremejane, Cañedo-Argüelles, et al., 2017). When a river stops

flowing and dries, aquatic dispersal ceases, and the strength of environmental filtering and biotic interactions increases in remaining wet habitats. When flow resumes, dispersal and ecological drift then prevail until sufficient colonists have reached previously dry patches and environmental filtering regains dominance, provided intermediate dispersal (Datry et al., 2016; Sarremejane, Mykrä, et al., 2017). Sampling perennial sites in river networks with nonperennial river reaches during low-flow conditions may even yield counterintuitive results. In prairie streams, for example, the abundance of stream fish was lower during wet years compared with dry years in the same river reaches: During dry years, individuals dispersed from intermittent to perennial reaches at the onset of drying and returned to intermittent reaches when flow returned (Hedden & Gido, 2020). Smaller upstream sites did not fit this pattern, potentially because of limited connectivity. Greater consideration of intra- and interannual flow variability is therefore required to capture the temporal dynamism of lotic metacommunities when building flow–ecology relationships.

Box 5.2. Existing e-flow program with a metasystem approach in the Murray–Darling Basin.

The Murray–Darling Basin (MDB) drains 1 million km² of southeastern Australia (**Figure 5.4**), supports 40% of Australian agriculture production and is home to more than 40 First Nations. The basin supports 50 native fish and 120 waterbird species (Murray–Darling Basin Authority, 2020b). Rivers across the basin are degraded by many anthropogenic stressors, including widespread overallocation of water entitlements for irrigation. The Millennium Drought (1996–2011) was a turning point in Australian river management, prompting the drafting of the Water Act (2007), which, in turn, established the Murray Darling Basin Authority (MDBA). Since 2012, the MDBA has overseen the implementation of a plan for basin-wide coordination of water resource management (Basin Plan 2012, 2021). The Basin Plan establishes water diversion limits and e-flows objectives for each of the MDB’s sub-catchments and groundwater basins, depending on storage levels and weather conditions. Achieving the diversion limits entails the recovery of approximately 15% of average total annual water withdrawals prior to the Plan. From 2014 to 2020, a total of 9.5×10^{12} cubic meters of e-flows were delivered in the basin through 666 actions (Barbour, Thompson, Brooks, et al., 2021; **Figure 5.4**).

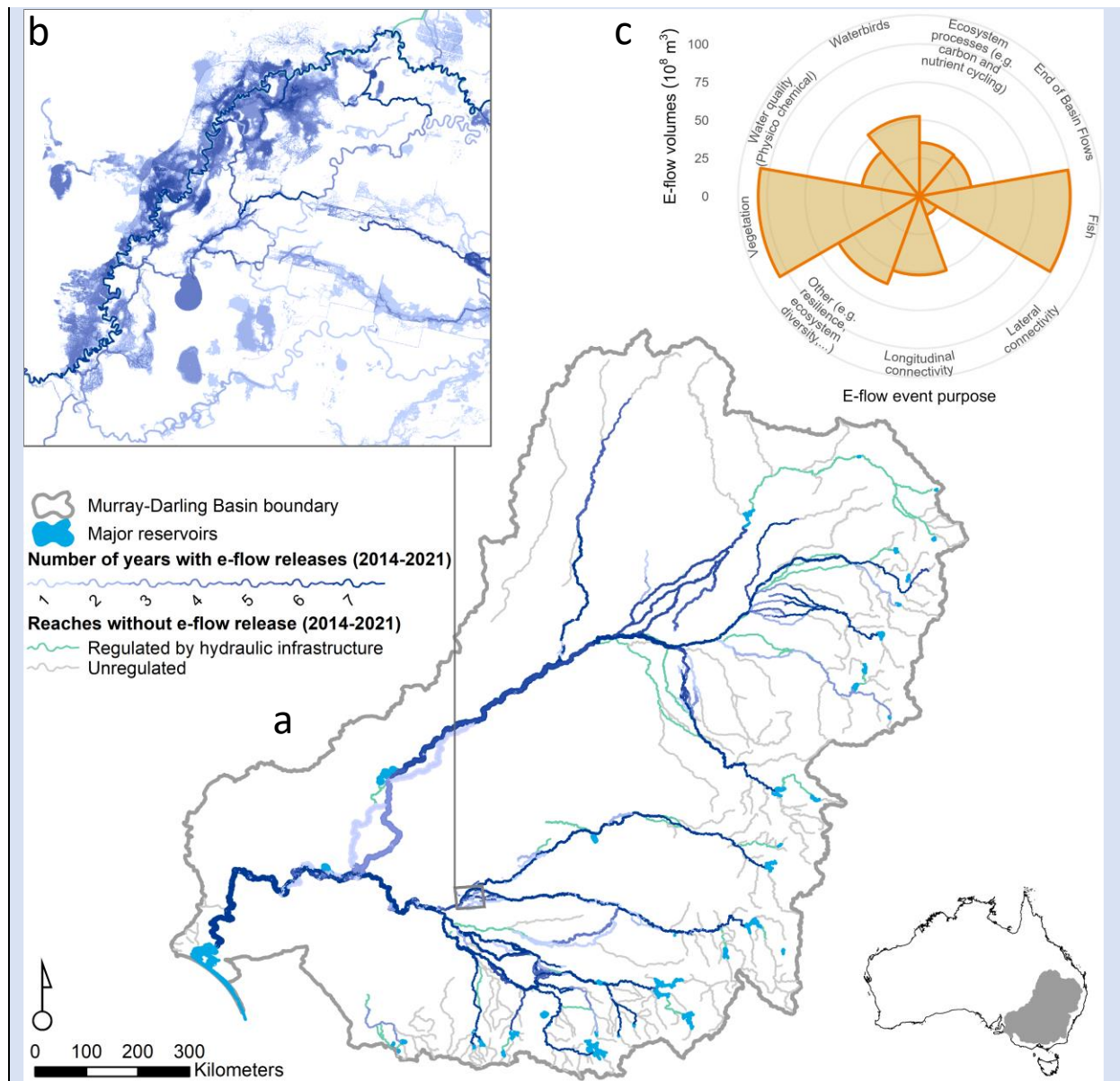


Figure 5.4. Distribution of e-flow releases across the Murray–Darling Basin.

Spatial distribution of e-flow releases from 2014 to 2021 across (a) the river network and (b) its floodplain. (c) E-flow volumes allocated to different ecological purposes (2013–2019; one event could have multiple purposes). The data were provided by the Commonwealth Environmental Water Office of the Australian Government and are available at <https://data.gov.au/home>.

The MDB e-flows program (Barbour, Thompson, Pollino, et al., 2021; Commonwealth Environmental Water Office, 2022; Murray–Darling Basin Authority, 2020a) broadly aligns with the metasystem approach and framework we present herein. First, the MDB Plan takes a basin-scale perspective. It relates local outcomes of e-flow events to large-scale objectives and accounts for the interactions of various metacommunity processes and influencing factors at local and regional scales (**Box 5.1**). Second, the program covers multiple main ecological targets with varying flow requirements: flow and connectivity, native fish, vegetation, and waterbirds (**Figure 5.4**). Third, the program was founded on an adaptive

management approach with a strong e-flow Monitoring, Evaluation and Research Program (Flow-MER; Barbour, Thompson, Pollino, et al., 2021), which collects spatially explicit data on hydrology, ecology and river–floodplain structure at sites across the basin, including information on longitudinal and lateral connectivity and the dispersal of species. Finally, a variety of e-flow management levers are spatially coordinated depending on the degree of regulation of rivers and management objectives. Nonetheless, the coordination of e-flow allocations and monitoring across the basin may benefit from greater integration of concepts and tools from the field of metacommunity ecology described in our framework. For example, although efforts exist to understand the metapopulation dynamics of native fish and waterbirds, and multiple population and flow–ecology models have been developed for the fish species of the MDB, spatially explicit models that account for the role of dispersal and biotic interactions in structuring metapopulations and metacommunities are still largely missing (but see Stoffels et al., 2015 for an example). These models could inform the prioritization of water allocations for recruitment in keystone sites while promoting connections that allow fish to move among populations (see framework section). In addition, the expected outcomes of the program are mostly species and area specific and do not yet incorporate basin-wide indices of biodiversity. Several of these limitations are slated to be addressed through the Flow-MER program. The most recent evaluation and research plan outlines several projects that aim, for example, to develop a multiscale approach to evaluate biodiversity, to further evaluate flow triggers for local and regional scale fish movement, and to develop integrative models of interactions among species, basin-scale and multispecies responses (Barbour, Thompson, Pollino, et al., 2021).

5.4. Integrating a metasystem approach to environmental flow design and implementation: An operational framework

No e-flow implementation exists, to our knowledge, that explicitly aims to protect or restore metacommunities, and relatively few implementations have targeted metapopulation dynamics (**Box 5.2**; e.g., Kendy et al., 2012; Norton et al., 2010 in the MDB). The prerequisites for e-flow programs to more effectively maintain or restore metasystem dynamics include focusing on preserving multiple populations or communities, incorporating spatially explicit biological and environmental information, and implementing spatially explicit management of water flows. However, achieving these requirements does not imply

that e-flows maintain or restore metasytem dynamics. To do so, e-flow programs must be explicitly tailored to this objective and must encompass more factors than local abiotic conditions. Below, we propose a framework to operationalize metasytem ecology in e-flow programs, from program definition and e-flow design to implementation and monitoring (**Figure 5.5**). Because e-flow programs operate under uncertainty, and because adopting a metasytem perspective adds another level of complexity to e-flow design, this framework functions as an adaptive management cycle. Accordingly, e-flow assessments function as near-term forecasts that are iteratively improved through implementation, monitoring, evaluation, and reporting (Dietze et al., 2018; Webb et al., 2017). In developing the framework, we build on standard methodological workflows for e-flow design (e.g., ELOHA; Poff et al., 2010) and previous proposals for adopting a metacommunity perspective in freshwater conservation and restoration (see in general: Bond & Lake, 2003; Chase et al., 2020; Cid et al., 2022; Patrick et al., 2021; Rolls et al., 2018; and specifically in riverine bioassessment: Cid et al., 2020). Our recommendations are also broadly consistent and complementary with other recent conceptual e-flow frameworks, such as the strictures and promoters framework by (Lester et al., 2020) and the climate-informed ecological resilience principles and associated indicators proposed by (Grantham et al., 2019).

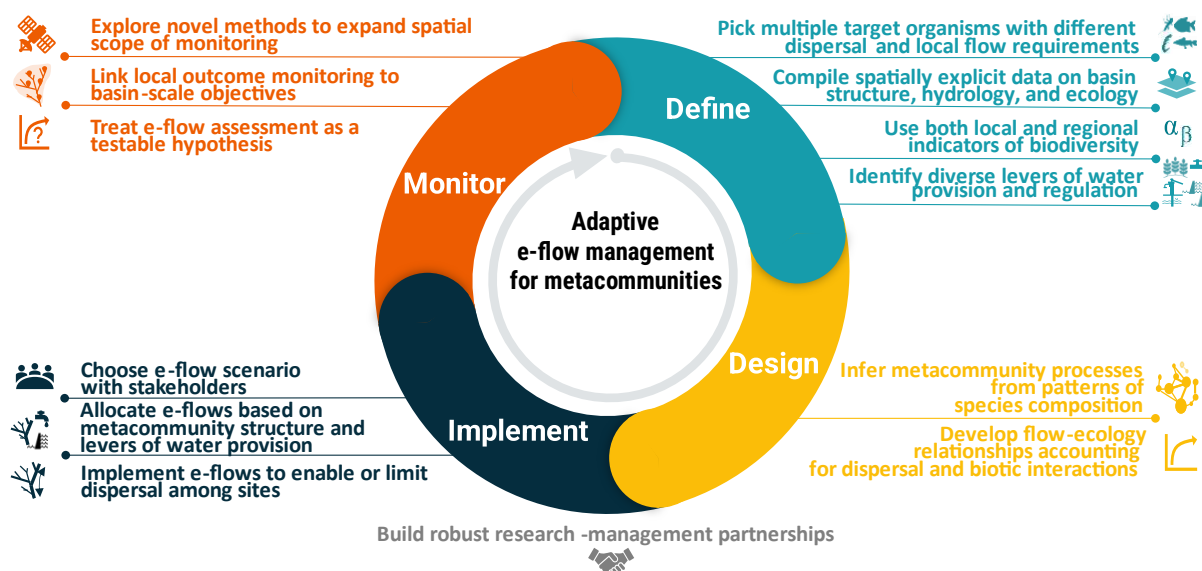


Figure 5.5. Operational framework for integrating a metasytem perspective in environmental flow (e-flow) design.

5.4.1. Define

Ecological target(s)

Once the overall objectives of an e-flow program have been determined (King et al., 2015), the first step of this framework is to select the ecological target for which to develop e-flow recommendations and the associated indicators to monitor the outcome of e-flow implementation. This selection should be made as part of a participatory process involving diverse stakeholders (Mussehl et al., 2022) and should reflect scientific, socioeconomic, and cultural requirements (Anderson et al., 2019; Finn & Jackson, 2011). Possible ecological targets range from one or more species (conservation targets such as the endangered Colorado pikeminnow *Ptychocheilus lucius*, or a small suite of umbrella species whose conservation is expected to benefit numerous co-occurring species; Obester et al., 2022) to communities (e.g., macroinvertebrates, fish), and entire ecosystems (e.g., ecosystems providing cultural value; First Nations Fisheries Council of British Columbia, 2020). Current e-flow programs are usually tailored to one or a few species rather than to entire communities, species assemblages, or ecosystems (Olden et al., 2014; Tonkin et al., 2021) and to local rather than regional measures of biodiversity. Careful selection of ecological targets is particularly important for designer e-flow programs (Acreman et al., 2014), which tailor flow regimes to specific ecosystem objectives, as opposed to e-flow approaches that attempt to mimic a natural flow regime. Designer e-flows that target only one or a few specific species risk benefiting one ecosystem component at the expense of others (Tonkin et al., 2021). From a metacommunity perspective, even if two ecological targets require the same local flow regimes, their dispersal ability, refuge use, and life cycle and seasonal movements may differ. For example, the New Zealand fish Canterbury galaxias (*Galaxias vulgaris*) and upland bully (*Gobiomorphus breviceps*) differ in their refuge use and, therefore, their flow needs: Both species move upstream as flows decline prior to channel drying, but bullies migrate from riffles to deeper runs whereas galaxiids burrow into the moist substrate (Davey et al., 2006; Lake, 2011). Therefore, slow but long-term drying may be more detrimental to galaxiids, whereas rapid drying would be more detrimental to bullies, even if in the short term (Lake, 2011). In general, long-lived and less-mobile species are more sensitive to local flow conditions whereas strong dispersers with life stages dependent on multiple habitat types are more sensitive to impairment of flow connectivity (Patrick et al., 2021). Beyond individual species, the metapopulation dynamics and metacommunity

structure of different guilds (e.g., upstream versus mainstem fish species; Ferreira et al., 2019) and organism types (fish versus macroinvertebrates; Hastings et al., 2016) may reflect contrasting levels of environmental filtering, biotic interactions and dispersal. To avoid relying on an ecological target whose conservation or restoration does not extend to other potential targets, one option is to use multiple target organisms with varied dispersal abilities and local flow requirements (Cañedo-Argüelles et al., 2015). Using multiple organisms to develop e-flow standards may be particularly relevant if some targets are selected primarily for their socioeconomic or cultural values (Finn & Jackson, 2011) with potentially little information on the metasystem dynamics driving their distribution and abundance. Databases listing the biological traits of species (e.g., macroinvertebrates: Sarremejane et al., 2020; fish: Mims & Olden, 2012; diatoms: Riato et al., 2022), including dispersal traits, can help guide this choice. Indicators of biodiversity at multiple levels may also be used to monitor the effectiveness of e-flow implementation on local and regional processes. Taxonomic richness (alpha diversity) is commonly monitored but may fail to indicate substantial turnover in community composition and may partly misrepresent ecological responses to the local flow regime in cases of dispersal surplus or dispersal deficit (Cid et al., 2020). In addition, taxonomic richness cannot track basin-wide heterogeneity in community composition, changes to source–sink dynamics, or altered temporal synchrony among communities that could weaken metasystem resilience (Ruhí et al., 2017). Beta diversity describes variability in species composition in space or over time, which is particularly relevant in monitoring the effect of e-flows on metasystem dynamics (Ruhí et al., 2017). A suite of other metrics in addition to beta diversity exists to characterize regional ecological features (Cid et al., 2022). Whereas those indicators are common in metacommunity research (Larsen, Comte, et al., 2021; Perkin et al., 2021), they are seldom used for e-flow design and monitoring. Because successful e-flow implementation depends on the involvement of multiple types of stakeholders and their coproduction of management objectives (Mussehl et al., 2022), communicating the relevance of seemingly arcane metacommunity processes and associated indicators is crucial to enable their inclusion as targets. Whether e-flows can be designed for broader targets than individual species or locations depends largely on the legal framework mandating the provision of e-flows. E-flow implementations in the United States often aim to fulfill mitigation requirements for threatened and endangered fish species listed under the federal Endangered Species Act

(Harwood et al., 2018). In Europe, the Water Framework Directive (WFD) does not mandate the implementation of e-flows unless needed to prevent or reverse ecological degradation as indicated by indices representing community health (it requires that riverine flow regimes provide conditions “consistent with the achievement of the environmental objectives of the WFD”; European Commission, 2015). Although vague, this requirement broadly aligns with metasystem thinking. In the MDB e-flow program, annual water management plans are required by law to establish e-flow allocation priorities across four main categories (river flows and connectivity, native vegetation, waterbirds, and fish), but additional objectives are also included in e-flow design (**Figure 5.4**). These include, for example, supporting populations of other native aquatic species (e.g., invertebrates, amphibians, platypus) and ecosystem functions (e.g., nutrient and carbon cycling, salt flushing). Widening the scope of e-flow policies to explicitly include multiple species and communities as ecological targets would help operationalize a metasystem perspective in e-flow programs. However, if the regulatory context requires that a narrow ecological target (e.g., a single species) be used to design the e-flow program, other aspects of this framework (e.g., metapopulation dynamics) can still be applied to support or restore metasystem dynamics for this target.

Compile available data and define monitoring needs

Designing and implementing e-flow recommendations from a metasystem perspective requires considerable data on the structure, hydrology, and ecology of the river basin. Compared with standard e-flow design frameworks, the main additional requirement is for most data to be spatially explicit. In other words, data should ideally be distributed across the region of study and the spatial relationships among sites (straight-line and river distances, structural and hydrological connectivity) considered. Structural data consist of a ground-truthed map of river reaches and other water bodies, natural and anthropogenic instream barriers, flow-altering structures and water withdrawal points, and land cover and land use. Information on the characteristics of flow-altering features (e.g., dams, flow diversions, wastewater treatment plants) is also important—for example, their operating curves and release capacity, as well as permitted and actual water withdrawals. This data compilation process should produce a map of a diversity of management levers that may be used for e-flow provision, depending on the financial and legal tools available to water resource managers. Because most e-flow assessments still deal with individual rivers downstream of a dam (Olden et al., 2014; Ramos et al., 2018), such data on spatially

distributed water sources are rarely collected. E-flow design requires a hydrological foundation: time series representing simulated naturalized baseline conditions and the current human-influenced hydrology of the system (Poff et al., 2010). Hydrological models should ideally be developed to generate discharge time series for all reaches in the river network rather than for individual sites. In river networks with extensive nonperennial reaches, long-term observational data describing in-channel conditions (e.g., flow, low flow, no flow, dry) of river reaches across a network can indicate how conditions change in space and time. The resulting information on temporary fragmentation and ecologically important features such as persistent aquatic refuges (Sefton et al., 2019) is key to conserve metasystem dynamics. Historical observations of this type are rare (Jaeger et al., 2021), but several citizen science initiatives (e.g., Allen et al., 2019), governmental programs (e.g., Sefton et al., 2019), and improvements in remote sensing (e.g., Marshall et al., 2021) and modeling (e.g., Yu et al., 2022) of surface water presence are rapidly improving our ability to design e-flows for nonperennial systems. Finally, projections of the future hydrology of the system are useful to ensure that e-flow recommendations are climate ready—that is, compatible with potential future water availability (Judd et al., 2022). Biological data are usually the most limiting type of data in e-flow assessments. Spatially distributed community data depicting the distribution or abundance of species across the river network form the basis of metacommunity analyses that can underpin e-flow design. Ideally, ecological and hydrological data collection sites should be colocated. To capture the spatiotemporal variability of metacommunity processes, sampling should ideally be distributed in space and time with information on straight-line and river distance among sites, across gradients of flow variability, alteration, and connectivity, and spread from mainstems to headwaters (with high dispersal often characterizing mainstem reaches and environmental filtering being more dominant in headwaters; Brown & Swan, 2010). Time-series data describing taxonomic community composition enable more advanced analyses (see the next section; Jabot et al., 2020; Ruhí et al., 2017) and are therefore preferable to static snapshots. Macroinvertebrate community data collected by biomonitoring programs can provide a useful basis to conduct metacommunity analyses (Patrick et al., 2021) and can be supplemented with additional data collection to meet these spatiotemporal criteria (see the monitoring step). Although statistical methods can estimate the role of dispersal in structuring metapopulations and metacommunities (in the design stage), quantitative measures of the dispersal rates of

species in a basin can provide valuable information for species- and site-specific assessments (Heino et al., 2015). However, field-based methods are costly and, therefore, mainly applicable to systems with considerable resources or high conservation stakes (e.g., protected species). In most cases, dispersal metrics calculated from species traits (e.g., fish: Radinger & Wolter, 2014); macroinvertebrates: Sarremejane, Mykrä, et al., 2017) can serve as useful proxies (Peredo Arce et al., 2021). In addition to quantitative estimates, trait information on the mode (aquatic, aerial, or terrestrial; active or passive), strength, timing, and direction (upstream, downstream, lateral) of species dispersal can also inform e-flow designs from a metasystem perspective (Sarremejane, Mykrä, et al., 2017). Most rivers are insufficiently studied to determine the relative roles of metacommunity processes, the influence of flow alterations on these processes, or the contribution of individual river sites to metasystem health. However, intensive monitoring is already taking place in many river networks and could be adapted to meet the needs of the framework we propose. For instance, 4 years of seasonal fish community data were sufficient to estimate the effects of flow on local extinction, colonization, and recruitment probabilities for the metapopulations of 42 fish species across 23 streams of the karstic lower Flint River Basin, Georgia (United States; Peterson & Shea, 2015). In addition, designing e-flows from a metasystem perspective can begin without comprehensive data. Data availability inevitably constrains analytical approaches, but simple methods can be informative and guide initial e-flow recommendations (see the “Implement” section). Additional monitoring can then generate new data as part of an adaptive management approach (Webb et al., 2017) whereby e-flow recommendations are periodically adjusted. As such, this step of the framework both compiles available knowledge and data and identifies gaps to fill.

Assess the relative need for e-flows

Although flow alteration is a ubiquitous cause of ecosystem degradation, river systems are subject to multiple additional stressors, which may undermine the effectiveness of e-flow programs if not also addressed (see Stewardson et al., 2017 for examples). Physical barriers to movement, invasive species, pollution, overfishing, increasing temperatures, sediment regime disruption, and riparian clearance may have additive or interactive (e.g., antagonistic, synergistic) effects with flow alteration (Birk et al., 2020). Targeted e-flows can alleviate the impact of some of these stressors by, for example, providing passage over barriers, flushing nutrients and other pollutants, regulating sediment load and controlling nonnative species.

However, given the cost of designing and implementing e-flows, it is critical to identify whether efforts may be better allocated to addressing another overriding stressor rather than flow alteration. If resources allow, managers can evaluate the benefit of complementing e-flows with other management actions (as was suggested in **Table 5.1**; Nicol et al., 2021) as part of an integrated basin management approach (Stewardson et al., 2017). Such a multipronged approach is already being explored in the MDB (Nicol et al., 2021) and other water-limited regions. In the San Diego River basin of California (United States), for example, multiple management actions were spatially prioritized in partnership with stakeholders to implement e-flows, protect habitat, and improve water quality across the basin (Stein et al., 2017).

5.4.2. Design

Infer metacommunity structure

This step aims to determine the relative strengths of metacommunity processes structuring community composition across the river network. Is the distribution and abundance of species strongly driven by environmental filtering, biotic interactions, dispersal, and/or ecological drift? How strongly are communities and populations linked, and are there source–sink dynamics among sites? Which sites are refuges during extreme flow events? Are species governed by different processes? An increasingly diverse toolbox is available to address these questions, depending on the quantity and characteristics of observational data and the resources available for conducting scientific analyses. Most empirical studies infer metacommunity processes by statistically analyzing patterns of species distribution or abundance among sites (Logue et al., 2011). An alternative approach involves reproducing the focal metacommunity using a spatially explicit mechanistic simulation model and testing a range of model parameters that control the relative strength of metacommunity processes, generating different scenarios of species distribution (e.g., Valente-Neto et al., 2018). The parameters associated with the scenario for which the generated patterns best match the observations are considered to most accurately reflect the processes structuring the system. Simulation models may better disentangle the relative roles of processes in empirical data, because similar ecological patterns can be driven by different processes (Valente-Neto et al., 2018). Once calibrated, such models can also simulate the effects of alternative water management scenarios on the metacommunity (Freeman et al., 2013). However, these models are currently too onerous for most management contexts in terms

of data, expertise, and setup time. Therefore, we consider them unrealistic for a general operational e-flow framework and do not discuss them further. Because the relative strength of metacommunity dynamics varies with spatial scale (see the “Controlling factors: Scale and heterogeneity” section), the units of analysis must be delineated. The biota of large basins such as the MDB is structured as potentially discrete metapopulations and metacommunities, depending on the dispersal capacity of the ecological targets and the connectivity of the system. In such cases, the basin must be divided into separate management units. For instance, population genetic studies have identified various levels of gene flow among fish species in the MDB: Golden perch exhibit high contemporary gene flow across most of the MDB, such that it should be managed as a single metapopulation (Attard et al., 2018). Other species, such as the eel-tailed catfish (*Tandanus tandanus*), exhibit genetic structure among catchments of the MDB but high levels of gene flow within those catchments (e.g., the Moonie River catchment, 15,000 km²), indicating that catchments of this size likely represent an adequate scale of analysis for e-flows and other management programs (Huey et al., 2011). Finally, for other species with small and demographically isolated populations displaying low genetic diversity, such as the threatened river blackfish (*Gadopsis marmoratus*), genetic studies can assist in the delineation of small management units within which to prioritize restoration measures (Lean et al., 2017). The scale of management must also be considered within basins. Focusing only on the communities within a fraction of the basin (e.g., only in the mainstem and larger tributaries) could overlook crucial spatial links (e.g., with headwater reaches that provide propagules and spawning grounds). Data describing the connectivity among reaches and subcatchments, whether potential (inferred from the landscape structure and the dispersal ability of ecological targets) or realized (inferred from actual dispersal or genetic structure), can enable selection of an appropriate scale (Cid et al., 2022; Hughes et al., 2013). The method most widely applied to infer metacommunity dynamics from observed patterns is variation partitioning (Peres-Neto et al., 2006). This approach decomposes the variation in occurrence or abundance-based taxonomic composition among local communities into three components: non-spatially structured environmental variation, spatially structured environmental variation, and pure spatial variation. The purely spatial component is hypothesized to reflect the effect of dispersal processes and ecological drift, whereas the non-spatially structured environmental variation expresses environmental filtering; and the

spatially structured environmental variation can result from multiple processes (Peres-Neto & Legendre, 2010). Although straightforward, this method can present statistical biases (Peres-Neto & Legendre, 2010) and allows limited inference of metacommunity processes if applied to a snapshot data set of species distribution (Guzman et al., 2022). Analyzing temporal variability in community composition, including through temporal approaches to variation partitioning, is therefore crucial to correctly infer metacommunity processes (Guzman et al., 2022; Jabot et al., 2020). Furthermore, applying multiple methods and analyzing multiple summary statistics, both descriptive (e.g., diversity metrics) and model-based (e.g., variation partitioning fractions), strongly increases the ability to infer metacommunity processes (Guzman et al., 2022; Ovaskainen et al., 2019). Two promising approaches for informing e-flow design are time-series analyses of spatial beta diversity and joint species distribution models (JSDMs). Temporal analyses of spatial beta diversity can be used both to infer the relative strength of metacommunity processes (e.g., through path analysis; Jabot et al., 2020) and to identify keystone sites (i.e., that consistently support high local diversity and contributing colonists to other sites, or containing unique species; Ruhí et al., 2017). Beta diversity analyses only require data on community composition. JSDMs are community-level extensions of standard species distribution models that leverage correlation in abundance (or co-occurrence) across taxa (Warton et al., 2015). As well as demonstrating high predictive performance in inferring metacommunity structure, JSDMs can reveal the potential strength of biotic interactions, expressed as residual species-to-species correlations (Guzman et al., 2022; Ovaskainen et al., 2019). In addition to data on community composition, JSDMs require hydrological and other environmental data as predictors of species distribution.

Develop flow–ecology relationships

Developing flow–ecology relationships requires flow regime characteristics to be related to the ecological indicators of interest while accounting for dispersal and biotic interactions. First, indices describing the flow regime and flow alterations are computed from discharge time series (e.g., Mathews & Richter, 2007). These metrics can be used as predictors of the ecological responses following a statistical (Olden & Poff, 2003) or expert-based preselection process (e.g., the functional flows approach; Yarnell et al., 2020). To capture the influence of dispersal, spatial autocorrelation in species composition is modeled by the statistical tool used to develop the flow–ecology relationship. Multiple model types can fulfill this

requirement, notably JSDMs (Warton et al., 2015), spatial stream-network (SSN) models (Isaak et al., 2014), and multivariate autoregressive state-space (MARSS) models (Holmes et al., 2012). JSDMs provide a well-developed way to establish relationships between flow statistics and species occurrence while accounting for the spatial distribution of sites and interactions among species (Ovaskainen et al., 2019). SSN models (Isaak et al., 2014), which are beginning to be used to develop flow–ecology relationships (Bruckerhoff et al., 2019; Larsen, Majone, et al., 2021), can account for autocorrelation that arises along both straight-line and network distances and from different dispersal modes. Differences in aquatic dispersal mode are modeled in SSNs by separately considering network distances among flow-connected (unidirectional flow, reflecting drift) and flow-unconnected sites (that are potentially on different streams and reflecting active instream dispersal; Isaak et al., 2014). Finally, MARSS models (Holmes et al., 2012) are particularly well suited to concurrently model the effects of temporal autocorrelation, spatial autocorrelation, and among-species correlation (provided sufficient sites and samples), as is evidenced by studies linking river flow regimes to metapopulation (Sarremejane et al., 2021) and metacommunity structure (Ruhí et al., 2018). MARSS models can also characterize the relationships between flow metrics and spatial beta diversity over time, and between flow metrics and site-specific contributions to beta diversity (Legendre & De Cáceres, 2013). Such analysis can identify how flow variability may create phases in which the metacommunity is dominated by regional dispersal versus local environmental filtering (Datry et al., 2016; Ruhí et al., 2017) or change the relative contribution of some sites to network-wide diversity (e.g., sites acting as refuges in different seasons or years). In river networks with extensive nonperennial reaches, in which low-flow refuge sites may play a key role in structuring metacommunities, temporary fragmentation among sites by drying could be incorporated into flow–ecology models if observations of in-channel conditions (e.g., flow, low flow, no flow, dry) are available (Sarremejane et al., 2021). Additional hydrological metrics, such as time series of pool area and volume, could also be used to predict ecological responses. If these additional predictors are used to develop flow–ecology relationships, links between discharge and in-channel conditions at monitored sites may need to be established to implement e-flow conservation actions (e.g., the amount by which surface or groundwater withdrawal must be reduced to maintain connectivity among pools). Finally, in those systems in which baseflow is particularly influenced by groundwater withdrawals and in which groundwater wells can

be regulated, groundwater simulations can establish links among groundwater withdrawal, flow alterations, and community responses (Falke et al., 2011).

5.4.3. Implement

Conserving or restoring metacommunity dynamics entails allocating water optimally across a river network and managing for dispersal in addition to meeting species' local flow needs—the typical focus of standard e-flow design. Even small-scale e-flows, when they are well targeted across a network, can fulfill network-wide objectives (e.g., in the MDB; Gawne et al., 2018). A few flow management projects already aim to maintain or restore dispersal among habitat patches for a particular species or to trigger fish migration, sometimes with explicit mention of metapopulation dynamics. These are mainly documented for fish in the United States and Australia, two countries with heavily altered hydrology and a long history of e-flow implementations (Poff et al., 2017). For example, e-flows have been implemented across the Susquehanna River Basin ($7.1 \times 10^4 \text{ km}^2$, northeastern United States) to conserve brook trout (*Salvelinus fontinalis*) metapopulation dynamics by promoting connectivity among habitat patches during summer low flows (Kendy et al., 2012). Similarly, e-flows maintain summer baseflow for passage over shallow riffles by endangered Colorado pikeminnow (*Ptychocheilus lucius*) in the Upper Colorado River Basin ($2.9 \times 10^5 \text{ km}^2$; U.S. Fish and Wildlife Service, 2020). Such movement increases access to suitable habitat and may contribute to maintaining gene flow between subpopulations. In the Lower Canning River (Western Australia), flow pulses ($2.2 \times 10^4 \text{ m}^3 \text{ d}^{-1}$ over 5 days) during summer aim to maintain water quality and provide sufficient depth over barriers to enable upstream migration by the freshwater cobbler (*Tandanus bostocki*; Norton et al., 2010). *T. bostocki* is the largest-bodied freshwater fish species in southwestern Australia, so these flows may also facilitate passage for other species. Across the MDB, e-flows are commonly implemented to promote connectivity and dispersal, including to enable access to refuges during low flows, to drown out barriers, to trigger migratory movements, to enable recolonization of river reaches from neighboring ones after local disturbance, to facilitate gene flow among subpopulations by long-distance dispersers, and to reconnect channels and floodplains with high flows (Commonwealth Environmental Water Office, 2022; Gawne et al., 2018). Facilitating dispersal is therefore already an occasional objective of e-flow design in line with a metasystem approach and could be included in more programs. Appropriate target sites for e-flow provision depend on the metacommunity structure. If analyses indicate naturally

limited dispersal among communities (or populations) and identify no keystone sites, then e-flow design should focus on maintaining a suitable flow regime across many sites (as determined by flow–ecology relationships) and providing flows that support that level of dispersal (Ruhí et al., 2017). But if analyses identify keystone sites that play a central role in supporting the metacommunity, then managers may prioritize e-flow provision at these crucial sites while maintaining sufficient flow for dispersal to the rest of the network. In the MDB, for instance, the Mid-Murray Floodplain Recovery Reach fish recovery plan focuses on ensuring suitable local habitat conditions for species whose populations are mainly driven by local recruitment, whereas e-flows are designed to trigger dispersal and ensure longitudinal connectivity for populations that rely on colonists from outside the local scale (Cornell et al., 2021; Lyon et al., 2021). Dispersal corridors that connect multiple sites through high dispersal rates, in particular, should be targeted for e-flow provision that maintains suitable abiotic conditions and connectivity for dispersal (Patrick et al., 2021). In the theoretical case in which insufficient water is available for e-flows to provide suitable conditions for two sites connected by high levels of dispersal, it may be preferable to provide adequate flow to one site—which can become a source of colonists for the other—rather than to provide unsuitable flows to both sites. Similarly, e-flow provision should prioritize promoting access to dry-phase refuges (e.g., perennial pools in naturally nonperennial rivers) during the drying period and their maintenance throughout the dry period (Rayner et al., 2009). Additional refuges may be restored (e.g., through targeted water pumping) to provide dispersal stepping stones between communities (Archdeacon & Reale, 2020). During droughts, which reduce water availability in river networks at a regional scale, even locally constrained e-flow releases may reduce the synchronous pressure exerted by the drought and enhance metasystem-wide viability (Marshall et al., 2021). Once sites have been selected, flow–ecology relationships can inform selection of the flow regime elements to conserve or restore. In the same way that designer e-flows can meet the local habitat needs of native species to the detriment of nonnative invasive species (e.g., Chen & Olden, 2017), designer e-flows may be tailored to promote and impair the dispersal of native and nonnative species, respectively. For example, restoring the timing of high flows can benefit the waterborne seed dispersal of native plant species whose phenology is adapted to a natural flow regime and limit the proliferation of invasive species (Lytle et al., 2017). If flow-dependent barriers to dispersal are present (e.g., rapids, low-head dams), evaluating whether their passability

should be increased (e.g., to restore dispersal among communities; Marshall et al., 2021) or decreased (e.g., to prevent a nonnative species from expanding its range) through e-flow provision, and when, is important. E-flows may also be designed to support biotic interactions other than competition and predation. For example, several mussel species in the MDB depend on host fish to complete their life cycle and colonize new sites, such that e-flows must be designed both to support critical mussel life stages in synchronicity with fish host species' needs and also provide pathways for host fish dispersal (Wright et al., 2022). The choice of scenario depends not only on stakeholder input (Mussehl et al., 2022) but also on the hydrology of the basin and the available management levers of water provision. For example, some perennial river pools that act as refuges in arid regions depend on occasional surface flows to persist throughout the dry season whereas others are primarily groundwater fed (Hamilton et al., 2005). Regulation of upstream surface water withdrawal or periodic releases from reservoirs may be needed for the former, whereas limits to groundwater withdrawal could be used to conserve the latter. The location of flow regulation structures, the ability to regulate surface and groundwater withdrawals and to alter land use will all influence where, how and at what cost e-flows can be allocated. To move beyond a strictly local approach, a diversity of management levers other than flow releases downstream of a single dam can be used for e-flow provision. Examples already exist of alternative sources of water for e-flow provision and include system-wide coordinated reservoir operation (Opperman et al., 2019); regulation of surface and groundwater withdrawals (e.g., in the United States: Kendy et al. 2012; in the United Kingdom: Gustard et al., 1987, implemented at least since 1963), including switching from surface to groundwater sources (McCoy et al., 2018); moving a diversion downstream (McCoy et al., 2018) or modifying the timing of withdrawal (European Commission, 2015); land use planning (e.g., switching to crops requiring less water, or temporarily or permanently taking land out of agricultural production; McCoy et al., 2018); targeted improvements in conveyance or irrigation efficiency (Opperman et al., 2019); release of wastewater treatment plant effluent (Hamdhani et al., 2020); diversion of domestic water from urban or suburban water supply networks (Norton et al., 2010); and even experimental storage of spring runoff in aquifers for later instream use (McCoy et al., 2018). Which water source can more easily be used for e-flow provision strongly depends on the legal and political context. Water withdrawal limits can be legally imposed in some countries and

localities, whereas other administrations rely on the buyback or leasing of water rights by government and nongovernmental organizations from willing sellers (Opperman et al., 2019). Finally, new coordination of e-flow releases across entire river basins can be achieved by strategically targeting hydropower dams undergoing relicensing through a centralized process. In the United States, for example, over 300 hydropower projects are expected to undergo relicensing between 2016 and 2026 (Schramm et al., 2016), providing an opportunity to coordinate e-flow objectives among dams with a metasytem perspective. In the MDB, environmental water is recovered to meet both local and basin-wide objectives with measures ranging from targeted infrastructure investments (e.g., efficiency gains from off-farm conveyance systems, on-farm irrigation, reservoir evaporation and seepage, urban water management) to voluntary surface and groundwater entitlement purchases (Murray-Darling Basin Authority, 2018). Then, specific e-flow targets are achieved by timing reservoir releases with unregulated streamflow, and by coordinating operating rules and withdrawals within and among catchments (**Box 5.2**; Murray-Darling Basin Authority, 2020a; Stewardson & Guarino, 2018). The increasing use of spatially distributed sources of water for e-flow provision is both a departure from the longstanding focus on single reservoir operation and another key requisite for metasytem approaches.

5.4.4. Monitor

Monitoring of e-flow implementations is pivotal to improve future management, to demonstrate the benefits of public investment to decision-makers and the public, and to inform ecohydrological science in general (King et al., 2015). E-flow programs are costly and often contentious, so their legitimacy hinges on transparent reporting of their benefits (O'Donnell & Garrick, 2017). The MDB plan, for example, will cost the Australian government approximately US\$9 billion from 2012 to 2026 (Ross & Connell, 2016). Despite their cost, most habitat and flow restorations go unmonitored, limiting the opportunities to develop evidence-informed best practices (Souchon et al., 2008). Nonetheless, guidelines and methods for monitoring the outcomes of standard e-flows are well established (King et al., 2015; Souchon et al., 2008; Webb et al., 2017). Within an adaptive management cycle, monitoring can continuously contribute to reducing uncertainties and adjusting e-flow recommendations and objectives (Webb et al., 2017). Analyses of metacommunity dynamics and flow–ecology relationships can provide quantitative forecasts that represent testable hypotheses to iteratively refine e-flows as they are implemented (Dietze et al., 2018).

Monitoring should therefore verify the actual delivery of water allocations (i.e., were discharge objectives attained?), the effectiveness of both short-term flow events (on, e.g., dispersal, recruitment) and the long-term flow regime (on, e.g., species distribution), and the validity of the assumptions and models underlying e-flow design (King et al., 2015; Souchon et al., 2008). In addition to previous assessments of stressors (see “Define” section), the monitoring stage can include continued assessment of whether nonflow stressors (e.g., water quality, instream barriers) may be affecting the ecological targets, compromising the evaluation of e-flow outcomes, and indicating the need for complementary non-flow-based measures (Nicol et al., 2021). Reflecting management targets, e-flow monitoring has historically focused on documenting the effects of discrete flow events on local habitat conditions (Olden et al., 2014; Souchon et al., 2008). To our knowledge, the only explicitly basin-scale, long-term e-flows monitoring programs are the Glen Canyon Dam Adaptive Management Program (although mostly focused on the mainstem effects of e-flows from a single dam; Melis et al., 2015), the Victorian Environmental Flows Monitoring and Assessment Program (Webb et al., 2010), and Flow-MER in the MDB (see **Box 5.2**; Barbour, Thompson, Pollino, et al., 2021; Gawne et al., 2020). Flow-MER uses monitoring data in seven areas across the MDB to assess both area-scale outcomes for river reaches and associated wetlands within the area and their contribution to the achievement of basin-scale objectives (i.e., outside of the spatial scope of individual flow releases). E-flow outcomes are compared with modeled scenarios that represent what outcomes would have been without e-flows, accounting for water availability each year. This annual evaluation considers how e-flow design could be altered to improve flow management outcomes. Additional funding is also allocated to novel research on ecological responses to e-flows (**Box 5.2**). The ultimate aim of the program is to improve understanding of basin-scale processes by comparing outcomes from isolated e-flow events with coordinated e-flow provision across areas (Gawne et al., 2020). Although Flow-MER (2019 –2022) and preceding monitoring programs in the MDB (2014 –2019) represent the largest e-flow monitoring effort in the world, the budget for their 2014–2022 implementation was approximately US\$35 million (Barbour, Thompson, Pollino, et al., 2021; Hart & Butcher, 2018), or less than 0.5% of the overall MDB Basin Plan 15-year budget, underscoring the modest cost of monitoring relative to the total investment for e-flow implementation. Assessing the outcomes of e-flow programs beyond a few sites across a river basin is cost prohibitive using traditional data collection methods, but

several novel data sources can be combined to increase the spatial coverage and density of e-flow monitoring. First, DNA-based monitoring could expand the spatial scope and density of community sampling across river networks (Carraro, Mächler, et al., 2020). Second, citizen scientists could generate abundant monitoring data to inform management and increase buy-in by diverse stakeholders (Mussehl et al., 2022). Lastly, satellite remote sensing can be used to track the delivery of e-flows and their effects on the distribution of and connectivity among habitats, and on the distribution and composition of riparian plant communities across the river network. All three of these approaches are already being trialed or implemented as part of the e-flow monitoring and research program in the MDB (e.g., Murray-Darling Basin Authority, 2020a; Watts et al., 2019). With sufficient representative sampling, the results from high-quality monitoring could be extrapolated to unmonitored sites for a truly basin-scale assessment (Webb et al., 2017).

5.4.5. Applicability of the proposed framework

We do not propose that every e-flow program should or could adopt all components of our proposed framework. It is unrealistic to fully cater to the specific metasytem dynamics of every river basin considering the cost of achieving this objective. Moving beyond simple hydrological rules of thumb (e.g., a fixed percentage of mean annual flow) toward greater ecological realism is already a major challenge for e-flow science (Poff, 2018). The development of transferable flow–ecology relationships is another key research priority for regional e-flow implementation (Poff et al., 2010). However, we contend that adopting a metasytem perspective from program definition and design to monitoring and evaluation could increase the effectiveness of most e-flow programs. This framework best suits e-flow programs focused on preserving multiple populations or communities linked by dispersal, equipped with spatially explicit data and multiple water management levers. Examples of e-flow programs with substantial resources already exist in many river basins, and system-wide approaches are increasingly adopted (Opperman et al., 2019). The substantial political and governance hurdles to integrating a metasytem perspective and managing flows across scales will probably be easiest to clear for such programs, which will then provide proofs of concept for other basins. Nonetheless, benefits can be gained from a metasytem perspective even when those conditions are not met, or where resources are limited. When a lack of data hinders analyses of metacommunity structure and processes, for example, managers still have multiple options. They can synthesize knowledge from experts, including

local stakeholders, and existing research to develop conceptual models that could guide target setting and identify potential ecological processes and factors that may influence the effectiveness of e-flow implementation. Planning can also be supported by conceptual and practical consideration of key ecological questions, such as: Do the species of interest require multiple habitats to complete their life cycle? If so, when and at what scale? Are there flow-dependent barriers to longitudinal or lateral movement? Are there nonnative species that may benefit from e-flows? Network analysis using topographic and remote sensing data can provide a priori assessments of barriers and key sites acting as refuges or connectivity hubs that could be targeted for more detailed e-flow assessments (Marshall et al., 2021; Yu et al., 2022). These assessments can be combined with knowledge of the life histories of the ecological targets to infer potential dispersal structure among populations or communities, which can help identify relevant management units (as demonstrated for more than 100 Australian aquatic species by Hughes et al., 2013). In the absence of ecological data, e-flows can also target natural spatiotemporal variability in flow regimes across a river network, rather than using flow metrics at a single site, to promote regional heterogeneity and resilience. In heavily fragmented systems, dispersal may still be possible for some species (e.g., golden perch in the MDB; Huey et al., 2011), and assessing the structure of the metasystem can help prioritize e-flows among sites. Finally, even if management is restricted to a single flow regulation structure for a single species, e-flows can still be designed to account for more than local habitat conditions, and trigger movement to other habitats, facilitate passage over barriers, or control invasive species.

5.5. Conclusions

Growing human water demand and ongoing global changes accentuate the competition for water among uses and make long-term implementation of e-flows programs increasingly uncertain. In most cases then, the main obstacle to e-flow implementation will remain political, not scientific (Dourado et al., 2023; Owusu et al., 2022). This difficulty in implementing e-flows further raises the stakes for program outcomes; whether the objectives of using scarce water for the environment are met affects the legitimacy of the programs and can determine their continued viability (O'Donnell et al., 2019). Therefore, careful design and robust monitoring that leverage advances in ecology to maximize the effectiveness of e-flow implementations are key to guaranteeing continued e-flows

implementation. In this article, we specifically propose that managing for metasytem dynamics beyond local environmental filtering—namely, biotic interactions, dispersal, and ecological drift—and accounting for connectivity, scale, and heterogeneity can increase the effectiveness of e-flow implementations. To achieve this objective, strong partnerships among researchers and managers are required that facilitate the integration of recent ecological research in management and enable program co-development through multiple adaptive management cycles (Webb et al., 2010). Incorporating metasytem dynamics in e-flow design may even increase the transferability of flow–ecology relationships by controlling for confounding factors. Although applications of metasytem concepts and models in conservation are still in their infancy (Chase et al., 2020; Cid et al., 2020, 2022; Patrick et al., 2021), we posit that increased adoption of this perspective will in turn fuel the development of streamlined methods and transferable knowledge that will increasingly facilitate metasytem e-flow assessments.

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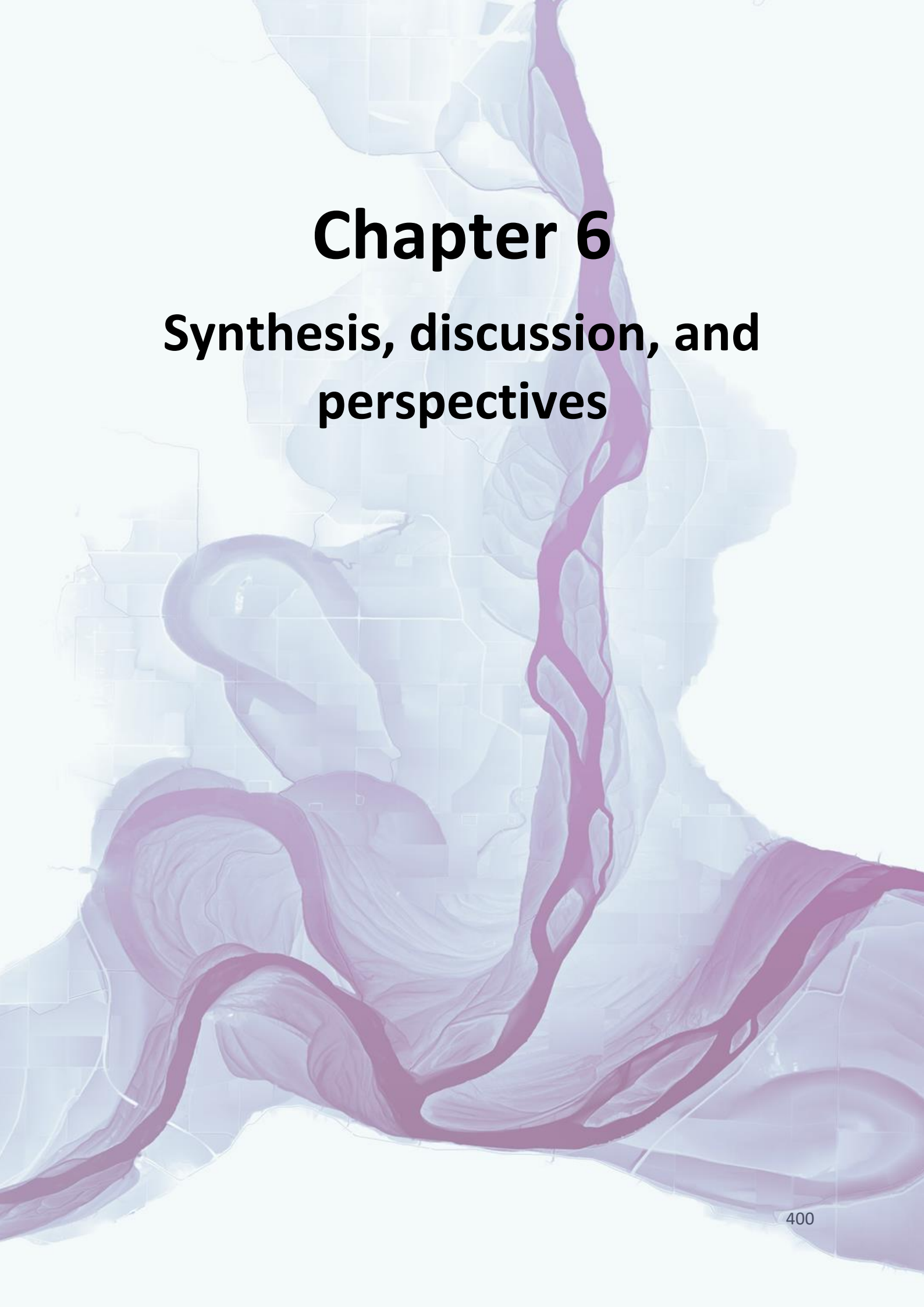
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Chapter 6

Synthesis, discussion, and perspectives

6.1. Introduction

While flowing water is the defining feature of rivers and streams, year-round flow is not (Messenger et al., 2021). Non-perennial rivers and streams (NPRs) are inherent to river networks, and recurrent flow cessation is a central process underlying the hydrology, ecology, biogeochemistry and ecosystem services of riverine ecosystems worldwide (Datry, Boulton, et al., 2023). These facts were not broadly acknowledged by the scientific community until recently. Together with the perception that watercourses are less valuable when dry (Cottet et al., 2023; Leigh et al., 2019), this lack of recognition has led to policy and management practices catering to perennial reaches at the expense of NPR ecosystems (Acuña et al., 2017). The overarching goal of this thesis was to advance our understanding of the global prevalence and diversity of NPRs, and to improve their integration in river policy and sustainable management. I leveraged an interdisciplinary perspective integrating hydrology, ecology, geography, and data science to address three main gaps:

- The lack of a global hydrological foundation for the science and management of non-perennial rivers and streams.
- The uneven representation of non-perennial streams in jurisdictional maps of watercourses defining the scope of environmental protection laws.
- The inadequacy of conceptual and operational frameworks for the design and implementation of environmental flows in river networks with high prevalence of NPRs.

In the following sections, I review the main contributions of my research chapters to addressing these gaps, reflect on some of the broad questions my dissertation raised, and discuss some of the potential future research perspectives that would further advance the study and management of NPRs.

6.2. Summary of research findings and contributions

6.2.1. A global hydrological foundation for the science and management of NPRs

Well before this thesis, scientists across disciplines remarked on the significant disparity between the ubiquity of NPRs and their scant representation in research (Clifford, 1965; Leopold & Miller, 1956; Tooth, 2000; Williams & Hynes, 1976). The global prevalence of NPRs was systematically cited to conjure their importance (Datry et al., 2014; Larned et al., 2010), but usually in vague terms in the absence of a rigorous estimate prior to this thesis.

Global assessments had indicated that 29% to 36% of the total length of rivers worldwide are non-perennial, with some suggesting that this figure could exceed 50% (Datry et al., 2014; FAO, 2014; Raymond et al., 2013; Schneider et al., 2017). However, these estimates were either hypotheses, geographically limited to certain areas, or incidental findings within larger studies, rather than dedicated global efforts to map NPRs. For instance, the models developed by the FAO (2014) and Schneider and colleagues (2017) assume that streamflow cessation only occurs in arid and semi-arid regions. Therefore, Chapter 2 of this thesis provides the first robust, quantitative confirmation that NPRs are the world's most widespread type of rivers and that they are prevalent in all climates, biomes, and continents. Even in the wettest climates, up to a third of headwater streams are non-perennial. The robustness of this finding was recently further confirmed. S. Liu et al. (2022) estimated that 55% of the global river network stopped to flow at least one day per year on average, compared to 51-60% in Chapter 2, with an entirely different discharge-threshold approach applied to another global hydrological model.

Chapter 2 was not about addressing a chip on the shoulder of NPR enthusiasts though; its implications go beyond an estimate of the total prevalence of NPRs. The resulting dataset represents a crucial hydrographic baseline for assessments of the global role and future fate of NPRs in the Earth system. It predicts the probability of intermittence for each mapped river and stream in the world (except Antarctica) for a total of 23.3 million kilometres. The fine grain of this assessment — the river reach — is essential for the future study and management of NPRs. It enables the linkage between predictions of intermittence with other sources of data at that scale, which in turn allows assessing and tracking the contributions of NPRs to biogeochemical and water cycles, as well as their role in fostering global biological diversity. For example, “only” the paucity of data on NPR ecosystem metabolism now stands in the way of robust estimates of their role in the global carbon cycle (Battin et al., 2023).

Chapter 3 goes one step further in addressing the lack of a global hydrological foundation for the study and management of NPRs by quantifying the diversity of flow intermittence regimes, a recognized challenge for the hydrologic community (Shanafield et al., 2021). Delineating distinct flow intermittence classes and analyzing their environmental characteristics promotes a more nuanced understanding of NPRs as spanning a large

spectrum of ecosystems. Nonetheless, this classification system has not been robustly tested against the criteria necessary to justify its use (Kraemer, 2020): objectivity (consistency among independent researchers in reaching the same conclusion regarding the quantity and definitions of distinct boundaries), predictivity (ability to predict other variables), and stability to the addition of new observations. A preliminary analysis of stability was conducted, but future efforts will need to further examine these criteria and refine this analysis. Despite its current limitations, Chapter 3 quantitatively demonstrates that the hydrology of NPRs varies in multiple dimensions other than the duration of flow cessation, which was the only differentiating characteristic included in global hydrological classifications (Poff et al., 2006; Puckridge et al., 1998) before Sauquet et al. (2021). It also confirms that flow intermittence regimes can coincide across continents and biomes all the while differing within the same biome or climate. These inter-regional differences have long been acknowledged: four decades ago, comparative analyses of global discharge time series across arid zones already identified that NPRs in Australia and southern Africa have similar annual flows and peak discharge that are more variable than in other parts of the world like the North American southwest (Finlayson & McMahon, 1988; McMahon, 1979). This thesis and future improvements (see *Future research directions* section) can provide a truly global picture of these differences across all NPRs. Further contributing to a sharper view of NPRs, Chapters 2 and 3 consider flow intermittence regimes more broadly than the recent formalization of the “drying” regime concept (Price et al., 2021) by including freezing and ponding (without drying), both widespread phenomena (Buttle et al., 2012). Finally, the methodology developed for Chapter 3 to assess the representativeness of gauging stations can be applied to any sample of locations. Combined with the typology, this approach can guide the design of conservation areas to encompass the diversity of global flow regimes, or support stratified sampling of the biotic community composition, biogeochemical fluxes, and ecosystem services supported by NPRs.

6.2.2. Taking stock of the uneven representation of NPRs in regulatory frameworks

Across the world, how people interact with rivers and streams is shaped by complex legislation mandating permits for conducting certain activities in and around watercourses or banning them altogether. One critical aspect of this regulatory framework is the definition and mapping of what constitutes a watercourse in the eyes of the law, as it dictates the

scope of legal safeguards for freshwater ecosystems. The inadequacy of environmental laws for the protection of NPRs has been alluded to before (Acuña et al., 2014, 2017; Doyle & Bernhardt, 2011; Larned et al., 2010; Taylor & Stokes, 2007). However, Chapter 4 of this thesis is the first assessment of the implications and interpretations of legal definitions on the actual extent and representativeness of protected watercourses at a national level, using France as a case study. The US is the only other country where such systematic cartographic assessments have been undertaken -- to quantify the jurisdictional scope of the US Clean Water Act (Fesenmyer et al., 2021; Greenhill et al., 2024). Yet these assessments were either theoretical (Fesenmyer et al., 2021) or based on a subset of reaches for which legally binding case-by-case decisions had been made (Greenhill et al., 2024). Chapter 4, by contrast, leveraged an expansive cartographic effort by local governments in France since 2015 to assemble a national map of watercourses that fall under the Water Law and assess cartographic interpretations of the definition of watercourses across two million reaches.

I estimate that NPRs comprise nearly 60% of the mapped hydrographic network length in mainland France but make up about 80% of hydrographic segments which have been disqualified as non-watercourses (i.e., excluded from regulatory protection under the Water Law). The disproportionate exclusion of NPRs from many of the departmental maps of watercourses in France does not come as a surprise considering the documented lack of recognition of NPRs (Cottet et al., 2023). Still, it provides evidence of the regulatory implications of this negative perception and highlights the stakes for the integrity of entire river networks.

In Chapter 4, I also show that interpretations of the same definition of watercourses vary across jurisdictions, and that these variations are statistically related to anthropogenic factors, including the prevalence of winter crops and irrigation. These correlations and documented disagreements among local stakeholders about these regulatory maps (Cinotti & Dufour, 2019) point to the importance of socio-political factors in shaping the scope of regulations. This phenomenon of variable implementation has been virtually unexamined elsewhere but has broad implications for the effectiveness of laws in protecting NPRs and their contributions to people (Nicolás Ruiz et al., 2021; Pastor et al., 2022; Steward et al., 2012; Vidal-Abarca Gutiérrez et al., 2023). Moreover, it represents a case study of the hydro-social cycle, the “socio-natural process by which water and society make and remake each

other over space and time” (Linton & Budds, 2014), and on the diversity of values ascribed to ecosystems (Pascual et al., 2023). Finally, in this chapter I examine legal definitions of watercourses in other countries to show that this issue is likely applicable to regulatory frameworks across the world.

Chapter 4 is interrelated with the other chapters in several ways. By quantifying the disproportionate exclusion of NPRs in regulatory frameworks, it further illustrates the need for the paradigm shift in river science, policy and management advocated in Chapter 2 and 3. In relation to chapter 5, all evaluations of successes and challenges to e-flows implementation underline the importance of a robust legal and enforcement framework (Arthington et al., 2023; Dourado et al., 2023; Harwood et al., 2018; Le Quesne et al., 2010; A. Owusu et al., 2022; A. G. Owusu et al., 2021; Pahl-Wostl et al., 2013). Adopting the metasystem perspective introduced in Chapter 5, in particular, requires a supportive legal framework. Specifically, it depends on a regulatory basis that recognizes the entire river network and its basin as the unit of management for water flow.

Jurisdictional maps that define the scope of the Water Law, examined in Chapter 4, are the main tool to ensure that the flow regime of running water ecosystems is protected, among other aspects of their integrity. The Water Law in France broadly regulates any facility, infrastructure, construction site and activity that may affect freshwater bodies by requiring permits (*Article R214-1 - Code de l'environnement - Légifrance, 2023*). For example, it regulates any action that can result in withdrawals from surface water or groundwater of at least 1,000 m³ per year, significantly modify the level of flow of a running water body, or result in input flows of any substance to watercourses (even if non-polluting). That said, a special decree was issued in 2019 to exonerate stakeholders from protecting e-flows in “atypical” watercourses whose lowest natural monthly flow is less than one-tenth of the average flow on inter-annual average in Mediterranean regions. It stipulates that no minimum flow is necessary for a maximum period of three months if all possible water-saving measures have been taken and the water withdrawal needs for drinking water supply or gravity irrigation cannot be met with a minimum flow of one-fortieth of mean annual flow (*Article R214-111 - Code de l'environnement - Légifrance, 2019*). This further broadens the exclusion of NPRs from legal e-flows requirements in large portions of the territory beyond those already resulting from jurisdictional maps.

6.2.3. Adapting e-flows frameworks to the ecohydrological dynamics of NPRs

Environmental flow (e-flow) programs have been implemented across the world to conserve and restore the quantity, timing and quality of water flows necessary to sustain river ecosystems (Arthington et al., 2018). Accelerating the design and implementation of e-flows is recognized as one of six priority actions to curb the ongoing loss of global freshwater biodiversity (Tickner et al., 2020). However, the effectiveness of e-flows programs may be limited by a singular focus on ensuring adequate flow conditions at local sites. This continued focus overlooks the growing body of research in metacommunity ecology, which shows that biodiversity and ecosystem functioning result from the interactions of both local- and regional-scale processes like species dispersal (Gounand et al., 2018; Leibold & Chase, 2017). The interplay of local and regional processes is particularly critical to the ecological structure and functioning of NPRs with high spatiotemporal variability in hydrological conditions. This variability creates a dynamic mosaic of habitats where dispersal and biotic interactions govern the abundance and distribution of species (Cid et al., 2020; Datry, Bonada, et al., 2016; Sarremejane et al., 2017).

Despite the importance of metacommunity dynamics in river ecosystems, no guidelines existed to explicitly account for them in designing e-flows. The aim of Chapter 5 was to fill this gap. This conceptual article sought to broaden the set of ecological processes integrated into e-flows programs with the end goal of better protecting the ecological structure and dynamics of river networks, in particular those with a high prevalence of NPRs. It first demonstrates how advances in metacommunity ecology can inform e-flows science and practice. I specifically discuss how metacommunity dynamics beyond local environmental filtering—namely, biotic interactions, dispersal, and ecological drift—and controlling factors—connectivity, scale, and heterogeneity—mediate species responses to flow alterations. Several of these concepts are illustrated with novel modeling simulations of population dynamics for two interacting species in a synthetic river network using a general metacommunity model.

I then provide a step-by-step framework to operationalize metacommunity concepts and tools in e-flows programs, from program definition and e-flows design to implementation and monitoring. Example recommendations include identifying diverse levers of water provision and regulation to allocate water optimally across a river network rather than only downstream of dams; inferring what processes drive species abundance and composition

across sites; and linking local outcome monitoring to basin-scale objectives. These recommendations are nuanced by reflecting about which measures may be more feasible in different regulatory contexts, linking to Chapter 4, and can be adapted even in river networks with limited in situ data. Throughout the Chapter, I use examples from freshwater conservation and restoration programs that demonstrate the processes or management measures discussed, with a particular focus on the basin-wide e-flow program of the Murray–Darling Basin in Australia. Across Murray-Darling Basin, e-flows are commonly implemented to promote connectivity and dispersal, thus broadly aligning with the metasytem approach and framework (Commonwealth Environmental Water Office, 2022; Gawne et al., 2018).

By synthesizing current knowledge in meta-system ecology and drawing from an extensive set of case studies on e-flows management and policies, this article creates a meeting point for scientists and managers, and across disciplines, to improve the management and conservation of NPRs.

6.3. Synthesis

6.3.1. Towards a new model of rivers in science, policy, and management

The overarching goal of this thesis was to “put intermittent rivers on the map” by questioning the river model underlying science, policy, and management. A model is an abstraction of reality, a way to grasp the intractable complexity of the world by focusing on the essential patterns and processes that are relevant to our objective. In ecology and river science, conceptual models seek generality, guide hypothesis testing and enable predictions, shaping how we collectively understand and manage river ecosystems (Lawton, 1999). In the process of trimming reality to gain understanding, however, some important elements may be erroneously deemed anecdotal and discarded. Flow cessation, and NPRs by extension, is one of those elements, that has historically been omitted from prevailing conceptual models (Allen et al., 2020; Datry, Boulton, et al., 2023).

Every chapter of this thesis tackles assumptions underpinning the river models framing science, policy, and management, which were tailored to perennial rivers considered in isolation from the rest of the network. Chapter 2 demonstrates that NPRs cannot be abstracted from our model of river ecosystems because they are the rule rather than the

exception on Earth. Chapter 3 takes a step towards nuancing our model of NPRs as spanning a continuum between aquatic and terrestrial environments. It also highlights the potential prevalence of freezing as a cause of flow cessation, which has only received cursory attention (Buttle et al., 2012; Tolonen et al., 2019). Chapter 4 questions the model underlying the legal definition of watercourses in regulatory frameworks across the world, which draw an artificial line between regulated and unregulated based on flow cessation and overlook the connectedness of river networks. Chapter 4 moreover exposes how these legal models, as abstractions of reality trying to discretize a continuous gradient, are necessarily confronted to local and individual mental models when implemented, thereby leading to the uneven protection of NPRs. Finally, Chapter 5 questions the conceptual model of rivers underlying e-flows program, that local flow conditions are the master variable governing river ecosystems. It instead calls for protecting and restoring flow regimes from a network-scale perspective that accounts for diverse ecological processes and complementary management measures.

This thesis contributes to an ongoing change of perspective that is gaining critical mass thanks to ongoing efforts. Notably, several large-scale coordinated research programs on NPRs started just before the beginning of my thesis in September 2020. The European DRYvER project (Securing biodiversity, functional integrity and ecosystem services in DRYing riVER networks), to which I participated, has mobilized multidisciplinary teams from 11 countries in 2020-2025 to collect, analyse and model data in nine river networks with a high prevalence of NPRs. Its goal is to investigate the impacts of climate change on the biodiversity, ecosystem functions and ecosystem services of NPRs (Datry et al., 2021). In the US, AIMS (Aquatic Intermittency effects on Microbiomes in Streams; 2020-2024) and StreamCLINES (2019-2023) are two large programs with coordinated data collection. The first explores the effects of river drying on water quality, biogeochemistry and microbiomes; the second examines the community structure, food web dynamics, and genetic connectivity of benthic macroinvertebrates (Burgin et al., 2022). Furthermore, Chapter 5 of this thesis was developed collaboratively as part of the Dry Rivers Research Coordination Network (RCN), a synthesis program on NPRs formed by over 40 ecologists, hydrologists and biogeochemists which ran from 2018 to 2023. These programs build on previous multidisciplinary efforts, like SMIRES (Science & Management of Intermittent Rivers and Ephemeral stream; 2016-2020) and the 1000 Intermittent Rivers Project (1000IRP), or those

in hydrology by the International Association of Hydrological Sciences (IAHS) and UNESCO EURO FRIEND-Water (Datry et al., 2017; Sauquet et al., 2020). Thanks to these initiatives, some of which my thesis contributed to, NPRs are entering the mainstream. Such a recognition of the prevalence and ecological importance of NPRs will hopefully trigger efforts to adequately manage them and reverse their exclusion from protective legislation.

6.3.2. From discretizing to integrating river networks

Discretization is part of most models, whether conceptual or mathematical. Partitioning objects, patterns, or processes into discrete categories helps us reduce multidimensional variability to a single label. Each grouping is thus associated with expectations as to the characteristics of its members, which presents several advantages. Mainly, it provides useful mental and linguistic shortcuts that facilitate communication, decision-making and management. For example, the classification of waterbodies is a central concept of the Water Framework Directive to evaluate the ecological conditions of freshwater ecosystems (Water Framework Directive Common Implementation Strategy Working Group, 2003). Discretization can also facilitate data collection, which is necessarily discrete, and subsequent data analysis and interpretation (Kraemer, 2020). For instance, the delineation of spatial and conceptual boundaries between ecosystems — terrestrial versus aquatic or lotic versus lentic — is a convenient discretization. These ecosystems are characterized by different processes which immediately come to mind (Rosset et al., 2017). Yet they are also physically connected and share numerous processes, spanning a continuum with no real boundary (Hotchkiss et al., 2018; Lamberti et al., 2010; O’Sullivan et al., 2022), such that discretization also has drawbacks. It can divert attention from forming general theories, introduce undue subjectivity, and obscure the connections between distinct groups or the diversity within those groups (Kraemer, 2020). In hydrology, for example, the concept of catchments as discrete hydrogeological units of analysis is being questioned in light of the prevalence of groundwater flow across catchments (Fan, 2019). Another important disadvantage of discretization is that categorical analyses have less statistical power and predictive ability than continuous methods (e.g., ANOVA versus regression analyses; Cottingham et al., 2005). Finally, discretization can result in less effective management strategies and research designs if applied dogmatically, or create expert jargon that hinders communication with the public (e.g., **Figure 6.1**).

FLOWING PHASE



Figure 6.1. Example of discretization of a continuous gradient of aquatic conditions in NPRs that represents real differences in patterns but results in jargon.

Aquatic states in NPRs as defined by Gallart et al. (2016) and their simplification in aquatic phases (Gallart et al., 2017). Photo credits: MIRAGE and TRivers projects. Reproduced from Bonada et al. (2020).

This thesis both leans into and steps back from discretization. It leans into discretization with Chapters 2 and 3 by emphasizing the distinctiveness of NPRs, and advocating for their recognition in science, policy and management; it steps back from it in Chapters 4 and 5 by promoting an integrated view of river networks including both perennial and non-perennial reaches.

The goal of “silo-ing” NPRs in Chapter 2 and 3 is to go against the historical treatments of lotic ecosystems as predominantly perennial, thus lumping NPRs within a homogenizing category. It pushes recognition of the critical importance of flow cessation on the functioning and conservations of riverine ecosystems, the same way that advocating for an

acknowledgement of inland waters as a distinct realm from terrestrial ecosystems in the recent Global Biodiversity Framework was crucial to set specific targets, monitoring and conservation (Cooke et al., 2023). Recognizing the distinctiveness of NPRs motivated the other large-scale research efforts previously mentioned, and was accompanied by special issues in journals and separate conference sessions, which enabled a constructive coalition around this topic across continents and disciplines (Fovet et al., 2021; Shanafield et al., 2020).

As the prevalence and importance of NPRs is increasingly recognized, an integration is now needed to move away from a dualistic model of perennial versus non-perennial ecosystems. An integrated view of river networks involves studying and managing all reaches, their floodplain(s), and their contributing catchment as a dynamically interconnected aquatic-terrestrial continuum, a meta-ecosystem with variable degrees of water presence and flow (Allen et al., 2020; Datry, Boulton, et al., 2023; O’Sullivan et al., 2022; Stegen et al., 2024; Wohl, 2015). It implies, for example, to shift the discourse from NPRs as entities (e.g., “NPRs are the world’s most widespread type of watercourse”) to flow cessation as a process (e.g., “most watercourses on Earth experience flow cessation”). Moreover, it implies a shift towards considering the connections among the components of a river network as equally important to its functioning and resilience as the components themselves (Datry, Boulton, et al., 2023). This perspective is not entirely novel; the connectedness and hydrological dynamism of river networks was already part of the flood pulse concept (Junk, 1989; Tockner et al., 2000) and Ward’s 4-dimensional view (Ward, 1989), among others. It is also at the center of modern metacommunity and metaecosystem ecology (Cid et al., 2022; Sarremejane et al., 2024). However, this recent development more fully integrates dry phases compared to previous models that deemed them largely inert, ecologically and biogeochemically (Datry, Boulton, et al., 2023).

An integrated network perspective encourages scientists and managers to think of ecosystems through the processes and scales most relevant to their application rather than through categories. From the point of view of energy, for instance, large reciprocal fluxes link river channels and their riparian area, with important temporal and spatial variations between wet and dry phases, blurring the line between these ecosystems (Allen et al., 2024; Baxter et al., 2005). Dry bed sections in perennial reaches at low flow may have identical

emission rates as those in NPRs but are usually not considered by scientists focusing on the latter (Arce et al., 2019). Chapters 4 and 5 of my thesis were intentionally written to emphasize this integrated network perspective. They are buttressed by earlier works on river network connectivity (Fritz et al., 2018; Leibowitz et al., 2018) for the former and on metacommunity theory (Leibold & Chase, 2017; Thompson et al., 2020) for the latter, while highlighting the distinctiveness and vulnerability of NPRs. Chapter 3, which currently categorizes NPRs to understand their hydrological diversity, is designed to be ultimately expanded to communicate and promote the representative study and management of the full diversity of global river flow regimes – both perennial and non-perennial.

6.4. Future research directions

In this final section, I discuss 6 research directions, among others, that emerged from this thesis to advance the understanding and management of global NPRs and their role in river networks.

6.4.1. Compilation and curation of streamflow time series from gauging stations

Global streamflow data are central to the study of rivers and streams but also unevenly distributed, fragmented and error-laden. Most gauging stations are on large, human-influenced, perennial rivers in developed countries, leaving much of the global river network unmonitored (Krabbenhoft et al., 2022). Although NPRs comprise more than half of the global river network, arid areas have the lowest station densities (Crochemore et al., 2019). Less than a fifth of gauging stations monitor flow in NPRs, and the average record length for gauging stations monitoring NPRs is 7 years shorter than for stations on perennial water courses globally (own computations based on the Global Streamflow Indices and Metadata archive; GSIM). This lack of empirical hydrological data precludes a comprehensive view of river networks across climates and biomes. The random forest model developed in Chapter 2 exhibited lower accuracy and higher bias in sparsely gauged basins, especially in boundary areas between climate zones, from mainly non-perennial regions to mainly perennial regions. Chapter 3 demonstrated the paucity of quality data on NPRs in the Global Runoff Data Center (GRDC) database, the largest free-to-access global dataset of streamflow gauging stations, which constrained my ability to evaluate the hydrological diversity of NPRs.

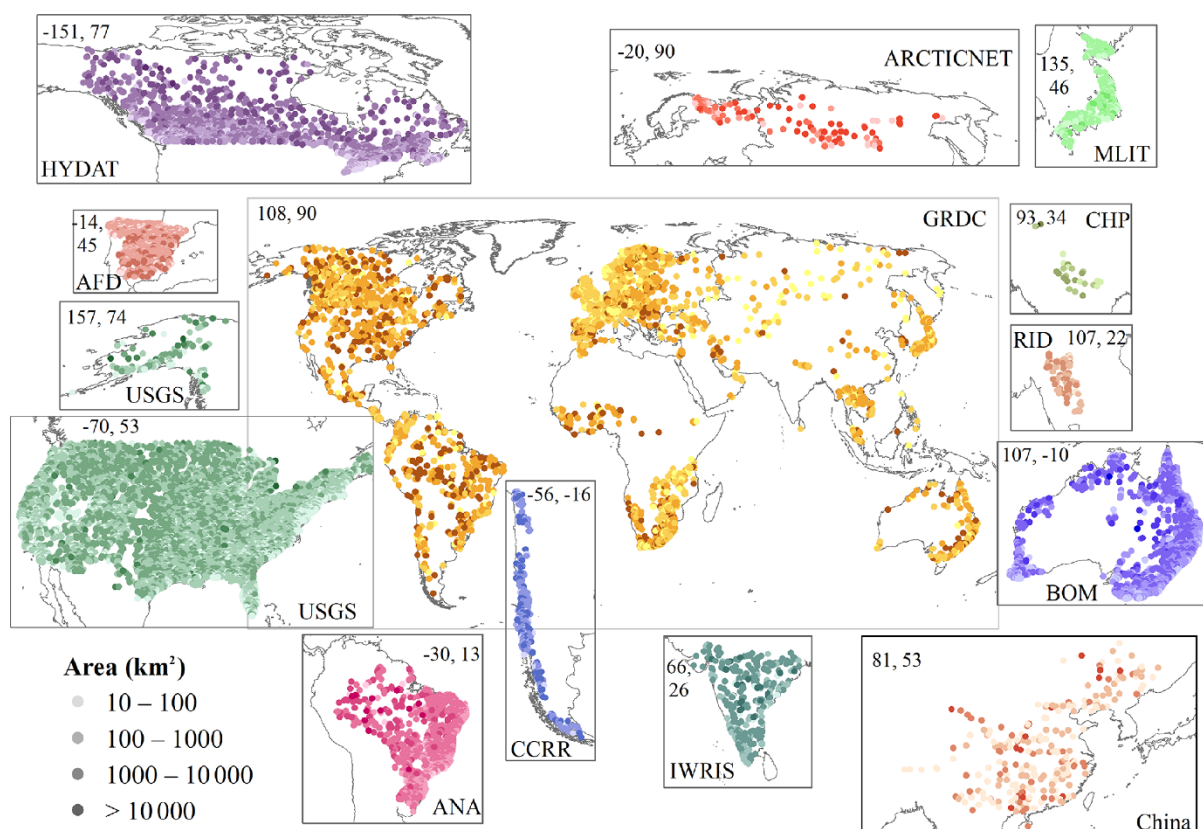


Figure 6.2. Compiling data from individual National Hydrological Services (NHS) yields more gauging stations than contained in the Global Runoff Data Centre database.

Stations compiled as part of the Global Streamflow Characteristics, Hydrometeorology, and Catchment Attributes (GSHA) (Yin et al., 2024). Each frame shows stations from a separate NHS.

The monitoring of river discharge is usually conducted at the national level by National Hydrological Services (NHS; Saarikivi et al., 2000). Each country's NHS determines its own monitoring strategies and operates its own network, often with nested levels of administrations and responsibilities (e.g., by federal states in Germany; Klingler et al., 2021). Many gauging stations also exist outside of those centralized networks (Kaiser et al., 2023). Therefore, the global availability of discharge measurements is dependent upon the willingness of NHS and other data providers to freely provide access to their data (**Figure 6.2**). In line with this imperative, the member countries of the World Meteorological Organization (WMO) committed to “broadening and enhancing, whenever possible, the free and unrestricted international exchange of hydrological data and products” (Resolution 25 Cg-XIII, 1999. Exchange of Hydrological Data and Products, WMO). This resolution was in part meant to bolster support for the GRDC (2015) to which voluntary contributions by member countries plummeted almost immediately after its establishment (**Figure 6.3**). The GRDC currently contains daily or monthly discharge records for approximately 10,000

stations worldwide, but most records date back to the 1970s to 1990s. There have been numerous calls to reverse this trend over the past two decades, to little avail (Fekete et al., 2012; Hannah et al., 2011; Rodda et al., 1993; Ruhí et al., 2018; Vörösmarty et al., 2010; Whitfield et al., 2012).

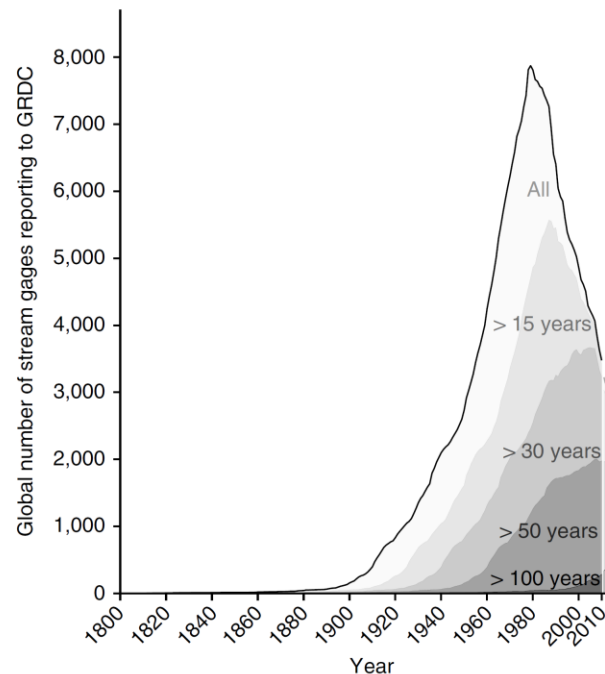


Figure 6.3. Global trends in streamflow gauging stations reporting to the Global Runoff Data Centre.

Stations are classified by age class (length of the discharge record, in years — grey shadings). The number of reporting stations peaked in 1979 and decreased sharply thereafter. Comparisons to 2010 (white vertical line) accounts for lags in data reporting, but trends to the present-day are shown. Reproduced from Ruhí et al. (2018).

The most notable early effort by academics to provide freely available global discharge data was GSIM (Do et al., 2018; Gudmundsson et al., 2018), which I used in Chapter 2. GSIM provides standardized metadata and time series of streamflow indices for ~31,000 streamflow gauging stations globally resulting from the collation and harmonization of 12 publicly available databases, including GRDC. Several more recent datasets have extended this approach to include additional databases, ancillary environmental variables, or missing data imputation by remote sensing, including Kratzert et al. (2023), X. Chen et al. (2023), Riggs et al. (2023), and Yin et al. (2024). Nevertheless, these compilations are all constrained to release summary indices of streamflow rather than re-distributing raw time series of mean daily discharge due to NHS' data sharing policies. While providing key information at the monthly, seasonal and yearly time steps, those streamflow indices are not geared to the study of NPRs as they only include the monthly number of no-flow days as an index of flow

cessation. In addition, none of these datasets have undergone in-depth quality assurance and checking aside from basic automated routines (e.g., in GSIM; Gudmundsson et al., 2018). No-flow observations are so notoriously prone to errors (Zimmer et al., 2020) that I deem those datasets unusable for robustly characterizing global flow regimes beyond the binary criterion used in Chapter 2. Therefore, I plan a major effort to curate global streamflow data from national hydrologic services. This effort will enable more comprehensive global studies of NPRs, including the continuation of Chapter 3 and the research directions I describe below. The analysis I performed in Chapter 3 to identify global regions where NPRs were under-represented in the global hydrometric network will help me to prioritize this compilation.

6.4.2. Integrating multiple sources of data on flow intermittence

Gauging stations provide crucial long-term data on river flow regimes, but come with several limitations for the study of flow intermittence (Jaeger et al., 2021; Zimmer et al., 2020). Besides being error prone for zero-flow observations, gauging stations do not provide information on the aquatic state of the reach which drives ecological and biogeochemical processes (e.g., connected pools, disconnected pools, dry bed but hyporheic flow, dry bed without hyporheic flow). Moreover, even if all the gauging stations that ever existed were compiled and curated, the resulting dataset would still cover only a small subset of the world's rivers and streams and exclude entire regions.

There are eight sources of primary data that can complement streamflow gauging stations for studying and managing the spatiotemporal dynamics of water in river networks: (i) *in situ* low-cost surface water sensors and time-lapse imagery from cameras on the riverbank, (ii) established networks of piezometric sensors monitoring groundwater levels, (iii) topographic maps, (iv) visual field surveys by citizen and government scientists, (v) field-based streamflow duration indicators, (vi) aerial and spaceborne remote sensing data, (vii) local traditional knowledge, and (viii) textual and photographic online data mining. No study to date has discussed such a comprehensive list of data sources or examined the opportunities and challenges associated with each of them — in terms of geographic extent, spatial and temporal resolution, reliability, expertise and labor requirements, and data pre- or post-processing. For example, satellite remote sensing is still constrained by a multitude of factors whose relative severity depends on the type of sensor, satellite platform, and algorithms

employed. Those limitations include, but are not limited to, obstruction of the river channel view from clouds and overhanging vegetation; limitation to larger rivers whose width spans multiple pixels; and relatively low revisit times impeding operational monitoring of daily discharge, flow initiation, or flash floods (Gleason & Durand, 2020). The relevance of each data source also varies by region and river type. Visual field surveys and local traditional knowledge are most relevant in populated regions whereas remote sensing is mostly applicable to large rivers outside of very arid or cold climates with limited overhanging vegetation. Yet these elements have not been systematically examined in any publication to my knowledge.

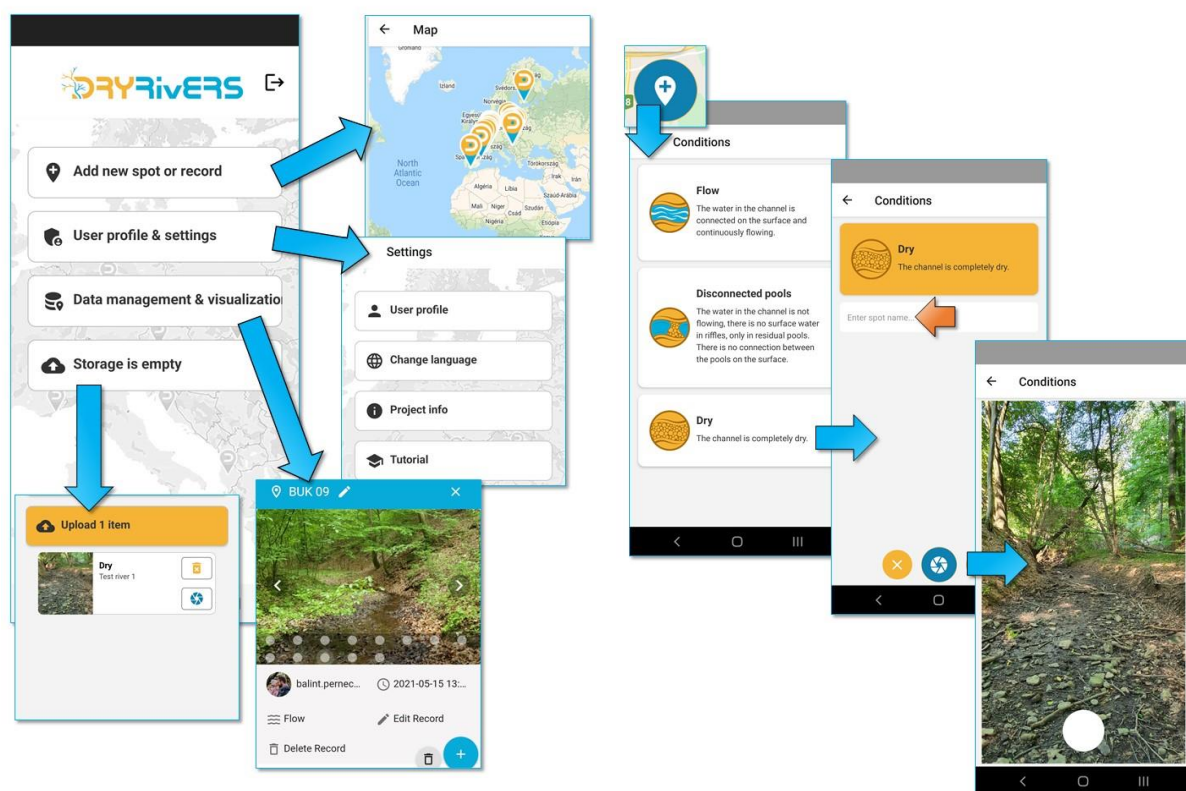


Figure 6.4. Screenshots of the DRYRivers app for citizen science observations of NPR aquatic phases (Truchy et al., 2023).

Photo courtesy of <https://www.dryver.eu/citizen-science/how-does-it-work>.

There have been, however, localized efforts to use sources i-vii, of which I cite examples below:

- i) *in situ* low-cost surface water sensors (Blasch et al., 2002; Jaeger & Olden, 2012; Jensen et al., 2019; Sabathier et al., 2023) and time-lapse imagery from the riverbank (Assendelft & Ilja van Meerveld, 2019; Herzog et al., 2022; Kaplan et al., 2019; Tauro et al., 2022);

- ii) established networks of piezometric sensors monitoring groundwater levels (Beaufort et al., 2018);
- iii) topographic maps (Hafen et al., 2020; Kampf et al., 2021) – Chapter 4;
- iv) visual field surveys by citizen scientists (Allen et al., 2019; Peterson et al., 2024; Truchy et al., 2023); **Figure 6.4**), government scientists (Beaufort et al., 2019; Sefton et al., 2019), research scientists (Martin et al., 2021), NGOs (Datry, Pella, et al., 2016), or combinations (Jaeger et al., 2021; McShane et al., 2017) ;
- v) field-based streamflow duration indicators, mostly macroinvertebrates and plants (Fritz et al., 2020, 2023; Mazor et al., 2021; Nadeau et al., 2015; Westwood et al., 2021);
- vi) aerial and spaceborne remote sensing data (Cavallo et al., 2022; Dralle et al., 2023; Fei et al., 2022; Gallart et al., 2016; Maswanganye et al., 2021, 2022; Tayer, Beesley, Douglas, Bourke, Callow, et al., 2023; Tayer, Beesley, Douglas, Bourke, Nik Callow, et al., 2023; Wang & Vivoni, 2022);
- vii) local traditional knowledge (Gallart et al., 2016; Hafen et al., 2020).

Textual and photographic online data mining has never been used for this purpose but would consist of leveraging the massive sources of information that social media and journalistic reports represent with deep learning methods to find georeferenced, timestamped observations of flow state. Flickr, for example, is a photo hosting and sharing online platform with over 10 billion photographs; it has already been used to harvest georeferenced pictures of specific species (Fox et al., 2020) and been combined with deep learning to detect images of flooding (Jony et al., 2020).

A global effort to compile and integrate these data sources would go a long way towards broadening the scope of hydrological studies of global river networks.

6.4.3. Global scale predictions of the spatiotemporal dynamics of flow intermittence

The model developed in Chapter 2 produced estimates of the long-term probability that every mapped river reach in the world stops to flow at least one day per year under natural conditions. Chapter 3 examines more nuanced temporal patterns, but only at gauging stations. To comprehensively study NPRs and their role requires going yet one step further and model the spatiotemporal dynamics of flow intermittence seamlessly across global river networks. Future modeling efforts should thus focus on producing time series of estimated

discharge and flow intermittence for all global river reaches, with particular attention to the spatiotemporal dynamics of flow cessation within river networks. Indeed, the spatial arrangement of NPRs (e.g., in the headwaters vs. middle reaches) and differences in the onset of drying (e.g., from upstream to downstream) across a river network shape ecological and biogeochemical responses to flow cessation but are hard to model (Datry, Boulton, et al., 2023; Messenger et al., 2021).

Two main modeling approaches can currently be distinguished to produce spatially distributed estimates of global discharge: process-based models on the one hand, and statistical (also called observation-based or data-driven) models on the other. Process-based models attempt to estimate water storage and fluxes across the different compartments of the terrestrial part of the global hydrological cycle. They rely on first principles as their structure is made up of sets of mathematical equations to represent hydrological processes which are fed climate and land cover data as principal inputs (Sood & Smakhtin, 2015). Statistical models, by comparison, are empirical in nature in that they are directly trained on *in situ* discharge measurements. By developing statistical relationships between the environmental characteristics within the catchment of streamflow gauging stations (e.g., climate, topography, land cover, soils, and/or geology), these models are able to produce seamless gridded estimates of streamflow or runoff, including for ungauged locations (Barbarossa et al., 2018; Beck et al., 2015; Ghiggi et al., 2019). Only a handful of global observation-based models exist to my knowledge (Barbarossa et al., 2018; Beck et al., 2015; Fekete et al., 2002; Ghiggi et al., 2019, 2021) and their use remains relatively marginal, whereas more than a dozen global process-based models are currently in use (Telteu et al., 2021).

Each of these modeling approaches comes with advantages and disadvantages. Process-based models are less sensitive to biases in the distribution of global gauging stations because they rely on first principles. However, these models still suffer from large uncertainties in modelling evapotranspiration (Schellekens et al., 2017; Wartenburger et al., 2018), groundwater-surface water interactions (Reinecke et al., 2019), and human water uses (Döll et al., 2016), all processes that are central to flow intermittence. In addition, the current spatial resolution of most models, 10 km to 50 km pixels, is inadequate to capture fine-scale catchment attributes that are relevant to flow intermittence and represent smaller

watercourses where flow intermittence is most prevalent. Statistical models are more flexible in their resolution but are very uncertain in sparsely gauged areas. One way to improve upon both model types, which was adopted in Chapter 2, is to employ a hybrid approach whereby the output grids from process-based models are statistically downscaled to individual river reaches and the resulting high-resolution estimates are used as predictors in a statistical model (**Figure 6.5**; Lehner & Grill, 2013; Linke et al., 2019).

Several models have already been developed to predict spatiotemporal patterns of flow intermittence at various spatial and temporal scales, either based on process-based models, statistical models, or a combination. PROSPER (Jaeger et al., 2019), for example, estimated the annual probability of flow intermittence from 2004 to 2016 at 30-m spatial resolution across the U.S. Pacific Northwest ($8 \times 10^5 \text{ km}^2$) with a statistical model trained with field surveys. Yu et al. (2020) leveraged a process-based model to predict daily flow intermittence at the river reach scale across $3 \times 10^4 \text{ km}^2$ of southeastern Australia and Tasmania; they coped with the inability of the model to predict zero-flow by determining spatially variable thresholds in modeled discharge below which a reach was deemed to stop flowing. As part of the DRYvER project as well, predictive models of flow intermittence were developed at two scales. One which I co-developed produced monthly estimates of the number of no-flow days across 1.5 million reaches in Europe during 1981-2019. We used monthly outputs from a global hydrological model as predictor variables for a random forest model trained on discharge time series from gauging stations (Döll et al., 2023). The other project in DRYvER implemented the same approach but to predict *daily* streamflow and intermittence in 3 meso-catchments (between 120 and 350 km^2) in Spain, France and Finland (Mimeau et al., 2024).

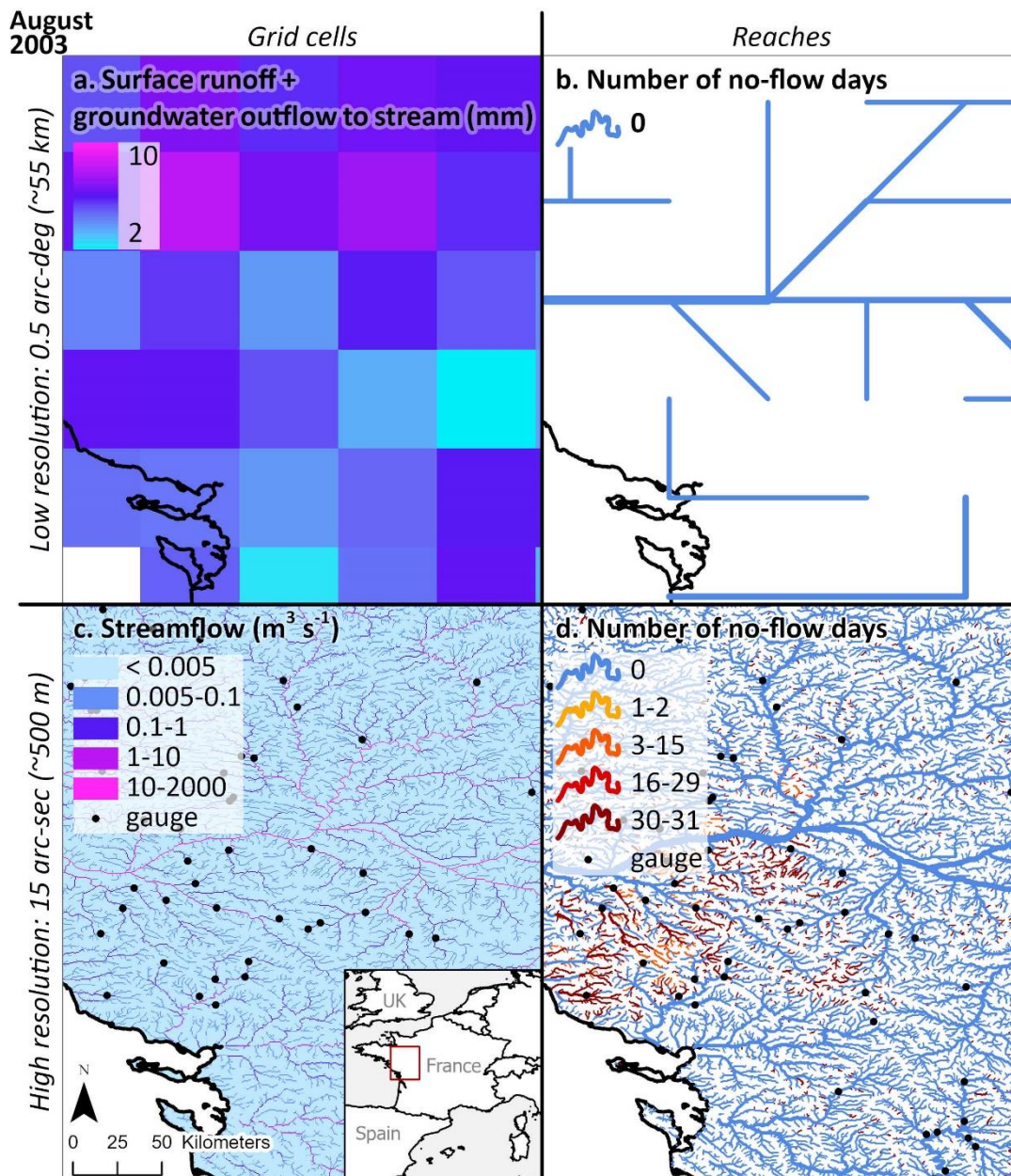


Figure 6.5. Illustration of downscaling of low-resolution outputs from a global hydrological model to the high-resolution stream network of RiverATLAS (Linke et al., 2019) and the resulting characterization of intermittence after applying a statistical model (Döll et al. *in review*).

Panels show low-resolution (0.5 arc-deg) grid cells with the sum of surface runoff and groundwater discharge (a), low-resolution reaches at the native resolution of standard global hydrological models, with their intermittence status (b), high-resolution (15 arc-sec) grid cells with downscaled streamflow (c), and high-resolution reaches with intermittence status in 5 classes (d). The figure shows the hydrological situation for August 2003. In c and d, the locations of the streamflow gauging stations used for validation of downscaled streamflow and as target for the statistical model are added.

One of my research objectives in the coming years is to participate in developing more advanced versions of these hybrid models at the global scale. Existing approaches could be improved by fine-tuning the statistical downscaling process from coarse pixels to river reaches, and by leveraging a greater diversity of predictor variables and training data.

Remote sensing data products, of water cover and soil moisture for example, could be used as predictors together with variables from process-based models. The primary sources of data mentioned in the previous sections — a larger network of gauging stations and alternative observation techniques — could be combined to improve model training and validation, depending on their reliability. The resulting reach-scale time series of flow intermittence could also be combined with remote sensing to produce estimates of the actual area of dry riverbed in large rivers, which is key to upscale carbon fluxes (Battin et al., 2023).

An additional way to improve these models would be to enhance the statistical models used until now to account for spatial autocorrelation and better represent the network-scale arrangement of flow intermittence. Accurately reproducing the spatiotemporal dynamics of flow and no-flow periods within river networks at large scale would open the door to many subsequent analyses. It would enable, for instance, to assess the relative role of temporary and permanent network fragmentation in driving biodiversity patterns as well as network-scale synchronization or desynchronization in metacommunity responses with different spatiotemporal patterns of flow intermittence (Datry, Boulton, et al., 2023; Gauthier et al., 2020, 2021; Larsen et al., 2021).

6.4.4. Improving our understanding of anthropogenic NPRs

This thesis was intentionally focused on natural flow intermittence despite the omnipresence of anthropogenic NPRs globally (Datry, Truchy, et al., 2023). For example, I spent several weeks selecting gauging stations under minimal anthropogenic influence for Chapters 2 and 3. The objective of this emphasis was two-pronged. First, the consequences of human activities on riverine hydrology are diverse in space and time. Flow alterations from water abstractions and return flows, land use change, and flow regulation by dams and weirs are superimposed upon the natural template shaping the distribution of NPRs (i.e., climate, lithology, topography, natural vegetation). This template is itself shifting with climate change, hence producing a wide array of flow intermittence patterns (Costigan et al., 2016; Shanafield et al., 2021). It thus seemed sensible to first focus on grasping the natural factors driving flow intermittence at the global scale before modulating these factors with human influence. Second, one of the goals of this thesis was to promote the recognition of flow intermittence as integral to river ecosystems, and to contribute to shifting the negative

perception of NPRs by the public. Conflating natural and anthropogenic intermittence would have gone against these objectives by potentially perpetuating the vision that drying is necessarily bad. Even with this approach, my research has sometimes erroneously been interpreted as alarming, commonly cited to simply say that the world's rivers are drying up.

Now that our grasp of natural flow intermittence is improving, an important next step is to advance our understanding of human impacts on flow intermittence, which has received comparatively little scientific attention. The greatest uncertainty in incorporating human water uses will come as global hydrological and hybrid models move to higher spatial and temporal resolutions (Döll et al., 2016). Country-wide statistics on water abstraction by sector need to be downscaled to the resolution of grid cells and reaches based on layers of urban cover, population, night lights, or irrigation, yet the relative allocation of withdrawals remains uncertain, particularly in areas with scarce data (Flörke et al., 2013). This issue will be compounded with greater integration of global groundwater models as the distinction between groundwater and surface water abstractions, as well as groundwater recharge from agriculture are subject to high uncertainties (de Graaf et al., 2017; Reinecke et al., 2019). Incorporating intra-annual variability in human water impacts is also key to model seasonal intermittence but a major challenge (Döll et al., 2016; J. Liu et al., 2017).

To incorporate the impacts of anthropogenic activities and climate change in statistical models will require disentangling their respective influence, yet they may have additive, synergistic or antagonistic impacts on flow intermittence depending on context. For example, the hydrological consequences of a shift from natural vegetation to crops depends on their respective impact on the water balance and runoff partitioning, and whether the latter are irrigated, and how (Duvert et al., 2022). We must progress on several fronts to effectively predict anthropogenically influenced flow intermittence regimes. Those include improved spatiotemporal data on human activities (particularly surface and groundwater withdrawals), their integration in both process-based and statistical models as part of the hybrid modeling framework, explanatory case-studies of individual flow time series in a wide variety of human-influenced catchments, and calibration of predicted discharge with remote sensing. Finally, in terms of climate change, one major modelling challenge will be to account for the shift from snow- to rain-dominated hydrology and the absence of cold snaps

causing full-channel freezing in the arctic, causing the perennialization of high-latitude streams (Feng et al., 2021).

Beyond hydrological aspects, we are just starting to comprehend the ecosystem responses to and management implications of anthropogenic intermittence (Datry, Truchy, et al., 2023). For example, evidence of long-term changes in biodiversity after shifts from perennial to artificially intermittent flow regimes or from increases in severity of intermittence remain fragmented (Aspin et al., 2019; Crabot et al., 2020); differences in ecological responses to anthropogenic versus natural intermittence, and the relative coping ability of perennial, naturally non-perennial and newly non-perennial ecosystems to intensifying droughts are not elucidated (Datry, Truchy, et al., 2023; Sarremejane et al., 2022); and the existence of tipping points or alternative stable states remain anecdotal (Bogan & Lytle, 2011; Zipper et al., 2022). A combination of long-term case studies and large-scale synthetic assessments will be needed to untangle the ecological patterns and processes resulting from human-induced alteration of flow intermittence.

In terms of legal protection and management of river ecosystems, key questions include: how can we establish environmental flows for transforming ecosystems whose hydrology and ecological communities are irreversibly changing (Acreman et al., 2014)? How do we differentiate natural and anthropogenic flow ephemerality when determining the legal protection status of watercourses? Does it even make sense to keep using reference conditions to guide ecological assessment and restoration efforts in irremediably altered ecosystems? Addressing these questions requires the joint participation of diverse stakeholders with scientists.

6.4.5. Towards robust estimates of global environmental flows

One of the initial goals of this thesis was to develop a framework to formulate e-flows guidelines for all NPRs globally. A single, spatially explicit, global assessment of e-flow requirements can contribute to water resources management in two main ways (i) by enabling a consistent top-down global analysis and comparison across basins and countries rather than relying on a bottom-up aggregation of disparate assessments, and (ii) as a first step in a multitiered framework for assessing and implementing e-flows (Opperman et al., 2018). However, global methods to evaluate e-flows requirements have not substantially progressed for nearly two decades. They still rely exclusively on simple hydrological criteria

which are unfit for NPRs (Acuña et al., 2020) and have limited context specificity or grounding in ecology (Messenger et al., 2024). As an illustration, semi-arid and arid regions are altogether excluded from the e-flows analysis recently developed by the United Nations Food and Agriculture Organization (FAO) to help member countries in calculating the SDG Target 6.4.2 water stress indicator (Eriyagama et al., 2024; Sood et al., 2017). Consequently, an improved global e-flows assessment method must be developed that accounts for NPRs and moves beyond simple hydrological estimation methods by leveraging the wealth of information from local e-flows studies.

I propose to adopt a method conceptually analogous to the scientific components of the ELOHA framework (Poff et al., 2010) but simplified and more reliant on extrapolation due to the constraints inherent in a global-scale analysis (**Figure 6.6**). Chapters 2 and 3, together with the research projects outlines in previous sections, would provide the hydrologic foundation necessary for the *scientific process*. To build flow-ecology relationships, a large-scale research effort is needed to systematically analyze the rapidly growing body of evidence on ecological responses to flow regimes and flow alterations in NPRs. Notably, additional research is needed to evaluate the degree of transferability of established quantitative relationships among species, basins, climates, and flow regimes (W. Chen & Olden, 2018; Crabot et al., 2021; Leigh & Datry, 2017; Yates et al., 2018).

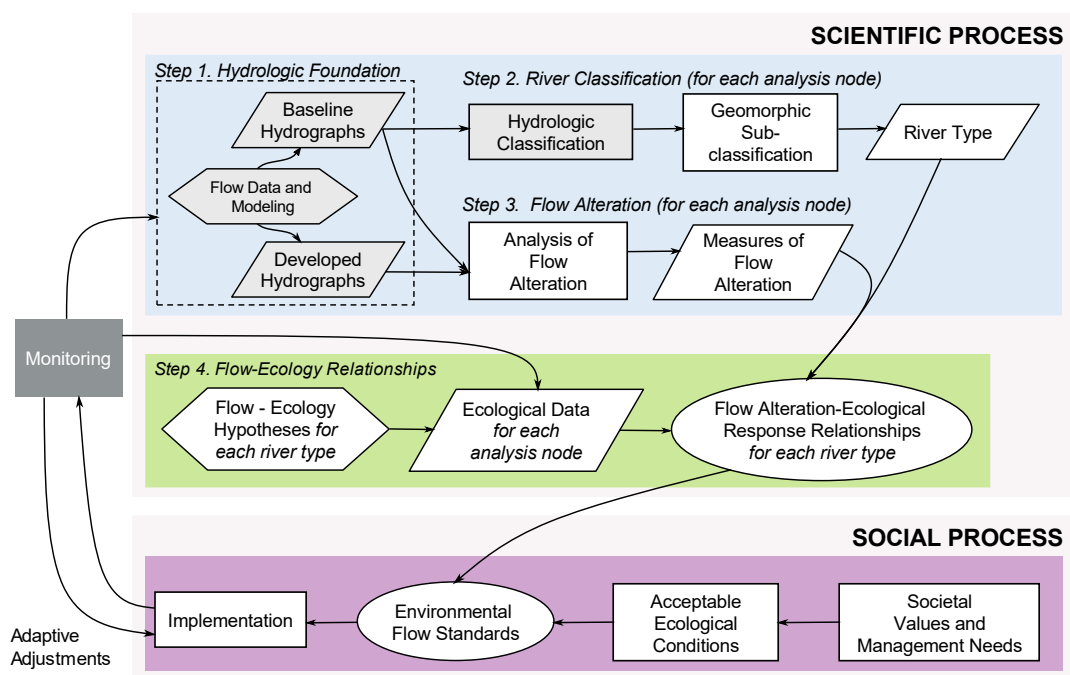


Figure 6. Summary diagram of the ELOHA framework.

Adapted from Poff et al. (2010). Hydrologic analysis and classification (blue) are developed in parallel with flow alteration–ecological response relationships (green), which provide scientific input into a social process (purple) that balances this information with societal values and goals to set environmental flow standards.

6.4.6. Bridging the gap from science to action

A weak point of this thesis is to repeatedly mention managers or managing river ecosystems (over 200 times in fact), and wanting to support management, without engaging managers directly. Chapter 4, for example, establishes that local interpretations of national definitions of watercourses are uneven. What has really been the perception and motivation of managers in assembling those jurisdictional maps then? Previous research by Mars et al. (2020) in a region of France alluded to these aspects, but this question would deserve further work. Similarly, how would a manager really go about implementing the operational framework introduced in Chapter 5? A single thesis cannot do everything, but addressing these questions is key to increasing the scope of my research. Doing so could leverage practices in translational ecology. Translational ecology deliberately involves ecologists, stakeholders, and decision-makers early on to collaborate in developing and delivering ecological research that contributes to improved environment-related decision making (Enquist et al., 2017; Wall et al., 2017).

A reviewer of Chapter 5 made the following comment during the second round of reviews: *“The paper is well written and if the intended audience is other academics, then it should be considered for publication in BioScience as it is not too dissimilar from Cid et al., 2020 referenced by the authors. [...] If the paper is intended to provide a potentially valuable tool for river ecosystem conservation and restoration through uptake by river managers (such as me), then I think the paper needs to be reconceptualized. My suggestion, which might not have been clearly stated before, would be to make the argument for an e-flows metasystem approach through case studies. Specifically, the authors could conduct the “Design” phase using the Murray-Darling Basin. This would provide readers a concrete understanding of what is missing from current regional e-flows implementation and allow the authors to describe theory with practice throughout the manuscript. The authors could then analyze another system that has local e-flows implementation (e.g., Fossil Creek or some other system well known by the authors) and show how a metasystems approach would benefit that local river or the large system in which it sits (as suggested by line 71: “could enhance the success of e-flows practices”). I understand this may require many more workshops by the authors and if this is undertaken, I would suggest river manager be included to help ground theory.”* I think that Chapter 5 in its current form was needed to lay

the groundwork for integrating a metasystem perspective in e-flows design. This is why, in addition to time constraints, I decided on this more conceptual approach, supported by examples from the literature and simulation modeling. Nonetheless, the reviewer's comment is entirely valid in pointing out that a test implementation with e-flows practitioners and stakeholders is warranted to bridge the gap between this prototype framework and a user-ready, mature version. Building a science-management partnership and engaging stakeholders in developing methods for e-flows design is a major factor determining the success of e-flows programs (Arthington et al., 2023; Webb et al., 2010). The Murray-darling Basin and the state of California are two regions of active experimentation where scientists and managers work alongside each other (many managers being scientists themselves), and where participatory methods are being developed for e-flows design (M. Mussehl et al., 2023, 2024; M. L. Mussehl et al., 2022; Stein et al., 2021; Webb et al., 2010). I hope to have the opportunity to collaborate with scientists, managers and stakeholders there on implementing a metasystem approach to e-flows design in the coming years.

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