Are landscape metrics reliable tools for modern conservation decision-making?

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Abstract

Under the pressure of climate change, Western conservationists are increasingly using remote sensing to monitor the state and status of ecosystems. In efforts to derive meaning from remotely-sensed imagery, many use landscape metrics as they can quantify the composition and configuration of different patches on land cover maps and are used to assess ecological processes. Considering the abundant use of landscape metrics, ensuring their reliability is crucial. In this thesis, I build upon past landscape metric validation studies which assessed the general behaviour of metrics when applied to land cover maps. Ultimately, all these works have tried to improve the 'statistical context' for calculating metrics, analysing scores, and acting upon them in sustainability policy. In Chapters 1 and 2, I revisit the origins of landscape ecology in ecology broadly, their history in global sustainability policy, and review past validation studies in landscape metric behaviour. In Chapter 3, I advance a validation study to assess previous gaps in landscape metric behaviour, including (1) the ranges of values in real landscapes, (2) the variability and (3) consistency in variability across landscapes, (4) the distributions best typifying responses, and (5) the predictability of metrics.

Procedurally, this study used Google Earth Engine, a cloud-computing geographic information system to composite sequential land cover maps for various unchanging landscapes, on which we computed landscape metrics. While general assumptions of landscape metric behaviour are often used, our results suggest landscape metric responses were not always generalizable, across all measures of statistical context we assessed. Considering the relieved computational burden, we argue future work should revisit early validation studies, while continuing to address pre-established gaps in knowledge. This is because a lack of statistical context to landscape metrics may undermine if they can be relied upon. In Chapter 4, I draw a comparison to past validation studies, and harken back to the data-driven multidisciplinary vision of landscape ecology at its seminal conference in Allerton Park, 1983. Ultimately, it is the goal of this thesis to assess landscape metric behaviour, as to provide epistemological development in the models of landscape ecology, while aiding practitioners who continue to use landscape metrics in modern sustainability decision-making.

Résumé

Sous la pression du changement climatique, les conservateurs de l'Ouest utilisent de plus en plus la télédétection pour surveiller l'état et le statut des écosystèmes. Pour donner un sens aux images à distance, beaucoup utilisent des métriques de paysage car elles peuvent quantifier la composition et la configuration de différentes zones sur les cartes de couverture terrestre et être utilisées pour évaluer les processus écologiques. Étant donné l'utilisation abondante des métriques de paysage, il est crucial d'assurer leur fiabilité. Dans cette thèse, je m'appuie sur les études de validation de métriques de paysage passées, qui visaient à évaluer le comportement général des métriques lorsqu'elles étaient appliquées à des cartes de couverture terrestre. En fin de compte, tous ces travaux ont cherché à améliorer le "contexte statistique" pour le calcul des métriques, l'analyse des scores et l'action en matière de politique de durabilité. Dans les chapitres 1 et 2, je revisite les origines de l'écologie du paysage dans l'écologie de manière générale, leur histoire dans la politique mondiale de durabilité, et je passe en revue les études de validation passées sur le comportement des métriques de paysage. Dans le chapitre 3, j'avance une étude de validation pour évaluer les lacunes précédentes dans le comportement des métriques de paysage, notamment (1) les plages de valeurs dans les paysages réels, (2) la variabilité et (3) la cohérence de la variabilité entre les paysages, (4) les distributions qui représentent le mieux les réponses, et (5) la prévisibilité des métriques.

Procéduralement, cette étude utilise ‘Google Earth Engine’, un système d'information géographique de cloud computing pour composer des cartes de couverture terrestre séquentielles pour divers paysages immuables, sur lesquelles nous calculons des métriques de paysage. Bien que des hypothèses générales sur le comportement des métriques de paysage soient souvent utilisées, nos résultats suggèrent que les réponses des métriques de paysage n'étaient pas toujours généralisables quelle que soit la mesure du contexte statistique que nous avons évalué. À la lumière du soulagement de la charge de calcul, nous soutenons que les travaux futurs devraient revisiter les études de validation précoces, tout en continuant à combler les lacunes préétablies dans la connaissance. Cela est dû au fait qu'un manque de contexte statistique pour les métriques de paysage peut

compromettre leur fiabilité. Dans le chapitre 4, je compare les études de validation passées et je me réfère à la vision multidisciplinaire axée sur les données de l'écologie du paysage lors de sa conférence phare à Allerton Park en 1983. En fin de compte, l'objectif de cette thèse est d'évaluer le comportement des métriques de paysage, afin de fournir un développement épistémologique dans les modèles de l'écologie du paysage tout en aidant les praticiens qui continuent à utiliser les métriques de paysage dans

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To Dr. Cardille, my supervisor, I want to extend my gratitude to you for your support and care you provided. It has been a great joy to return to your foundations of landscape metric behaviour from over 15 years ago and rekindle this question as to whether landscape metrics **are** reliable. I do hope future students of yours will carry this torch forth. I am also grateful for your pragmatism, as to ensure my thesis research can meaningfully contribute to current practice: we have a planet to save!

To Dr. Fahrig, my committee member, thank you for your support throughout our meetings, and your advice on how to articulate this argument. To the 40+ conservation practitioners I had the privilege of connecting with throughout this thesis, I am grateful for your insight. I hope to continue dialogue about how we can ensure these pivotal conservation decisions are based upon rigorous, reliable, and most importantly, environmentally-relevant measures of ecological state and change.

To Brandon, this non-computer scientist is especially grateful for your help in learning to code.

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"If I appear to see further than other mortals, mayhap it is because I stand on the shoulders of giants" – Sir Isaac Newton

These are *my* giants.

Contribution of Authors

While this thesis has been written in a manuscript-format and chapters are written by me, the student. There is one (1) manuscript that is in preparation to be submitted, upon acceptance of this thesis per the nominated reviewers to this thesis. This manuscript has been formatted according to the requirements of Springer's *Landscape Ecology.* I am the first and corresponding author on this article, along with Dr. Cardille (as a second author).

While under Dr. Cardille's supervision, I designed, implemented, and carried out the analyses constituting the validation study. I drafted all the figures and tables. Dr. Cardille provided feedback on the study findings, and suggested feedback and revisions to both text and figures. Both Dr. Cardille and I collaborated on the ideation and conceptual framework for this publication.

The study introduction, literature review, and discussion has been independently researched, organised, and written by me. Dr. Cardille has provided suggested revisions to all contents of this thesis.

1. Introduction

Landscape metrics have an extensive record of use in conservation management (Leitao and Ahern 2002; Sundell-Turner and Rodewald 2008; Wiens 2002), as practitioners use them to quantify landscape patterns to elucidate the state and status of ecological systems (Turner 1989). At the turn of the century, a concerted effort to monitor ecological resources led to the development of many landscape metrics, which are the statistical models applied to categorical land cover maps to characterise landscape composition and configuration (Forman and Godron 1986). Foundationally, landscape metrics assume a relationship between landscape structure and ecological processes (Turner 1989). Landscape metrics have been used in various applications, including land cover description, ecological inventorying (e.g., amount of forest), change analysis, assessing the fragmentation of natural areas and effects to ecological connectivity, in addition to relating structural metric responses to individual species- through metapopulation processes (Uueema et al. 2009). Most popularly, landscape metrics are used in North America's 30-in-30, to determine which 30% of land should be protected by 2030 (Davis et al. 2022; Pither et al. 2019).

While used extensively, implicit assumptions of universal behaviour, as opposed to rigorous and environmentally-relevant validity testing, has supported a broad adoption of landscape metrics. Over the last 30 years, isolated works by conservation practitioners and academics have attempted to quantify the behaviour of landscape metrics (Bogaert 2003; Cardille et al. 2005; Cushman et al. 2008; Fortin et al. 2003; Hargis et al. 1998; Neel et al. 2004; Tischendorf 2001; Wu et al. 2002); however, we still do not have a general description of landscape metric responses, thus limiting their interpretability. What remains unknown is the expected range of landscape metric responses, the expected distribution of landscape metric responses, and the attendant models which best typify landscape metrics over time.

Concomitantly, these knowledge gaps make it difficult to know when a score on a given day can be relied upon, where it sits within a range of expected values, or if it is an outlier. Subsequently, this means conservation practitioners can be using measurements subject to Type 1 and Type 2 hypothesis errors: where metric scores suggest a change when the landscape is unchanging, or where a landscape metric response remains stable despite landscape change, respectively (Gardner and Urban 2007). Compounded with adverse amounts of conservation decisions being made in our critical decade of climate action (Steffen et al. 2017), ensuring their reliability is thereby crucial.

Building upon past landscape metric validation studies, I aim to assess the general trends of landscape metrics across the various elements of statistical context. These include (1) measurements of the range and general dispersal across; (2) measurements of the consistency in variability of metric responses, across all landscapes; (3) the distributions of metric responses, across all landscapes; and (4) the predictability of metric responses, using the acquisition date of the land cover maps on which metric scores are derived. In this thesis I present the development of a validation study to assess metric behaviour across sequential images for many landscapes in North America.

1.1 Thesis Objectives

My thesis aims to contribute to the body of knowledge on the statistical context of landscape metrics. The specific objectives for each chapter are as follows:

- **Chapter 1**: To review the origin of landscape ecology in ecology broadly, review the history of past landscape metric behaviour studies, in addition to the current context on which landscape metrics are used.
- **Chapter 2:** To assess whether general trends exist in measures of landscape metric statistical context across: (1) the range, central tendency, and distribution of metrics responses; (2) the consistency in variability of metric responses; (3) the distributions of metric responses and (4) the predictability of metric responses, using the acquisition date of the land cover maps on which metric scores are derived.
- **Chapter 3:** To discuss the historical multi-disciplinary and data-driven impetus for landscape ecology, broad implications for future landscape metric validation studies.

1.2 Literature Review

1.2.1 Origins of Ecology

To first understand landscape ecology, it is essential to understand the origins on which the field was derived from ecology and first principles, its relationship to design and land use planning, and the subsequent emergence of computational tools to assess land cover patterns and explore ecological processes.

Foundationally, ecology is the study of interactions between organisms with each other and the abiotic and biotic environment. Intentionally broad, ecology was defined holistically to encompass the variety of natural processes occurring in the natural environment. It is meant to be grounded in first principles of biology, chemistry, and physics which enable many of the species-environment interactions, and on which deductions about the state and status of ecological processes can be meaningfully built (Odum and Barrett 1971).

Initially, the interest in ecology grew out of humankind's interest in curiosity and epistemological advances of knowledge, broadly. This is noted among early writings in ecology including Carl von Linnaeus' Systema Naturae (1762), von Humbolt & Bonpland's *Essay on the Geography of Plants* (1807) and White's *The Natural History of Selborne* (1890). Ecology has since become the basis to understand how anthropogenic, western-initiated human influences impact the natural environment (Bazzaz 1998). However, ecological systems are innately complex, hierarchical (Miller III 2008), and thus difficult to comprehensively frame (Meadows 2008). With a growing knowledge of natural systems there was an attendant emergence of ecology subdisciplines, assessing ecological systems at various scales and contexts (e.g., population, community, landscape, and global ecology).

1.2.2 Origins of Landscape Ecology

As the subdiscipline of ecology, landscape ecology examines the patterns among the landscape, and their interaction with ecological systems. It is considered a coarse assessment of ecological organisation, larger than the individual, population- or community-ecology scale. Procedurally, landscape ecologists are looking top-down and *ex situ*, describing how different types of patches (i.e., like-land covers) are composed and configured within a matrix (i.e., surrounding area composed of different land covers). Often, approaches include measuring the amount of area (e.g., how much of Canada is forested), how diverse is the landscape (e.g., is it all forest, or are other land cover types common, and in what proportion), in addition to how the configuration of patches influence organism function(s) (e.g., home range size, genetic diversity and flow). While landscape ecology textbooks often reference Troll (1950) as the first instance where ecological processes were examined at the landscape scale (Wiens et al. 2007), foundations of hierarchically classifying ecological systems are seen earlier in the 1930s among geography journals.

In Western countries, geographers argued that separating systems into discrete scales, based on their functional relationships, allowed further examination of processes (James 1933; Unstead 1935). Through isolating ecological systems, such as, in the case of community-ecology, allowed the examination of community-specific effects (e.g., predation and prey dynamics, carrying capacity). However, this would garner less focus on the nested organism-level or population-level processes (e.g., genetic diversity among the population). This presumption of isolation allowing deeper investigation of ecological systems was readily adopted at the landscape scale. By the 1950s, Troll (1950) had parsed the natural environment into hierarchical landscape units, which presumed specific functions occurred at discrete scales. Troll (1950) included a list of common landscape hierarchies, such as K. H. Paffen's eight-tier system of "landscape cell-small landscapes - singular landscape - large landscape - landscape group- landscape region - landscape zone - landscape belt", or P. E. James' four-tier hierarchy "locality - district - subregion - region" (1950, pg 80). From Troll (1950), it became common that ecosystems could be evaluated and described at the landscape scale, which predicates that ecological patterns can discern ecological functions. The notion that form follows function has been evidenced by evolution through natural selection at the species and community-level, not necessarily at the landscape level.

At the organism-, population- and community-level, it is known that the form of an organism is subject to evolution through the process of natural selection, where preferential individual traits permit persistence in a given environment. Thus, organisms with these traits, evolved through cladogenisis or andogenisis, are those more likely to persist. Ecology textbooks provide early evidence for this relationship, including how species of Galapagos finches, through adaptive radiation and convergent evolution, had shorter and tougher beaks to crack through shells and access food (Odum and Barret 1971). Another common example is how a darker-coloured peppered moth began to outpace light-bodied moths, as this pigmentation, a product of natural selection through industrial melanism (Cook 2018), provided these varieties a competitive advantage among the soot-covered habitat of Industrial England (Odum and Barrett 1971). In evolution through natural selection, at the organism- through community-level, these examples illustrate how fundamental the notion of form follows function is to natural systems. While not explicitly said, this notion has been adapted to the other scales and contexts of ecology, including landscape ecology, where visual ecological patterns at the landscape-scale are assumed as indicative of ecological processes at the landscape-scale (Forman 2011; Gustafson 2019; Turner 1989, 2005). For example, Forman (1995) wrote how landscape patterns, or “what we see today, was produced by flows yesterday” (Forman 1995). Like any other sub-discipline of ecology, Forman (1995) has long-believed landscape ecology has “roots in ‘first principles’ or background theory, and also [is] supported by a reasonable amount of empirical evidence”. In support of his claim, he convened the 1983 Allerton Park Workshop, which has since been summarised by Turner (1989). Since the 90s, there is extensive case-specific proofs to support this relationship between landscape patterns and ecological function (Cui et al. 2021, Davies et al. 2021; DiFiore et al. 2019; Fronhofer and Altermatt 2015; Huber et al. 2014; Keane et al. 2017; Miguel et al. 2018; Wiersma 2022; Yuan et al. 2015), in addition to several books and educational materials on how ecologists could benefit from a landscape ecology approach (Gergel and Turner 2002; Turner et al. 2001).

1.2.3 Landscape Metrics

Landscape metrics are the statistical models ecologists employ on land use and land cover maps to study the composition and configuration of the landscape (Forman and Godron 1981). Compositionally, this involves assessing what patches or values are present, and in what abundance. Configurationally, ecologists investigate the spatial structure of the landscape, such as the orientation, placement, and shape of patches. Although there are different methods to represent landscapes, landscapes are still predominantly viewed as discrete patches (i.e., as in the Patch-Matrix Model) (Antrop 2021; Driscoll et al. 2013; McGarigal et al. 2009). More comprehensive models of landscapes exist, such as viewing the surface as a series of continuous values as opposed to discrete categories (i.e., percent forested vs binarily classified as forest or not). Nevertheless, the focus of this thesis is on the use of Patch-Matrix Model metrics (Kupfer 2012).

The Patch-Matrix Model (Forman and Gordon 1981,1986) is derived from Clementsian ecology, where similar groupings of species are thought to have similar ecological functions, and thus, can be grouped accordingly. This is a means of simplifying ecological systems. The Clementsian model was originally used to describe the succession of plant communities towards a climax ecological community, through autogenic (i.e., forces internal to a biotic community, such as soil nutrients and texture) and allogenic processes (e.g., forces external to the biotic community, such as anthropogenic global warming) (Naveh and Liebermann 2013). The Clementsian model asserts that at any given point, the composition of an area can be used to stratify it into a discrete ecological category (e.g., as forest, shrubland, wetland, or marsh). Readily, this idea has been adopted by categorical land cover maps, and the metrics thereunto qualifying landscape composition and configuration (Hakkenberg et al. 2017; Oberg 2019).

Under the Clementsian model, the metrics applied to land cover maps are interchangeably defined as ‘surface metrics’ and ‘landscape indices’ (Uuemaa et al., 2009). Some researchers describe them as surrogates for ecological processes (see Lindenmayer and Franklin 2002). While an inference, or assumed ‘surrogate’ (2002), all methods ultimately abstract and further reduce the complexity of natural systems into a score (Kupfer 2012; Riitters et al. 1995; Sanderson 2020; Turner and Gardener 2015; Wu and Hobbs 2002).

In practice, landscape metrics are used to both describe landscapes and deduce ecological function. In the former, metrics can be used to, for instance, quantify the amount of habitat area or habitat fringe, the clumpiness or intactness of habitats, the density of patches, the variability of land cover types, the interspersion of patches within unlike patches (e.g., fen ecosystems within a coniferous forest), in addition to the diversity of land cover types (McGarigal and Marks 1995). The latter are used to explain, for instance, how fragmented a landscape is, how connected a habitat is. Since the outset of the landscape ecology, there has been a concerted effort to not just describe landscape patterns but understand ecological processes, including “the functional interactions of the natural landscape” (Troll 1950). In effect, landscape metrics rely upon the assumption of a reciprocal relationship between spatial patterns and ecological function (Gustafson 2019).

1.2.4 Landscape Metrics in Conservation Planning and Decision-Making

There is nearly a fifty-year history of using landscape metrics within global sustainable development, both directly (e.g., using metrics from FRAGSTATS software, per McGarigal and Marks (1995)) and indirectly through monitoring and quantifying global land cover change. Briefly, we recount the history below.

In 1983-85, the Brundtland commission worked with United Nations countries to categorise land as worthy of enhancement, prevention, and restoration using satellite monitoring (Imperatives 1987). The Brundtland commission built upon the motive of the first UN convention on the environment a decade prior, which was one of the first instances where international unity sought to work towards sustainable development (McNamara 1972). In their seminal report, *Our Common Future*, there was an express interest to inventory the abundance of land covers in each of these categories (Imperatives 1987). Moreover, the United Nations Environmental Programme’s (UNEP) Earthwatch Subprogram (Sec. 4.3), monitored the connectivity and interspersion of these habitats (i.e., examining potential habitat refuges for species departing disturbed and/or modified areas) (Imperatives 1987; UNEP 1975).

More, the report indicated the importance of identifying the “many ecosystems that are rich biologically” and “severely threatened”, (Imperatives 1987, pg 125-128). In 1992, the United Nations Sustainable Development (UNSD) organisation convened the Rio Summit or the Earth Summit, where 178 governments committed to improving monitoring efforts of ecological systems, namely fragmentation, connectivity, in addition to the abundance of resources (e.g., area as forested, forest change) (Lafferty and Eckerberg 2013). In 2004, the Organization for Economic Development (OECD) countries agreed upon a universal set of environmental indicators, which supported the use of metrics to capture “habitat alteration and fragmentation through [summarised] changes in land use and land cover” (OECD 2004, pg 30). Most recently, the Terra Carta, per the One Planet Summit, gave explicit mention to “monitoring natural resource capital, including by satellite” (HRH the Prince of Wales 2021, pg 17). Indeed, policy instruments have and continue to uphold the utility of landscape metrics not solely for monitoring but assessing and evaluating the integrity of natural systems (Gökyer 2013; Mayer et al. 2016).

Building upon extensive top-down multinational support, landscape metrics are also used in modern conservation planning, environmental policy, and land-use planning applications (Leitão and Ahern, 2002; Sundell-Turner and Rodewald, 2008). Pragmatically, their use spans scales of global efforts through to local conservation entities. For instance, the joint effort of Canada and the United States, the Great Lakes Commission (GLC), uses changes in extent and proximity of land covers to water bodies to predict changes in water quality (Lopez 2005). The organisation supports how a “GIS-derived landscape metric, such as percentage of cropland area among watersheds, can be correlated with water quality parameters… [and] be analysed as a causal (predictive) relationship” (Lopez 2005, pg 11). Other multinational efforts include the Joint Research Commission (JRC) of the European Union (EU), where landscape metrics were used as biodiversity indicators (reviewed in Cassatella and Peano 2011).

At the national scale, the United States Environmental Protection Agency set forth a proposal to use landscape metrics, as some, “such as dominance, fractal dimension, and contagion have been proposed in the USA as indicators of watershed integrity, landscape stability and resilience, and biotic integrity and diversity" (Lopez et al. 2006). To date, many are still used in local hydrology management divisions of the United States Environmental Protection Agency (reviewed in Lopez and Frohn 2017). In Canada, the Forest Service used landscape metrics as indicators, as the patterns and their change provided insight into "land use, habitat, and biodiversity" (Wulder et al. 2008); the perceived utility of landscape metrics for forest monitoring and forecasting has since been echoed in other countries, such as the United States (Kupfer et al. 2012), India (Reddy et al. 2013), and China (Li et al. 2021). As evidenced above, landscape metrics are used in a variety of conservation contexts to both monitor and assess the integrity of ecological systems. Thus, the importance of ensuring landscape metrics is reliable is axiomatic.

1.2.5 Assessing Behaviour of Landscape Metrics

In addition to the profuse use of landscape metrics in conservation ecology and land management contexts, there is an attendant body of literature calling into question the reliability of landscape metrics. Mostly, implicit assumptions about general landscape metric behaviour, as opposed to rigorous and environmentally-relevant validity testing, has been used to substantiate landscape metric validity. In 2004, Neel et al. echoed McGarigal et al. 's (2002) concern on how "the ecological interpretation of [landscape] metrics has been plagued by a lack of thorough understanding of their theoretical behaviour" (Neel 2004, pg 435). Research has only evaluated landscape metrics' behaviour, such as through metrics' generalised responses to changing scales (Wu et al. 2002), examining landscape metric self-similarity (e.g., collinearity and explanation of variation) (Riiters et al. 1995; Cushman et al. 2008), and how metrics respond to aggregation of patches in the landscape (i.e., are forest patches dispersed throughout a landscape or contained in one area) (Neel et al. 2004).

In 2002, Wu et al. introduced general measures as to how landscape metrics should respond to changes in scale, dubbed "scalograms". The authors measured landscape metric responses in four landscapes within the United States, and categorised landscape metric responses according to three "types" depending on how a line of best fit could be matched to a plot of metric score by an independent scale parameter (spatial extent or spatial grain) (2002). These types of response include i) linear or exponential, ii) 2nd and 3rd order polynomials and iii) erratic responses (where no line of best fit can be assigned) (2002). Problematically, since publication, the generalised conclusions about how landscape composition and configuration metrics respond to changes in scale, has served as the basis for uncertainty estimates for landscape scores (Šímová and Gdulová 2012), and has been used to rescale metric scores for environmental analysis (Argañaraz and Entraigas 2014). More, while expectations of landscape metric responses to spatial extent and grain are largely accepted, research has found discursive metric responses when applied to different imagery products and different study contexts (Corry and Lafortezza 2007; Frazier 2016; Peng et al. 2010; Shen et al. 2004) this draws into question the universality of scaling dynamics and the work which has used the general scaling behaviour. Beyond spatial resolution and extent, select works have examined temporal responses of metrics; however, the scale as a predictor to metric response is typically assessed singly (e.g., just by spatial scale), rarely concurrently with spatial extent, resolution, and time (Gustafson 2019; Newman 2019): this negates the potential interaction of different scale parameters to influence landscape metric behaviours.

In 2008, Cushman et al. assessed the collinearity of landscape metrics, given how interrelated and redundant landscape metrics are often applied for landscape monitoring efforts. Out of the FRAGSTATS library of class- and landscape-level metrics, Cushman et al. (2008) identified 24 and 17 independent configurations, respectively. In part, this was done to combat the 'shotgun-approach' of computing landscape metrics, where all metrics within the FRAGSTATS platform are computed, regardless of their relevance to the study at hand. Examples of a shotgun approach are numerous (Blaschke and Drăguţ 2003). For instance, Lustig et al. (2017) used twenty-five different landscape metrics as to examine which patterns best predict allochthonous species spread in novel environments.

Finally, Neel et al. (2004) assessed the response of landscape metrics to different aggregation dynamics. Ideally, this was to elucidate if metric responses were related to the aggregation of patches in a landscape and the size of area included in a computational window. Neel et al. (2004) note how there were also individual efforts to assess the responses to aggregation with specific metrics

(Gustafson and Parker 1992; Hargis et al. 1997; Riiters et al. 1995; Saura and Martínez-Millán 2001). The consummate of all these works then, and since, hold that there remains limited understanding of metric behaviour. This is important because if practitioners can understand landscape metric behaviour, it may “aid in selecting and interpreting metrics that are sensitive to changes resulting from a phenomenon of interest” (Neel 2004, pg 454).

Worth noting, there have been other efforts to assess landscape metric general behaviour, including the doctoral dissertation of Porter (2011) who measured the effect of classification noise (i.e., the certainty in a pixel being classified as one category as opposed to another) and how it may translate into landscape metric scores, in Iowa, USA (2011).

Notwithstanding these works, there has not been further research into landscape metric behaviour (personal communication, Cushman, February 15, 2022). Rather, the discussion on landscape metrics has shifted to developing new methods (Hanson et al. 2022; Saura et al. 2017). As evidenced by the lack of discourse since these works, there is perceivably less interest in assessing whether the growing amount of landscape metrics, including older methods which are consistently used (Kedron et al. 2018; Uueema et al. 2009), are suitable for environmental monitoring and modelling.

1.2.6 Published Concerns on Landscape Metric Use

To date, there have been instances in the literature where practitioners voice concern on the use of landscape metrics. For example, Sawyer et al. (2011) notes how “conservation planners are faced with a critical question: will [landscape metrics] improve placement of linkages/corridors by explicitly incorporating habitat effects on movement, or will they result in misleading and potentially costly recommendations for conservation by concealing invalidated assumptions?” (2011, pg 669). Considering the overview of programs using landscape metrics **(Section 1.2.4**), the magnitude of impact that using landscape metrics will have on pivotal conservation decisions has grown.

Indeed, landscape metrics' results are still considered tangible to explain ecological concepts to policy makers, decision makers, and the voting public composed predominantly of Western non-scientists (Nassauer and Corry 2004; Mayer et al. 2016). However, there is a "lack of evidence that pattern indices imply ecological processes", and that "planners and designers should be exceedingly cautious in making ecological inferences from landscape pattern index values" (Corry and Nassauer 2005). Rather, the variability or the uncertainty is not adequately incorporated into a reported landscape metric value (Lechner et al. 2012).

In addition to the assumption about the reciprocal relationship of pattern and process, there are concerns about how individuals contextualise a score for their landscape. For example, Cardille et al. (2005) note how the "inability of potential [landscape metric] users to establish the spatial or statistical context of real-world landscapes appears to be a major factor inhibiting a full exploration of and experimentation with the ever-growing library of satellite-derived land-cover data" (Cardille et al. 2005, pg 987).

More, Leitao et al. (2012) notes how "through the use of tools like FRAGSTATS we have the power to measure and report more about landscape pattern than we can interpret in terms of effects on ecological processes" (2012, pg 62); however, the authors still suggest landscape metrics can be used in planning contexts despite this link.

Recently, I critiqued some of the Western logic which underlies landscape ecology broadly (Serre 2021), arguing how some individuals advance the use of landscape metrics, often out of ease of application and interpretation as a substitute for the evidence necessary to support a link between what a metric is measuring, and the ecological process under investigation. Since, Wiersma (2022) has provided a comprehensive review of individual studies supporting a link between landscape pattern and ecological phenomena. However, as there are conflicting landscape metric validation results (specifically with regards to scale), many of these individual case studies, such as the 87 referenced in Wiersma (2022), are thought to "not be fully replicable experiments" (2022, pg 8). Beyond these few examples, the debate on the utility of landscape metrics is limited: metrics are assumed to be sound measurements of ecological processes. Putting aside contention over whether land cover patterns can help ascertain the underlying ecological processes occurring in a landscape, continued validation is needed to address gaps in metric behaviour and build external validity for existing landscape ecology studies. Indeed, all disciplines which subscribe to the Western scientific method, cannot use clout to supersede empirical evidence: continual, rigorous, and repeatable evidence is needed (Ioannidis 2005).

1.2.7 Anecdotal Concerns on Landscape Metrics from Practitioners

Considering the minimal published discourse, we sought to speak with conservation practitioners directly. From October 2021 to February 2022, we conducted twenty-eight semi-structured individual and group interviews with Western conservation practitioners who use landscape metrics.

Overall, the goal of these interviews was to capture the perspectives on the reliability of landscape metrics in Western conservation management, given the dearth of published rhetoric since 2010. We interviewed a total of forty-three conservation practitioners who work at local and regional levels (Niagara Escarpment Commission, Toronto and Region Conservation Authority), in addition to national (incl. United States Environmental Protection Agency, Environment and Climate Change Canada, Canadian Forest Service, United States Department of Agriculture, United States Fish and Wildlife Service), and international scales (incl. the International Joint Commission, Ducks Unlimited, Yellowstone to Yukon, Centre for Large Landscape Conservation, the Nature Conservancy). Through thematic coding of all interview responses, all forty-three Western practitioners identified how there is still a lack-of knowledge in landscape metric behaviour, and a decrease in overall discourse around how to meaningfully interpret a landscape metric score. Moreover, some practitioners identified how metrics are assumed to be environmentally-relevant, not proven as such (~81% of individuals).

It is important to acknowledge the bias this presents to the thesis as the perspectives shared by practitioners helped to guide this research. Even if we do not interpret these interview responses as objective evidence, and solely unsubstantiated anecdotal accounts, it was from talking with these practitioners that we sought out the foundational literature and evidence, that is peer-reviewed, to support whether generalised trends in landscape metrics exist. More, it is from conversation with these individuals that I seek to take a deep dive into the early foundations and assumptions of landscape ecology. While these perspectives helped guide the context for this review, the information presented within this thesis is solely the summation of published, peer-reviewed work, not these anecdotal accounts.

1.2.8 Ease in Computing Landscape Metrics

Landscape metrics were first seen as a unified set of analytical tools in FRAGSTATS, a program released by McGarigal and Marks (1995) which sought to integrate the variety of landscape-, class-, and patch-level metrics into a unified software for both experts and non-experts. Since the launch of FRAGSTATS, landscape metrics have been integrated into a variety of programs, including common statistical analysis software of R (R Core Team 2016), through the *SDMtools* (VanDerWal et al. 2019) and *landscapemetrics* (Hesselbarth et al. 2019) packages. There are also numerous standalone platforms to calculate landscape metrics, including APACK (Mladenoff and DeZonia 2000) and PatchAnalyst (Rempel et al. 1999). Simultaneously, software plugins have been written to link into common geographic information systems (GIS) of ArcMap (Yu et al. 2019), ArcGIS (Adamczyk and Tiede 2017), and QGIS (Jung 2013). Most recently, this list includes cloud-computing platforms (Deng et al. 2019) and cloud-computing GIS, such as Google Earth Engine (Theobald 2022). Together, the variety of means to calculate landscape metrics with existing programs makes their application to categorical map analysis significantly easier for users. However, when FRAGSTATS was launched, McGarigal and Marks (1995) included an extensive rhetoric on the potential misuse of landscape metrics, and the importance of context in metric selection and interpreting a score. Upon review of the documentation and publications surrounding each of these programs, this dialogue has not been carried forth.

1.3 Conclusion

Landscape metrics have been, and continue to be, commonplace in conservation ecology, land management and sustainability policy as they measure habitat composition, configuration, in addition to assessing ecological function. Supporting their use, several works have identified general trends in landscape metric behaviour; however, landscape ecologists and practitioners are still operating without sufficient knowledge of landscape metric behaviour, which may undermine the reliability of metric scores. Building upon these past landscape metric behaviour studies, there is a need to continue assessing landscape metric behaviour. This would contribute epistemologically to the development of landscape metrics and computational landscape ecology tools. However, more broadly under the pressure of Western-initiated climate change, practitioners ought to have greater knowledge about the tools they are using to evaluate what land should be protected, where biodiversity hotspots are, and which landscapes best facilitate habitat connectivity.

2. Do Landscape Metrics Exhibit Universal Behaviour?: Assessing the Variability, Consistency, Distribution and Predictability of Landscape-level metrics in Real Landscapes.

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Abstract

To date, many patch-matrix-model (PMM)-derived landscape metrics are still used in conservation management and land management decisions. While past studies have assessed the generalised behaviour of landscape metrics, gaps in metric behaviour remain. It was our objective to address some of the gaps in the generalised behaviour of landscape metrics. These include: the range of values for metrics in real landscapes, the consistency among the variability of landscape metrics across landscapes, the distributions which best typify responses, in addition to assessing how predictable metric responses are using the acquisition date for the land cover maps in which scores are derived. Together, all of these measures go to advance our statistical context of landscape metrics. Procedurally, we computed 65 landscape-level metrics across large (>150), successional land cover collections for N = 680 landscapes across North America in Google Earth Engine (108,922 total land cover maps). Subsequently, we assessed the distributions and model fit using generalised linear models. In part, our results are to provide preliminary estimates to expected ranges, variability, and consistency of variability for landscape metric values across many real landscapes. However, across all measures of statistical context, landscape metrics did not always exhibit generalizable trends. Most notably, we found landscape metrics only seldom were described by a normal distribution

(30% of metrics): an implicit assumption of many studies that use PMM-derived metrics. We discuss how these various components of statistical context, namely the lack of generalizability, may undermine the reliability of landscape metrics to practitioners and how contingent assessments of behaviour are necessary.

2.1 Introduction

Conservationists and land managers are increasingly using remote sensing technologies to monitor the state and status of ecosystems (Cavender-Bares et al. 2022; Kerr and Ostrovsky 2003). In efforts to derive meaning from remotely sensed imagery, many use landscape metrics as they can purportedly quantify the composition and configuration of different patches on categorical landscape maps, and then be used to understand ecological processes (Forman and Godron 1981; Lindenmayer and Franklin 2002; Turner 1989). Compositionally, this involves assessing what patches (or similar land covers) are present, and in what abundance (Forman and Godron 1981). Configurationally, the patterns and arrangement of patches are examined for how they affect function (e.g., organism movement) (1981). In this context, we are referring to the subset of landscape metrics which are computed on categorical land cover maps at the patch-, class- and landscape-level.

The adoption of landscape metrics echoes the growing and global environmental monitoring effort. For instance, in Canada, the federal government committed to “30-in-30:” to protect 30% of land and water resources by 2030 (Environment and Climate Change Canada 2022). Similarly, in the Convention on Biodiversity (CBD) post-2020 Biodiversity Framework, they aim to improve “the integrity of all ecosystems… with an increase of at least 15 percent in the area, connectivity and integrity of natural ecosystems” (Power 2022). Indeed, landscape metrics are tools we use to measure progress towards connectivity targets, in addition to what constitutes ecological integrity and which natural areas to protect (Pither et al. 2021). Thus, if we are to continue using landscape metrics, assuring their reliability is crucial.

However, many argue that implicit assumptions, as opposed to rigorous and environmentally-relevant validity testing, have been used to substantiate landscape metric validity. For instance, Neel et al. (2004) voiced concern on how “the ecological interpretation of [landscape] metrics has been plagued by a lack of thorough understanding of their theoretical behaviour” (Neel 2004, pg 435). Cumulatively, research has evaluated landscape metrics’ behaviour through their response to changing scales (Wu et al. 2002), examining landscape metric self-similarity (e.g., collinearity and explanation of variation) (Cushman et al. 2008; Riiters et al. 1995), and how metrics respond to aggregation of patches in the landscape (i.e., are forest patches dispersed throughout a landscape or contained in one area) (Neel et al. 2004). Furthermore, as landscape metrics are often derived from classified satellite imagery, Porter (2011) suggested that classification noise (i.e., the certainty in a pixel being classified as one category as opposed to another) may translate into landscape metric scores (2011). However, these landscape metric behaviour studies subscribe to the notion of universal landscape metric behaviour: that there are *universal* scaling patterns, and *typical* distributions of metrics, *typical* covariances among metrics, and *consistent* responses to classification noise, no matter where a metric is applied.

Fundamentally, this abuts against the purpose for which landscape metrics were derived. In the documentation of FRAGSTATS, the original program to calculate land cover metrics, McGarigal (1995) noted how “In a real landscape, the distribution of patch sizes may be highly irregular” and how summary statistics such as [mean and standard deviation] make assumptions about the distribution [of a metric] and therefore can be misleading” (1995, pg 13) By design, landscape metrics were intended to measure individual responses in landscapes. Over 25 years ago, Hargis (1997) harkened back to this original documentation, calling for an understanding of “the attainable values of each metric, and how these values are altered within landscapes containing different sizes and shapes of patches, and different modes of disturbance” (1997, pg 185). In 2005, Cardille et al. noted how we still do not understand the “frequency distribution of metric [responses] in relevant subsets of landscapes”, which limits landscape metric users in their ability to contextualise a score they derive from any given landscape (2005, pg 984): this call remains unanswered. Rather, individual papers report the ranges of values in their landscapes of interest. Consequently, we do not know whether universal ranges exist or not, and in what frequency. Thus, many practitioners are operating without the adequate statistical context, including the expected ranges of their values and the distributions best typifying responses. This may undermine their ability to draw meaningful inference from landscape metrics in their area of interest. Thus, there is a need to assess whether the growing amount of landscape metrics, including older methods which are consistently used (see Kedron et al. (2018) and Uueema et al. (2009) for review), meet assumptions of universal behaviour.

In this study, we seek to meaningfully build upon the foundational efforts which have called-for or attempted-to assess the universal behaviour of landscape metrics. The goal of this study was to (1) describe the variability of landscape metric responses, across different landscapes, in addition to (2) describe the distribution of landscape metrics in a variety of real landscapes, over time. More, we (3) intended to explore how predictable landscape metric responses are.

Exploratorily, we devised a validation study, where we assessed the variance explained by each landscape metric, and how consistent this variance was across a variety of sample landscapes in North America. Then, we assessed which distributions best typify landscape metric responses, over time, in each landscape. We hypothesised that within a given landscape, repeated metric responses for a landscape would be best-described by a normal distribution, as this is the universal and implicit assumption governing their current use. We also assessed how often landscape metric scores of a repeated area were predictable, when accounting for seasonality and inter-year changes. We hypothesised landscape metrics in unchanging landscapes would be predictable by seasonality, as this would suggest real landscape signals driving a score, rather than error caused by noise among the land cover classification or metric. Concomitantly, these tests aim to address whether universal trends in landscape metric behaviour exist. Additionally, we hope to contribute to a body of 'statistical context', which may be used by ecologists and land managers who employ landscape metrics.

2.2 Methods

We computed landscape-level metrics on a variety of landscapes within Southern Canada and the United States. We included areas within 25º to 50º in latitude and -126º to -58º in longitude, encompassing a total of 16,182,053.77km^2. This includes landscapes across many of the ecological regions of North America, including northern forests, north-western forested mountains, marine west coast forests, eastern temperate forests, great plains, deserts, mediterranean California, tropical wet forests, and southern semi-arid highlands (Bailey 1998). We started with N = 1000, 5120m x 5120m terrestrial landscapes (256 Sentinel-2 pixels in width and length), which cover ~26,215 km^2 of this vast and different area.

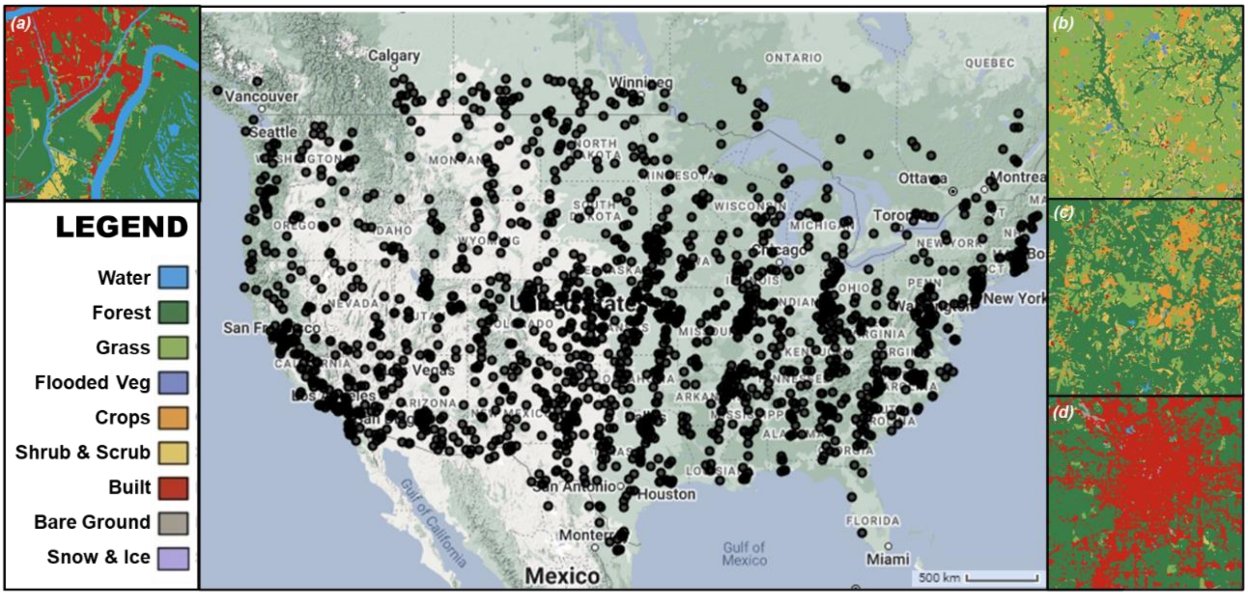

Figure 2.1 Stratified sample locations (N = 1000) across the global human development index (gHM) (Kennedy et al. 2020). Inset maps are 1:200000 scale, Dynamic World (Brown et al. 2022) land cover maps for (a) Houma, LA, (b) San Antonio, TX, (c) Charlotte, NC, and (d) Atlanta, GA.

2.2.1 Sampling Procedure

Within this terrestrial boundary, we selected sample landscapes with a high frequency of repetitious land cover maps, and those subject to different anthropogenic pressures. As our land cover maps are from Dynamic World (Brown et al. 2022), a database of classified land cover maps for every sequential Sentinel-2 image, we first isolated areas with a high-frequency of Sentinel-2 images. Tiling all yearly images of Sentinel-2 in the study extent for each year, we masked unsuitable areas scenes where the yearly return was less than 30 images/annum. Subsequently, we sought to represent a variety of anthropogenic stressors and the degree of anthropogenic modification (from 0-1) that conservation practitioners work within, from completely naturalised to highly urbanised, for instance. We then conducted a stratified sample of points within these high-imagery coverage zones, using the global human modification (gHM) dataset. This dataset is a 1km x 1km cell raster layer, which culminates how modified a landscape is across various indicators. These include predominantly-western human settlement, agriculture (presence of livestock, cropland), transportation (road and rail infrastructure), mining and energy production, in addition to electrical infrastructure (power lines, night time lights) circa 2016 (Kennedy et al. 2020). The resulting landscapes were used in image compositing.

2.2.2 Image Collection Assembly

We assembled all landscape composites in Google Earth Engine. Google Earth Engine is a cloud-computing geospatial platform (Gorelick et al. 2017), which enabled us to retrieve classified images, filter collections, and subsequently compositing the time series of land cover maps for each landscape. The Dynamic world catalogue was filtered for images within each landscape's extent, and for images captured between May 1st and November 30th, for each year, from 2017-2021. Each image collection was then filtered to exclude images with more than 10% cloud cover in the entire scene, using the Sentinel-2 cloud-detection quality band.

Dynamic World is a near-real time classification algorithm applied to incoming Sentinel-2 imagery, which maintains the source spatial resolution (i.e., pixel size) of 10m (Brown et al. 2022). Dynamic World images are land cover maps, with a thematic resolution of nine, including (1) water, (2) trees, (3) grass, (4) flooded vegetation, (5) crops, (6) shrub and scrub, (7) built, (8) bare, in addition to (9) snow and ice (2022). The data product has a time frame matching the launch of Sentinel-2 LIC, to current day (circa June 27, 2015). Dynamic World has a revisit time of 2-5 days, allowing for frequent land cover-maps of the same landscapes. See **Figure 2.2.**

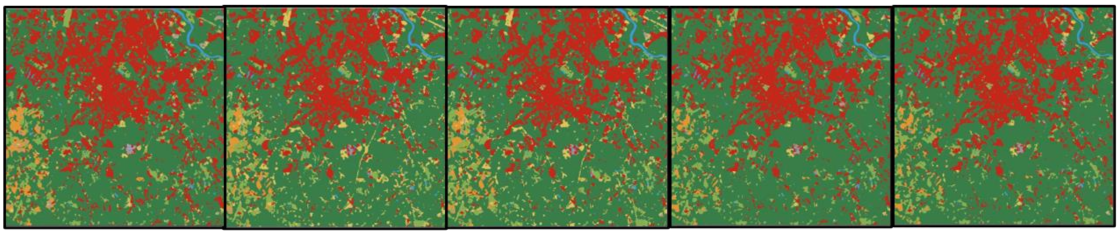

Figure 2.2: Illustrating the successional Dynamic World (Brown 2022) land cover maps, derived from Sentinel-2 imagery, for Kearney, NE; maps are at a 1:200000 scale.

As a near-real-time classified imagery product, Dynamic World is subject to having masked pixels when cloud cover is present in Sentinel-2 images. As full land cover maps are required for landscape metrics, we excluded images with more than 5% of masked pixels in our landscape analysis window. For images with less than 5% of masked pixels, these images could be 'backfilled' to create the complete land cover maps requisite for calculating landscape-level metrics. We illustrate the process below in **Figure 2.3**.

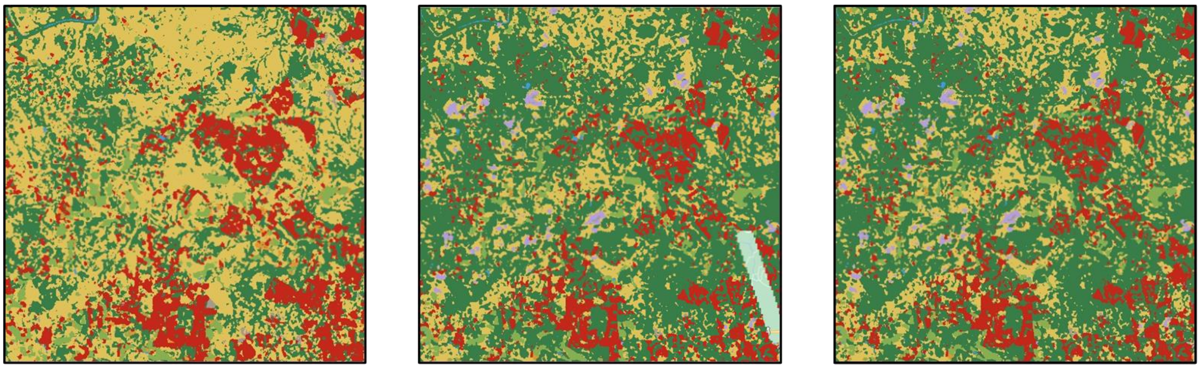

Figure 2.3: Demonstrating how masked clouds were filled in Dynamic World (Brown, 2022) images. In this instance, a prior scene (left) is used to fill the masked pixels in the bottom-right of a July 27th image (middle); the 'backfilled' scene has no masked pixels (right): all maps are to 1:114286 scale.

Images were backfilled if there was an unmasked image within one month prior to the image requisition date; this was to minimise the potential influence of intra-year change (i.e., plant growth and senescence). If there were not any images to perform the backfill, the partially-masked land cover image was removed from the composite of images in each landscape. Images were masked to the sample landscape bounds and exported from Google Earth Engine. We note this as a limitation as it generates some amount of self-similarity of sequential land cover maps within each landscape.

Once backfilled, we visually inspected all images (N = 109,100). Some image collections had scenes with pixels classified as snow and ice, which was inconsistent with our seasonal filtering, climate normals for the geography, and our visual inspection of true-colour images which suggested cloud cover was being falsely classified. These images were systematically removed from collections using a threshold median absolute deviation (MAD) on landscape metric scores. In total, N = 178 images were misclassified (>0.2%). A full procedure for misclassified image removal is provided in Supplemental Information (see **Section 6.1**)

Subsequently, landscapes with less than *n* = 30 images in any given year were excluded. This ensured each landscape had a minimum of *n* = 150 successional land cover observations, on which summary statistics and model fit could be computed for each of the sixty-five landscape-level metrics. In total, N = 108,922 Dynamic World images were used across N = 680 landscapes.

2.2.3 Generating Landscape-level Metric Results

Using the *landscapemetrics* R package (Hesselbarth et al. 2019), we computed all sixty-five landscape-level composition and configuration metrics for each image, within each landscape. Categorically, landscape-level metrics can be divided into aggregation metrics (n = 15), area and edge (n = 8), core are metrics (n = 12), shape metric (n=16), entropy (n= 3), diversity (n = 8) and unique metrics (n = 2) (e.g., mutual information and relative mutual information): this does not mean they do not overlap. A full list of metrics and their respective calculations is provided in Hesselbarth et al. (2019). *Landscapemetrics* is used to supplement the since-deprecated FRAGSTATS program. It includes all the original landscape-level metrics first synthesised in McGarigal and Marks (1995). In this study, we focussed explicitly on landscape-level metrics, not class- or patch-level metrics. All patch adjacencies were calculated using queen’s case rules (direct and corner adjacency), more, the sample boundary was not included as a habitat edge as these were subsamples of real landscapes. All other parameters were default per the *calculate_lsm* function (Hesselbarth et al. 2019).

2.2.4 Describing Landscape Metric Behaviour

For each metric response, in each landscape, we computed summary statistics, including median and coefficient of variation (CV). We preferred non-parametric summary statistics as we did not want to assume any normality when describing landscape metric results (Baskent and Jordan 1995; McGarigal and Marks 1995). While we could have used a median absolute deviation (MAD) or interquartile range (IQR), the requisite transformations to get metrics to the same scale (all metrics to 0-100) use parameters that assume a normal distribution. In this study, we wanted to measure the metric's tendency of the distribution towards its mean as it is measured by practitioners, not once results are normalised (thereby redistributing the data from what is measured). Thus, we used a stringent CV of 10% to classify metrics as either tightly dispersed or variable. We then aggregated to the median CV value, across all landscapes, as a measure of how generally dispersed a metric is.

More, we assessed the consistency of the CV measurements for each metric, across all landscapes, using a coefficient of quartile deviation (CQD) thereunto all responses for a given metric. The coefficient of quartile deviation (CQD) is a percentage to quantify a non-parametric measure of dispersion from the median value (Arachinge et al. 2022). To calculate CQD, for each metric, we used the difference between the 75th percentile and 25th percentile CV measurements, divided by the sum of these percentiles (Arachinge et al. 2022). As the CQD is measured on each metric, we could summarise the consistency in dispersal (as CV) across all real landscapes. As a standardised 'variance of variances', a high CQD signalled metrics where, across all landscapes, the variability in metric response is inconsistent (i.e., some landscapes have a small variance in a metric value, others may be large). Comparatively, a low CQD signalled metrics where the variability in any given landscape is consistent (i.e., the exact range of values may not be the same, but the variance explained is similar). In this study, we used the often-used threshold of CQD = 0.5 to separate instances where variances are considered preferable (or consistent) or not preferable (or inconsistent variability) (Montgomery 2020). Ratifying support, this value of 0.5 is the generic threshold for CQD values in statistical software, Minitab (Alin 2010), derived from the McKay–Vangle confidence interval of CQD <= 0.5 (Bonnet 2006). Lower thresholds may be used; however, we chose the more conservative threshold to allow metrics to be more variable across landscapes, which would permit more context-specificity, which is the intent under which landscape metrics were derived. For example, metrics with a CQD > 0.5 represented inconsistent variability in a metric response, across landscapes; metrics with CQD <= 0.5 indicated consistency in the variability for a metric, across all landscapes.

Subsequently, to assess the predictability of landscape metric responses in each landscape, observations for each metric were fit using generalised linear regression models. We used these models as they seek to fit a variety of common functions (e.g., Log, Logit, CDFLink, identity, inverse power, inverse squared, and power) to different possible distributions of the data (incl. binomial, gamma, gaussian, inverse gaussian, negative binomial, poisson, and tweedie). Both the image's day-of-year and year of each image were used as model predictors for landscape metric scores. Day-of-year was fit as a random effect, as the intended use of any validation study is to extrapolate beyond the study subset: in our case, we wanted to discuss metric behaviour in North American landscapes, broadly. More, we had a sufficiently large number of observations for each metric, afforded through prefiltering of suitable geographies. Further, using day-of-year as a random effect does not assume true homogeneity among the dependent variable of metric response; allowing for one landscape to change appearance differently from other landscapes. This applies to the patterns of change, rate, and overall timing. This rightfully permits the assumption of ecological heterogeneity, which is foundational to any landscape ecology research (Lack 1969; Tews et al. 2004; Wiens 1997). Year was fit as a continuous, fixed-effect.

For each landscape, per metric, best-fit models were determined using the lowest Bayesian information criterion. Further, we required day-of-year to be a statistically-significant predictor at an $\alpha = 0.05$ (95% CI). From the tests for best-fit, we could derive which distributions best typified a landscape metrics' response in a given landscape.

Subsequently, we computed the proportion of observations as significant outliers using a Student's-t statistic. We calculated studentized residuals for each best-fit model, where the expected value from the model is subtracted from the observed target value at each increment of the predictor variable (i.e., days of year, years). Then, the residuals are divided by the adjusted standard error. We employed a threshold for significant studentized residuals, where observations greater than 1.96 were labelled as significant-outliers to the model with 95% confidence (per Cardille et al. 2001; Deutsch et al. 2021). In terms of a landscape metric score, the proportion of observations as significant outliers was used to interpret the number of days where metric values cannot be adequately predicted using the best-fit model. Thus, the relative proportion of observations as externally studentized residuals is used to describe the reliability of a score when predicting landscape metric responses. Herein, these results are only described comparatively to other landscape metrics observations, calculated with the same number of observations, and the same number of landscapes.

2.3 Results

By all measures of statistical context we assessed, there is varying evidence for either general behaviour or site-specific contexts of metrics. First, we describe the range of values for different landscape metrics, their spread, and the consistency among landscapes. Second, we describe the distribution of landscape metric responses with successional images of the same landscapes. Third, we present the results of the generalized linear models and how well landscape metrics are predicted by seasonality.

2.3.1 Variability in Metric Values

From our assessment of median coefficient of variation (CV) for each landscape metric, using a stringent CV <= 10% threshold to typify dispersal, thirty-nine metrics were considered highly dispersed from the central tendency, on most instances. Inversely, twenty-six metrics had a high tendency of values around the central tendency. More, to describe the variability in landscape metric responses, we include the real ranges of metric responses across real landscapes (see **Table 6.1).** In many instances, the number of observations for each metric (>100,000) approaches the central limit theorem, as the frequency distributions for most metrics appear normally-distributed. In aggregate, metrics varied on the size of the dispersal kernel, and potential skew. There are select instances where metrics do not appear normal in aggregate, including *division*, *mesh, msidi, msiei, siei,* and *sidi*. Conversely, patch richness density (*prd*) had gaps within its distribution, suggesting certain values would never occur. Nevertheless, the number of observations comprising these distributions (>100000), limit any use of these general distributions to contextualise the expected frequency of a landscape metric response within a given landscape.

Out of all 65 landscape-level metrics, fifty-five were consistent in their variability across landscapes, as determined by being below this threshold (see **Table 6.2**). Predominantly, metrics (*n* = 30) had a high median CV across all landscapes, while being consistent in this variability across landscapes. Examples include the measures of the adjacency of 'like' patches (*pladj*), the number of patches (*np*), the patch complexity (*parfrac*), the thematic complexity of patches (*ent*), proportion of disjunct core areas (*dcad*), and the probability of cells have 'like' class distinctions (*contag*). Some metrics (N = 24) had a low median CV measurement, across the landscape measured, indicating consistently low variability from the central tendency. There were two instances where metrics were inconsistent in a low median CV value across different landscapes (e.g., the complexity of landscape pattern (*condent*) and the total core area (*tca*)). Eight metrics had a high median CV value and were inconsistent in their variability across landscapes. In other words, metrics that, in aggregate, tend to be tight or distributed to the central tendency can either be consistent or inconsistent in that variability across landscapes.

2.3.2 Distributions of Landscape Metrics

Per the lowest Bayesian information criterion, our data suggests that metrics were either exclusively or near-exclusively described by one type of distribution, described by several distributions, or rarely and inconsistently described by any distributions. Only in instances where metrics are exclusively described by one distribution do we consider this a generalised behaviour.

Of all the landscape-level metrics, we could describe fifty-five metric's distribution in all instances (see **Table 6.3**). There are exemptions to this, such as in landscape metrics describing the distance to nearest 'like' neighbours (*enn_cv, enn_mn, enn_sd*), which were described 99% of the time. Most often, landscape metrics were best described by one kind of distribution; for instance, twenty metrics were described exclusively by one distribution, and twenty-five were described predominantly by one distribution with minimal description from other distributions (=<5% of instances). In some metrics, not all landscapes could be typified under the distribution types permitted by generalised linear models. These include the measures of size and abundance of patches (*area_mn* and *area_sd*), the size of core areas (*core_mn* and *core_sd*), in addition to the size of all core areas (*tca)*.

In general, our results do not agree with the working presumption that landscape metrics can be used under a general assumption of normality. Of the 65 landscape-level metrics we evaluated at this spatial (~25km^2) and temporal scale (5 years), nineteen metrics' distributions were best-described as gaussian, across all landscapes: only nine metrics were described exclusively by gaussian distributions, across all landscapes. These nine included metrics describe the compactness of a landscape patches (*circle_mn circle_sd*), the complexity of patch configuration (*condent*), the spatial connectedness of patches (*contig_sd*), patch area and overall landscape compactness (*gyrate_mn, gyrate_sd*), in addition to measures of deviation from a maximum compactness of patches (*shape_mn* and *shape_sd*).

Typically, landscape metrics were best typified by gaussian, inverse-gaussian and negative-binomial distributions. Select instances occur where a metric was described by one of the aforementioned distributions, in addition to a binomial distribution, such as with *enn_sd* (0.15% of instances) and *tca* (30.5%), in addition to those describing patch richness (*pr* = 0.30%) and relative patch structure (*mesh* =

2.84%). Similarly, eight metrics are, though selectively, described by poisson and tweedie distributions: this never exceeded 1% of landscapes.

As landscape metrics are often used under the guise of normality, there is seldom published research as to whether landscape metrics are normal or not. In a rare example, a report to the European Commission on assessing the ability of landscape metrics to quantify heterogeneity in remote sensing data for the global human settlement layer project, Degen et al (2018) suggested *pr*, *shdi*, *ta* (total area), and *prd* (as patch richness density) are four metrics that are not normally distributed within their study extent. While we did not evaluate total area (as the landscape window is consistent in every image, every landscape), our results support the claim that these three metrics are not normally distributed. Specifically, *shdi* was better typified by a negative binomial function (78.38% of instances), *pr* and *prd* were never best-fit as a gaussian distribution. Ultimately, minimal published rhetoric on metric distributions limits comparability of these results. Landscape metric distributions are often evaluated using the aggregation of landscape metric responses across a single landcover product (see Cardille et al. 2005), rather than typifying responses in successional land cover maps for a single area.

2.3.3 General Linear Model Fit

In general, no metric response was consistently predictable using day-of-year and year as predictors (see **Table 6.4**). Year was significant on the best-fit models only minimally (9.2% of instances); the inclusion of year rarely improved the best-fit model type (0.47% of instances). This supports our assumption that the landscapes we sampled, for the most part, were not predictably changing over the study years. In this context, this was interpreted as the landscapes remaining stable throughout the evaluation period, and the reflected variability in landscape metric scores being a product of seasonal variation.

On average, metric responses were 46% predictable. This varied across metrics: some were highly predictable, such as the difference in size (*area_cv* = 83%) and core area among patches (*core_cv* = 83%), the number of patches (*np* = 82%), in addition to the perimeter-area ratio of metrics (*para_mn* = 87%). Others were less predictable: including *area_mn* (0.5%) and *area_sd* (4.0%), *core_mn* (0.5%) and *core_sd* (4%), *pr* (12%), *prd* (19%) and *tca* (18%).

Moreover, whenever a model could be fit, the base function varied across landscapes. Of all possible generalised linear model functions, log, identity, inverse-power, and inverse-squared functions best fit the shape of landscape metric responses. CDFLink and Logit functions were rarely fit to landscape metric results (e.g., *prd* was best-fit by a CDFLink function <1% of instances). For instance, *area_cv* is a metric consistently predicted (83% of instances); however, it is best-fit by log and inverse-squared functions, on 63.9% and 36.0% of instances, respectively. The relative abundance of which function best fit responses were variable across all landscape-level metrics.

Of the models that fit landscape metric responses, we then compared the average proportion of significant studentized residuals (when the observation was >= 1.96). For most landscape metrics (82%), the average proportion of observations as significant outliers was less than 5%. This signifies on the instances where a metric is significantly predicted by seasonality, the best-fit model has a low proportion of outliers, while maintaining, on average, significance in the predicted score. Comparatively, ten metrics had an average of over 5% of observations that were significant outliers. For these metrics, the high proportion of outliers violates the 95% confidence interval of the Student's-t test that would suggest these metrics are predictable.

2.4 Discussion

Throughout this study, we made an explicit focus to just describe landscape metric behaviour using a sample of landscapes across parts of North America. Firstly, we described the range of expected values for a metric. Secondly, we described the magnitude and consistency in the variability of a metric (how variable, on average, and how consistently variable, among all landscapes). Finally, we described the distribution of landscape metric values, and how well they can be predicted when controlling for seasonality in responses. Together, all these efforts aim to expand the statistical context to landscape metrics which are used by experts and non-experts alike.

This builds upon the numerous efforts which have tried to quantify landscape metric behaviour in both simulated and real-world landscapes (Bogaert 2003; Cardille et al. 2005; Cushman et al. 2008; Fortin et al. 2003; Hargis et al. 1998; Neel et al. 2004; Tischendorf 2001; Wu et al. 2002). Despite the tremendous efforts to date, we still do not have a comprehensive understanding of landscape metric behaviour. As we argue, these elements of statistical context we assessed may work independently and concurrently to influence how an ecologist or land manager (or "practitioner") may view the reliability of a landscape-level metric.

Within this discussion, we will discuss (1) the results of landscape metric behaviour in aggregate (incl. variability, ranges of values in real landscapes, and aggregate distributions of metric observations across all landscapes); (2) how the consistency among the variability in landscape metric responses lend predictability; (3) how information about the distribution of a metric can improve how contextualising whether a score is frequent or rare for a landscape; and (4) the value of being able to predict a metric score using information about the image acquisition date.

2.4.1 Aggregate Landscape Metric Behaviour

Firstly, in aggregate, the frequency distributions for metrics revealed that most metrics approached normality, as stipulated in the central limit theorem. However, this was likely as a product of the number of observations (~100,000) (LaPlace 1810). Our responses confer with Cushman (2018), who used 25 different landscape areas, varying in size and thematic resolution, and computed 100,000 different analysis windows within these areas. Using the length of total edge (*te*) metric, Cushman (2018) showed how the frequency distribution of this metric response converges to normal or gaussian, per central limit theorem. We build upon Cushman's (2018) analysis through showing the aggregate distributions of all metrics (see **Figure 6.1**). Predominantly, most metrics exhibited similar convergence to a normal distribution. There were some instances where metrics had visible gaps within their distribution, when not relict of the incrementation of possible values (i.e., patch richness density (*prd*)). While most metrics converged on central limit theorem in aggregate, the application of metrics to individual real landscapes did not always meet a normal distribution.

2.4.2 Consistency and Generalizability of Landscape Metrics

Secondly, we assessed the consistency among landscape metrics' variability. For the most part, metrics were consistent in their variability across landscapes. However, there are nuances in what consistency among responses tells us about a landscape metric, which are worthy of discussion. At a foundational level, we do not know whether inconsistency among the variability of metric responses means that a metric is more sensitive to a wide range of landscape composition and configuration elements (i.e., number of edges, interspersion of patches), and thus a better measurement. Nor do we know whether the high variability indicates inconsistency in how a metric responds to signals in a landscape, and thus is less reliable. Often, low CQD values are interpreted as indicating model stability (Bonett 2006; Roach and Griffith 2015); following this hypothesis, if the variability is consistent in one metric, this would be comparatively more stable than landscape metrics exhibiting inconsistent variability. This predicates, however, that the measured response from a metric is accurate: this is something we did not measure. While some have attempted to quantify or describe the effects of land cover classification noise (Griffith 2004), even suggesting ways to reduce it (Brown et al. 2000), these exploratory approaches are not enough to infer how our landscape metric scores are determined by product of classification noise, the metric, and or actual signals from the landscape.

As the precision of the metric cannot be ascertained, we believe it is thus important to assess the predictability of responses. For example, if a practitioner knew the variability of their chosen metric in each landscape is consistent with the expectation in other landscapes, they may have higher confidence in correctly interpreting a score. We believe this, as the inverse, would be no certainty in what to expect for a range of values of a metric, as the variability is different across landscapes.

This is further muddied when considering the downside to consistency. If a given metric's central tendency and variance is very consistent across all landscapes, this may undermine the reliability of the metric, as it would suggest a lack of an ability to respond to individual contexts. This was the purpose by which landscape metrics were derived (McGarigal and Marks 1995). Furthermore, a low CQD indicates only consistency in variance, not whether the responses are very distributed (high median CV) or proximate (low median CV) to the central tendency.

Given these limits, we therefore cannot conclude whether certain metrics are more reliable based on their central tendency, range of values, and consistency among the variability metrics exhibit across landscapes. We only can say some metrics are more predictable than others; though, whether the predicted response is an actual landscape signal or propagated noise from the land cover classification or the metric itself is indeterminable solely using this information.

2.4.3 Further Contextualizing Scores with Distributions

Thirdly, we aimed to describe the distribution of landscape metric responses. Most often, landscape metrics were typified by just one, general, distribution; rather, they were described by many different distributions, or there were instances where metrics were rarely matched to any suitable distribution within a generalised linear model at all. Most notably, we found our landscape metrics, in each individual landscape, did not exclusively meet a normal distribution. We recognize that select studies have used non-parametric measures to summarise landscape metric responses (e.g., Baskent and Jordan 1995; Betts 2000; Shaker et al. 2020), or show how in their individual contexts, landscape metrics responses were not normally distributed (Hasset et al. 2012; Remmel and Fortin 2013). Nevertheless, landscape metrics are still used as if they follow a normal distribution extensively (D. Theobald; University of Colorado Boulder, personal communication, December 16, 2022).

We assert that metrics best-typified by one distribution, most of the time, may be easier for practitioners to contextualise than metrics typified by multiple distributions most of the time, or those unable to be fit to a distribution at all. In the previous section, we described the expected spread from central tendencies (median

CV) for each landscape metric, in addition to the consistency and magnitude of variability among values (CQD). Equipped with this knowledge, an individual could compute a metric like *cai_mn*, one consistently predicted by a gaussian distribution, and compare the result to the expected frequency of that measurement to elucidate if that response is more expected or rare. With a metric like patch richness density (*prd*), which is determined by inverse gaussian and negative binomial distributions (56% and 44% of instances, respectively), even where the individual has a low median CV in addition to consistency in the variability across landscapes, they may not be able to elucidate if their score is likely or unlikely, as practitioners often do not have frequency distributions for metric responses (K. Zeller, United States Department of Agriculture, February 7 2022). See **Figure 2.4** below.

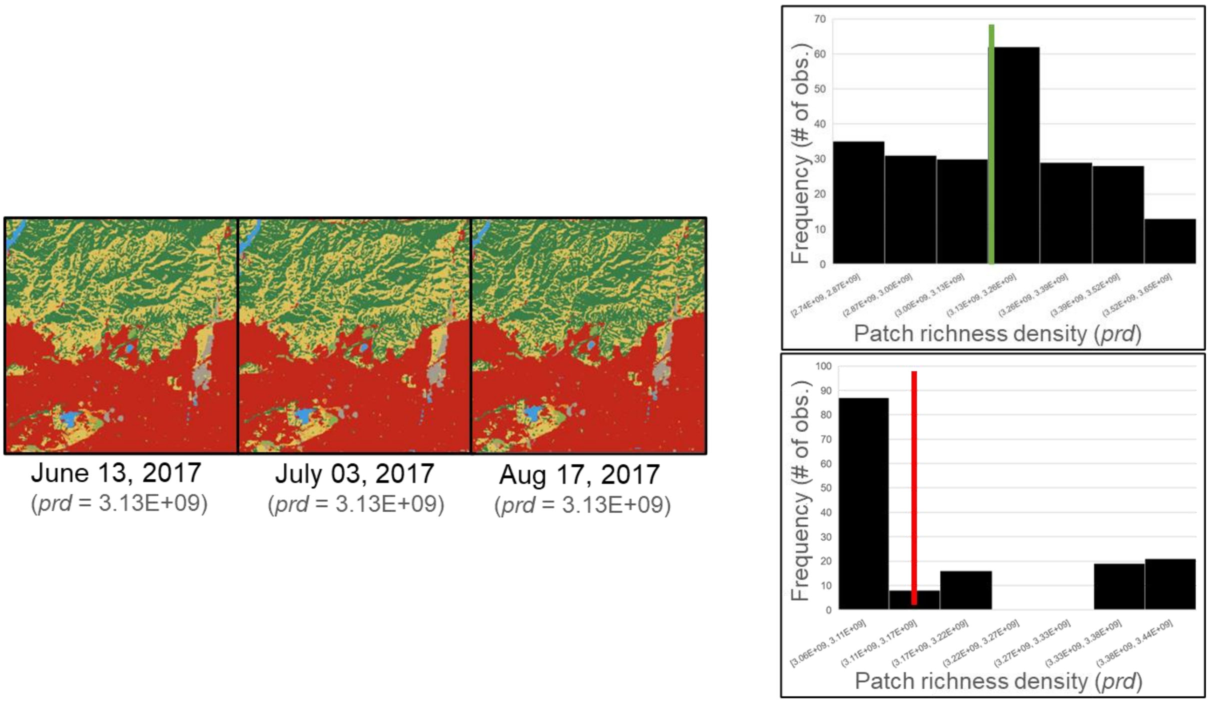

Figure 2.4. Successive Dynamic World images for Pasadena, CA with their respective patch richness density scores (left): images are at 1:200000 scale (25km^2). In this landscape, the frequency distribution indicates these '*prd'* scores are common and possible (top right, n = 229 images); in nearby Anaheim, CA these '*prd'* scores, while possible, are rare (bottom right, n = 151 images).

The consequences of a practitioner not being able to discern if values are expected or unexpected are twofold. Primarily, we worry that when real changes in landscapes do occur, responses that should be considered in low (or rare) frequency are contextualised as often, conflating a false-negative to no change (Type II error). Additionally, when no change is happening in a landscape, a common frequency distribution may suggest a value is rare, when it is in fact, frequent: this could be used to suggest landscape change when the environment remains stable (as a Type I error).

Thus, based on comparative reliability, when scores are variably described by different frequency distributions, a practitioner's inference of a score, on any given day, will have less context than one consistently described by one distribution. Again, if the result of a metric is relied upon, this may lead to individuals falsely inferring change in an unchanging landscape, or falsely indicating stationarity in a changing landscape, respectively.

2.4.4 Predictability and Reliability of Landscape Metrics

Fourthly, we aimed to explore how predictable landscape metric responses were using day-of-year (accounting for seasonal change) and year (isolating inter-year change) as predictors. As we have shown metric scores vary within a given year, understanding apparent trends in seasonality and year-to-year change are important to assessing whether a response is expected or unexpected. As mentioned above, the absence of understanding the expectation of a response can lead to practitioners making Type I and II hypothesis errors. Often, landscape metrics were not predictable using either variable. In all instances where model responses are predicted, the variability exhibited by landscape metrics is best determined by landscape responses to seasonality (as the most significant predictor), and seldom improved by predictors of year. When the response is not fit by model, it is also possible that seasonality and year has some effect (though non-significant); however, it is not clear how the metric response is affected by other variables. Again, we do not know whether the score is a real landscape signal or predicted better by other variables not included in the models (such as classification noise).

As metric responses were predictable only in 46% of instances, on average, there is not sufficient confidence to say that landscape metrics predictably respond to either seasonality or year. Using these predictors to assess whether a metrics' score is expected or unexpected (from classification noise, effect of a metric to maximise or minimise the effect, or real change) is effectively up to a coin toss.

More, as part of evaluating the comparative fit of models, we assessed their proportion of significant studentized residuals. For most metrics (n = 53), when a landscape metrics' response to seasonality is predictable, the average number of observations as outliers does not violate the 95% confidence interval in the estimate of a metric response. This means that when metrics were predictable, the model significance was often not violated. However, ten metrics had a proportion of observations as significant studentized residuals (or outliers), greater than 5%. Concerningly, these ten metrics were also those best-fit by a function most often.

However, as no metric was predicted by a single function, or consistently across all landscapes, the proportion of observations that are fit is irrelevant, as a metric response is unpredictable. The practitioner is both not able to know, in which instance, their landscape is or is not fit by the predictors, but they also do not have a sense of the base function that fits metric behaviour. This limits one's ability to determine if a score is a product of seasonality or other influence(s) (i.e., from classification noise, effect of a metric to maximise or minimise the effect, or real change in the landscape).

Overall, some metrics have consistency among their range of variability and the distributions which best-typify a response on a given day. As discussed above, many metrics are often consistent in their ranges of variability, but all are not. Moreover, individual metrics are predominantly typified by multiple distributions at varying frequencies, which would suggest not all landscape metrics exhibit generalised behaviour. These factors combine to limit the predictability and precision of landscape metric responses. Furthermore, no metric is consistently best-fit by any generalised linear model function. What is therefore necessary is further work to assess the statistical context of landscape metrics, using different data products, and landscapes of interest, as to examine what site-specific contingencies there are to landscape metric behaviour. Only then can any practitioner have sufficient statistical context to interpret a landscape metric value, from an image acquired on any given day, and know if it is expected or not.

2.4.5 Limitations

Most of our limitations within our study are consistent with other landscape metric behaviour validation studies (see Wu et al. 2002). Predominantly, our analyses are subject to the modifiable areal unit problem in both zonal (size of landscape included for analysis) and scale (classification resolution and the simplification of landscape details) (Jelinski and Wu 1996). While we controlled for a consistent landscape size and resolution, future research should assess the ranges of values, distributions, and predictability of landscape metrics at different landscape study sizes and land cover resolutions. For instance, we do not know how metrics tend towards normality with the size of the study extent or pixel size.

Second, our image collections allowed scenes with >5% of masked pixels to be backfilled by a previous image and included. While a common procedure in assembling consecutive land cover classifications for large areas (Pasquarella et al. 2022; Zhou et al. 2022), backfilling images permits self-similarity throughout the time series. However, this would have only minimised the variability among landscape metrics, representing a conservative estimate of metric uncertainty.

More, while we aimed to systematically sample land covers across North America, certain land covers may be less frequently sampled due to cloud cover. These include mountainous regions with clouds (as a product of orographic lift), waterbody-adjacent areas (as a product of the lake-effect), or land covers with smog and haze (Jombo et al. 2023; Taylor et al. 2023).

Fourth, we used a specific land cover product, Dynamic World (Brown et al. 2022), as it was a ready-made land cover classification. Like other land cover classifications, Dynamic World has inaccuracies in the land cover classification. Thus, any attempt to quantify landscape composition and configuration are undoubtedly affected by the accuracy of this imagery product. To parse the effect of noise caused by the image classification, future work assessing the behaviour of landscape metrics should assess responses across varying classification accuracies.

Finally, we used the global human modification index (gHM) (Kennedy et al. 2020) to represent different scenarios in which landscape metrics may be applied in conservation applications. An assumption we are making is that no real change occurred after this data layer was assembled in 2016. While year was often an insignificant predictor (suggesting no change since 2016), this could also be that noise percolation had a stronger effect, thus nullifying the predictive ability of year as a variable.

2.5 Conclusion

When landscape metrics were originally developed, their purpose was to capture signals of what is happening in the landscape (McGarigal and Marks 1995). This would suggest landscape metrics were intended to be site-specific. In various areas of interest, landscape metrics have been applied to understand how the suite of abiotic, biotic, anthropogenic processes culminates into signals detected from land cover maps (Turner 1989). In this study, we aimed to build upon the foundations of other works which assessed the statistical context of landscape metrics and assess whether universal trends in metrics exist. Most notably, our evidence conflicts with the existence of universal trends in the statistical context of landscape metrics. For instance, prior to our study, there was an implicit assumption that landscape metrics meet a normal distribution: our results suggest only some metrics meet this general behaviour. Beyond normality, we presented many logical considerations considering the various elements of statistical context we assessed. In other words, landscape metric responses were neither entirely general nor site-specific.

In addition to others who assessed the behaviour of landscape metrics (e.g., Neel et al. 2004), we harken back to Cardille et al. (2005) who asserted “we do not think that landscape metrics, as currently understood, are a panacea for ecological analysis”, and rather “the inability of potential users to establish the spatial or statistical context of real-world landscapes appears to be a major factor inhibiting a full exploration of and experimentation with the ever growing library of satellite-derived land-cover data” (2005, pg 987). We sustain Cardille et al.’s perspective as there were minimal generalizable trends among landscape metrics. Moreover, when metric behaviour is generalizable, it may be that certain metrics will propagate similar ranges of values, or populate a similar distribution, no matter where they are applied, and thus are not sensitive to the environment in which they are used. While consistency among metrics in their explained variability and the distribution best-typifying responses can lend predictability, we still do not know whether the response is from the actual landscape. Thus, while some metrics may be more predictable, further work is necessary to build upon our understanding of predictability and consistency, to assess metric accuracy. To assess accuracy of a measurement, we encourage future works to isolate the effects of (1) land cover classification inaccuracy and (2) thematic resolution on landscape metric responses. While landscape metrics will undoubtedly still be used in conservation decisions, a concerted and attendant effort needs to be made to continue building an understanding of their statistical context and behaviour.

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2.7 Statements and Declarations

2.7.1 Funding

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2.7.2 Competing Interests

Bryant M. Serre and Jeffrey A. Cardille declare no relevant financial or non-financial interests to disclose.

2.7.3 Author Contributions

Both authors contributed to the study conception and design. Material preparation, data collection and analysis were performed by Bryant M. Serre. The first draft of the manuscript was written by Bryant M. Serre, and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

2.7.4 Data Availability

As part of providing information about the statistical context of landscape metrics, all computed values, per metric, per landscape, are provided in the appendices. All data, code or summaries are available upon request to the corresponding author.

3. Discussion

3.1 Overview

Landscape metrics are commonly used to assess the patterns and functionality of ecological systems, consistently applied in modern conservation management, ecology, and land-management decisions (Leitao and Ahern 2002; Sundell-Turner and Rodewald 2008; Wiens 2002). Indeed, the use of landscape metrics will ultimately affect how humankind adapts and mitigates the effects of our Western-initiated climate change. As landscape metrics constitute elements of this decision-making process, the importance of ensuring their reliability is self-evident.

Though, it is only because of the profligate legacy of white males in positions of power, who have degraded the environment, that we must now address the environmental issues of today. While it is often cast that all science has systemic gender bias and exclusion, the notion of it being widespread is not sufficient reason to ignore it now in a discussion of landscape ecology. In 1987, Jim Thorne had reviewed one of the foundational texts in landscape ecology to argue how the field of landscape ecology is “refreshing and imaginative because of the use of personal observation, the lack of gender bias, and the clear well-illustrated examples (Thorne 1987, pg 154). However, a deep examination of Forman and Gordon (1986) reveals sparse mention of research conducted by women, nor were there any women in attendance of the first meeting of landscape ecology in Allerton Park, Illinois three years prior (see Rissler et al. 1984 for attendees). It has only been recently that landscape ecology has accepted scholarship through women, which has advanced the foundations established by men.

It is in this informed context of historical bias that we may now contextualise how the results of this thesis fit within the scope of past landscape-metric validation studies. Moreover, I hope to articulate how future research can expand our understanding of landscape metric behaviour. More generally, I will discuss the need for future validation studies under the context of landscape ecology’s origin: a field poised to be a multidisciplinary, data-driven field not dissimilar to others in the environmental sciences.

3.2 Modern Assessments of Landscape Metric Behaviour

As mentioned, landscape metrics are used in a variety of modern, pivotal, conservation management policies and global agreements. This is evidenced by the numerous programs which have employed landscape metrics over the last two decades (Kupfer et al. 2012; Li et al. 2021; Lopez et al. 2005; Lopez et al. 2006; Lopez and Frohn 2017; Reddy et al. 2013; Wulder et al. 2008). Qualifying their use, there are several landscape metric validation studies where the responses of metrics to different contexts is assessed and generalised, such as (1) in varying spatial extents and (2) spatial resolutions of land cover maps, (3) in the collinearity of metrics, and (4) in how metrics respond to different aggregations of landscape patches (Cushman et al. 2008; Neel et al. 2004; Wu et al. 2002). This harkens back to the original focus of landscape ecology in which practitioners sought to deduce general patterns of ecological processes using information from the landscape mosaic (Wiens 2008).

While past studies support generalised behaviours among landscape metric responses, which may improve how we understand metric scores, there is an attendant 20+ year-long discourse which has stressed the need to continually evaluate these assumptions to ensure landscape metrics can be relied upon (reviewed in Gustafson 1998, 2019). In hopes to contribute to this discourse, this thesis aimed to assess the statistical behaviour of landscape metrics, including addressing some of the common gaps in knowledge previously identified (Cardille et al. 2005; Gustafson 2019; Turner 2005). Namely, these include the range of values for metrics, an understanding in the consistency of metric responses across different landscapes, in addition to the distributions which best typify landscape metric responses. Moreover, we sought to understand how predictable landscape metric scores are, using information about the time of acquisition, per the land cover maps from which they are derived.

In contrast to past findings of general behaviour, our results indicated landscape metrics were not always consistent in their variability across landscapes (84% of landscape-level metrics were consistent). Metric responses were also often typified by multiple distributions; namely, landscape metrics were rarely described as gaussian. Using generalised linear models, we assessed how likely metric scores could be predicted using information about the acquisition date of the image. As metric scores varied within a given year, we thought there may be effects of seasonality which drive variability within a score. Using generalised linear models, we tried to predict the response of a metric score, in landscapes that seemingly do not change over time, as to help practitioners contextualise whether a score on a given day can be predicted, and is within the expectation of seasonal variation, or if it is unpredictable. Fortunately, landscape metrics were mostly insensitive to the image acquisition year (predicted responses 9.2% of instances with a best-fit model): this lends support to our study approach where we focused on landscapes not changing over time. By day-of-year, metric responses were predicted around half the time (54% of the time, on average, across metrics): this suggests that metric responses may have seasonal variability, and thus influence a score depending on when the land cover map is composited. In Chapter 3, I argued how these various elements of statistical context interconnect, and showed some examples where both expert and non-expert users of landscape metrics may be limited in knowing what distribution or function predicts a score, and thus, how they would evaluate whether a response is expected or unexpected.

In part, our conflicting results may be a product of a larger sample size and the use of a ready-to-use classified land cover product. Previously, landscape ecologists were working under the impressions that to answer larger theoretical “questions in landscape ecology [would] require the ability to acquire and manage large quantities of data;” namely, the high cost of computing and storage needs were cited as limiting factors to advancing the field of landscape ecology (Risser et al. 1984, pg 6). It has not been until recently that frequent land cover information is both accessible and easily interpretable by landscape ecologists (Crowley and Cardille 2020). With the privilege of access to cloud-computing software (Gorelick et al. 2017) and a near-real-time land cover product (Brown et al. 2022), we were able to conduct a large-scale study of metric behaviour. This allowed us to interpret ~100,000 land cover classifications, across 680 real landscapes, to describe the behaviour of 65 landscape-level metrics across our study area.

Previous related studies of metric behaviour occurred in a setting of substantially more limited data availability. Working in the early 2000s, when Landsat data was not freely available, Wu et al. (2002) were able to test only “five landscapes with contrasting natural and socioeconomic settings'', with only a single corresponding land cover map for each landscape they assessed the changes in pixel size and spatial extent on the response of 19 landscape metrics. Upon their analysis of these landscapes, they advanced that “metrics fell into three general categories: Type I metrics showed predictable responses with changing scale, and their scaling relations could be represented by simple scaling equations (linear, power-law, or logarithmic functions); Type II metrics exhibited staircase-like responses that were less predictable; and Type III metrics behaved erratically in response to changing scale” (2002, pg 761). The authors suggested their results need to be “verified by additional studies with both real and artificial landscapes'' (Wu et al. 2002, pg 778).

Despite their admonition to use their results only as preliminary evidence of landscape metric behaviour, the dearth of subsequent tests of metric behaviour led landscape ecologists to interpret their results as evidence of general landscape-metric scaling behaviour (Frate et al. 2014; Frazier and Wang 2013; Ma et al. 2018; Rutchey and Godin 2009; Zhang and Li 2013), in spite of studies reporting conflicting evidence to scaling trends (Corry and Lafortezza 2007; Frazier 2016; Peng et al. 2010; Shen et al. 2004). While the concept of general behaviour is now widely accepted, the process through which it gained acceptance appears to contradict the original principles of a multidisciplinary and data-driven field of landscape ecology.

3.3 Revisiting Landscape Ecology at Allerton Park, Illinois

In April 1983, the first unified meeting of landscape ecologists was convened in Allerton Park, within Piatt Country, Illinois. In efforts to formalise a discipline and the research direction of this new field, this meeting brought together a diverse expertise of scientists, largely as landscape ecology was not thought of as “a discrete discipline or simply a branch of ecology, but rather the synthetic intersection of many related disciplines” (Risser et al. 1984, pg 9). Members of the Allerton Park workshop knew that if this emerging field sought to address a “broad range of issues and scientific questions", that it would need to build "upon data and ideas from diverse fields such as ecology, geography, and wildlife management" (Risser et al. 1984, pg 10). It may be worthwhile to remind the reader that this field was initiated by a botanist-turned-landscape architect and an economist (Forman and Godron 1981), who went back to the foundational work in geography and climatology (see Troll 1950). It was only upon this varied expertise that data from all ecologists and biologists could then be used to advance theories, namely in the fundamental assumption that landscape patterns are a product of ecological functions (Forman 2011; Gustafson 2019; Turner 1989, 2005).

More, landscape ecology was emerging at a time where, for nearly a century the field of ecology had been critiqued by male physicists, chemists, and biologists for reducing the complexity of systems for the purpose of comprehension, and for the early assumptions which transferred this study and description of Nature into a science (Cowles 1904; Cragg 1966; Fretwell 1975; McIntosh 1980; Rosenzweig 1976; Stauffer 1957). Notably, Peters (1976) critiqued how this line of inquiry in ecological sciences had conflated "several major tenets of modern ecological thought", including theories of evolution through natural selection with concepts of landscape diversity and spatial heterogeneity, in ultimately unscientific ways. (i.e., without the burden of evidence to support) (Peters 1976, pg 8).

However, the goal of landscape ecology was never to reduce ecological complexity, rather, it was the opposite. At Allerton Park, landscape ecologists had asked these critics to "eschew parochial views about landscape ecology" and instead, come to them in the pursuit of "intellectual development of this complex, interdisciplinary field" (Rissler et al. 1984, pg 10). While the impacts of anthropogenic climate change were not thoroughly recognized in the mid-80s, landscape ecology rightly galvanised upon the two decades prior of environmental action within both the United States and Canada. In the 1970s, the United States had celebrated its first Earth Day with bipartisan support (Beyl 1992), and North America saw the establishment of paramount environmental regulators and researchers, including the United States Environmental Protection Agency and the Canada Centre for Inland Waters (Beyl 1992). It was on this society-wide goal to improve the state of the natural environment (Flippen 2000) that landscape ecology brought together broad interdisciplinary expertise.

As with any science, it is known that differing expertise permits the ability for different interpretations of the data one has in front of them (Bammer et al. 2020; National Academy of Sciences and National Academy of Engineering & Institute of Medicine 2005). Indeed, addressing complex environmental issues requires the collective expertise of multiple disciplines and lived experiences among individuals, as it is this diversity that allows for a more comprehensive framing of ecological systems, and thus, more accurate interpretations of ecological phenomena (National Resources Council 2001). Understanding this, landscape ecologists held that there need be a standard for all intellectual development in the field, where any hypothesis must “withstand the scrutiny of interest groups and be generalizable over large geographic areas” (Rissler et al. 1984, pg 10). This initial effort can be directly linked to the many studies to date which support (1) the link between ecological processes and the resulting landscape patterns (reviewed in Wiersma 2022), in addition to (2) general trends in metric behaviour (Bogaert 2003; Cardille et al. 2005; Cushman et al. 2008; Fortin et al. 2003; Hargis et al. 1998; Neel et al. 2004; Tischendorf 2001; Wu et al. 2002).

I harken back to this with the intent of showing the value that cross-disciplinary expertise brought to landscape ecology. It evidences the importance of widespread data to support the claims on which we continue in the pursuit of knowledge within this field. Even broadly, to support any scientific advancement, all theories must be subject to “ultimate destruction when it is proven wrong, or to logically justified acceptance when finally [they are] vindicated by facts” (Opik 1977). In 2008, Wiens’ review of Allerton Park embodies this notion, as he argues the landscape ecologists of today often use general principles, despite how the ecological “complexities and contingencies of landscapes make generalisation difficult” (2008, pg 128). To ‘course correct’ the field, Wiens (2008) suggested that with the diverse expertise in modern landscape ecology, landscape ecologists should instead return to “develop[ing] contingent principles and theories, [in addition to] ideas that may apply to a suite of landscapes that share common features or to particular domains of scale, but not more generally” (2008, pg 128). Beyond landscape ecology, the value of trans-disciplinarity is not unique; rather, it echoes a broader historical lineage of intellectual development in natural science research, such as in the field of limnology.

3.4 Parallels to Modern Limnology at Lac Leman, Switzerland

At the first meeting for limnology (*Internationale Vereinigung für Limnologiae)* in 1922*,* August Thienneman convened a variety of scientists, where he proposed *Archiv für Hydrobiologie,* a unified journal to publish on limnological studies (Berg 1950). On *Hydrobiologie,* Thienneman served as sole editor for 40 years (Berg 1950). Under his aegis, the discipline examined lakes as closed, simplified structures; it was the perspective that lakes are readily comprehensible and understandable in isolation to their surrounding watersheds (Berg 1950). At the time, in post WWI Europe, Thienneman's observations were based solely on a few lakes in Germany, on which he then concluded generality to all freshwater lakes. It was later that multi-decadal observations of inland lakes in the Laurentian Great Lakes basin (Birge and Juday 1934), as synthesised by Evelyn G. Hutchinson, showed that lakes varied extensively. As Hutchinson's analysis suggested, lakes were not closed, generalizable systems; rather, they were intrinsically linked to the surrounding watersheds' morphology, geology, and climate which drives site-specific differences among lakes (Hutchinson 1957-1993). Through Birge and Juday's data, and the collective expertise of chemists, biologists, bacteriologists, physicists, and instrument-makers that Hutchinson pulled together to analyse their lake observations (Kalff 2002), the original paradigm of lake classifications was rejected, and modern limnology emerged. Hutchinson's work was exemplary for how it crossed not just disciplines, but cultures, levels of formal education, class, and gender as to build upon a foundation that was strong enough to incorporate all authentic knowledges of limnological work prior (Carpenter 1924; Merrill 1893; Monti 1929; Patrick 1948).

Consequently, much of the effort that had gone into advancing limnological studies under Thienneman's editorship of *Hydrobiologie* became irrelevant, as all research published in this journal had to vociferously subscribe to his general assumptions about lakes (Berg 1950). It is only in the re-establishment of "modern" limnology, that Hutchinson re-centred dialogue on how individual lakes is uniquely, and comprehensively, affected from organism-level traits up to broad scale atmospheric conditions (Hutchinson 1957-1993). Hutchinson argued that (1) simplistic classifications of ecological processes were not enough, and that (2) individuals cannot examine an ecological system in isolation of other elements of their biotic and abiotic system(s) (Hutchinson 1957). Concomitantly to Hutchinson's reorganisation of limnology, his student, Jack Vallentyne, had pleaded with Thienneman's contemporaries to not just get fascinated by what a given organism can do, but go in, and deeply understand the notions of biology, chemistry, and physics which constitute pelagic systems (1957). To do so, would warrant tremendous interdisciplinary expertise. Vallentyne (1957) argued something as simple as water's physics and chemistry are often the last study for the limnologists, as "the beginning student is attracted by the diversity of aquatic life: the whirligig beetles, bottom living insects, fish and other fantastic forms of life" (1957, pg 218).

While this narrative serves to illustrate the complexity of ecological systems, it also emphasises the need for transdisciplinary expertise and contexts, as it was similarly expressed in the foundational meeting for landscape ecology. While the peer-based critique of scientists who fail to comprehensively frame ecological systems is both necessary and just, this could be avoided through transdisciplinary science. It is the collective expertise and diverse contexts that individuals bring to environmental science inquiries that historically permitted a more accurate understanding of ecological phenomena and improved the environmental-relevance of all research (Likens 2001; Lindenmeyer et al. 2012; Wetzel and Likens 2000). It is for this reason, over the last 40 years, some landscape ecologists have returned to the notions of Allerton Park and Wiens' critique, arguing how an integrative field like landscape ecology requisites trans-disciplinarity (Brandt 2000; Field et al. 2003; Hobbs 1997; Nassauer 1995; Naveh 1978; Termorshuizen and Opdam 2009; Turner 1987; Wu 2021). It is apt that many sources reference Jantsch's (1970, 1972) definition of multidisciplinary, who was a classically trained astrophysicist.

3.5 Future Research on Landscape Metric Behaviour

Herein, we discuss several future research directions in landscape metric behaviour. Firstly, as the results do not support generalised trends in landscape behaviour, it is rightly suspect that past assumptions of landscape metrics be re-validated with greater amounts of evidence. Leveraging cloud-computing technologies, we have shown that there is sufficient capability to calculate landscape metric scores across North America; this could be scaled up to a global assessment. Indeed, evaluating landscape metric behaviour in this way would contribute to the development of "contingent principles and theories" of metric responses to geographic location and varying scale parameters (Wiens 2008, pg 128).

Secondly, work should continue to return to the many unaddressed gaps in metric behaviour, posited by landscape ecologists over the last 20+ years (reviewed in Gustafson 1998, 2019). For example, this would include a more comprehensive assessment of response of scaling trends among landscape-metric scores in response to different (1) temporal scales (over time), (2) spatial scales (i.e., different sizes of the landscape analysis window), (3) pixel sizes (i.e., the size of pixels used in land cover classifications), in addition to (4) thematic scales (how many land cover categories are used). Moreover, we argue these impacts of scale should be tested concurrently, rather than independently. To date, the behaviour of a metric responses to scale is often measured by only one of these criteria (Bailey et al. 2007; Du et al. 2006; González-Moreno et al. 2013; Moreno-De Las et al. 2011; Obeysekera and Rutchey 1997). Singly assessing scale knowingly reduces ecological complexity: for instance, if changing the spatial extent of observations, larger landscapes may exhibit different responses to resolution than smaller landscapes. In support, Holland et al. (2004) noted how "often little or nothing is known about the scales at which a species responds to structural characteristics of its environment", which has consequences not only for "the effectiveness of study designs," but on the then-inferred dynamics of the ecological processes which we are potentially misrepresenting (2004, pg 228). Devising a means to assess the interactive effects of multiple scale parameters on a metric score may improve the environmental-representativeness of both landscape metric validation studies and other landscape ecology studies generally (Bissonnette 2019; Frazier et al. 2014).

Third, it is hoped future research of patterns in real landscapes can elucidate how classification error relates to landscape metric results. Classification error remains a fundamental issue in ascertaining the predictor of a landscape metric score (Hess 1994; Lechner et al. 2012). For instance, if a practitioner had two images of the same landscape with different producers' accuracies (i.e., the reported accuracy of land cover map as validated through external observations), it is likely classifications within these two land cover maps would be different. As a product of this difference, we would expect landscape metric scores to vary. However, we do not have the ability, from either of these images, to discern the true, “accurate” signals from a landscape. If we could evaluate the impact of increasing or decreasing producers’ classification accuracy on landscape metrics, we may be able to better understand how much error responses are subject to. It is with these classifications (derived from remote-sensing practitioners) and real landscape observations (from conservation ecologists and local knowledge keepers who are boots-on-the-ground), constituting a transdisciplinary knowledge, that we may discern real signals in a landscape from scores influenced by classification error. This reduction of noise remains a prominent focus in remote sensing, and thus should be further examined in landscape ecology as landscape composition and configuration metrics ultimately derive their meaning from remotely-sensed imagery products (Cardille and Fortin 2016; Lee et al. 2018).

3.6 Towards an Interdisciplinary and Data-driven Landscape Ecology

To reiterate, metrics are increasingly utilised in both local and international sustainability policies. While general trends have lent confidence to interpreting scores, if wrong, the consequences may undermine the effectiveness of current adaptation and mitigation strategies to Western-initiated anthropogenic climate change. If any practitioner is to rely on a score, derived from a land cover map, which is a product of a specific image acquisition period, it is important for them to know if that score is something frequent and within a range of reasonable expectation or not. If a score is unexpected, this could indicate change in a landscape, which should be evaluated, with a broad interdisciplinary expertise, as to assess how this landscape change may affect ecological processes. However, practitioners are currently operating without this requisite understanding to determine what is expected, in addition to what is a real signal or a product of noise within our image classifications. Through these proposed future research directions, we acknowledge that ensuring the reliability of these metrics is not just crucial, but also attainable if we return to the discipline's data-driven multi-disciplinarity. I cannot underscore enough the importance of continued dialogue, across disciplines, to ensure ecological processes are sufficiently and accurately captured in landscape metric scores, so that they may be relied upon for local-to-international sustainability strategies. Larger than landscape metrics, the success of our efforts to confront climate change will depend on our ability to genuinely embrace a transdisciplinary approach, to leverage the collective expertise and perspectives of diverse individuals, and to remain committed to the pursuit of scientific inquiry that is both data-driven and multidisciplinary in nature.

4. Conclusion

This thesis seeks to contribute to the growing body of knowledge of landscape metrics' behaviour in real landscapes. Ideally, we also hope to provide information that can situate the statistical context of landscape metrics to the many practitioners, conservation ecologists, land-managers, and policy makers, both expert and non-expert, who employ these tools extensively. In **1.2 Literature Review**, I reviewed the foundations on which landscape ecology sits in ecology and biology, the current assumptions of the discipline, past validation studies, as well as the many local through international uses of landscape metrics towards past and current conservation mandates. In **Chapter 2**, I put forward a novel landscape metric validation study, which aimed to address several gaps in knowledge of landscape metric behaviour. These include (1) the expected ranges of values for metrics in real landscapes, (2) metric variability in a given landscape, (3) the consistency of that variability across many landscapes, (4) the distributions which may typify metric responses, and (5) how often a score can be significantly predicted by seasonality. In all dimensions of statistical context, the results do not support that generalizable trends in landscape metrics always exist. Beyond epistemological development, I hope these results provide real information to practitioners, in which they can use to determine suitable metrics for use and interpret scores with. In the section **3. Discussion,** I discuss some of the broad and implicit assumptions of landscape ecology, in addition to the 20+ years long critiques of landscape ecology and the near century-long critiques in the study of ecology. In this chapter, I draw a parallel between the origins of landscape ecology at Allerton Park, in Illinois (USA) and limnology on the shores of Lac Leman (Switzerland). I do so with the intention of discussing the importance of transdisciplinary expertise to the root of many environmental scientific endeavours, and the value it may bring now to assessing whether landscape metrics are reliable. More, I discuss facets of western scientific advancement including the sufficient burden of evidence, the importance of questioning our underlying assumptions, and the holism of environmental factors which influence a metric's score. This section ends on future research directions particularly in landscape metric validation studies, considering the work previously done, as conducted in this thesis, and the gaps in knowledge that practitioners believe remain unresolved. It is on the rigorous foundations of knowledge about how metrics measure and respond to landscapes, that we may make more environmentally-representative and significant decisions to preserve land, restore biodiversity, and wholly fight against the effects our self-initiated anthropogenic climate change on human and natural environments alike.

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6. Supplemental Information

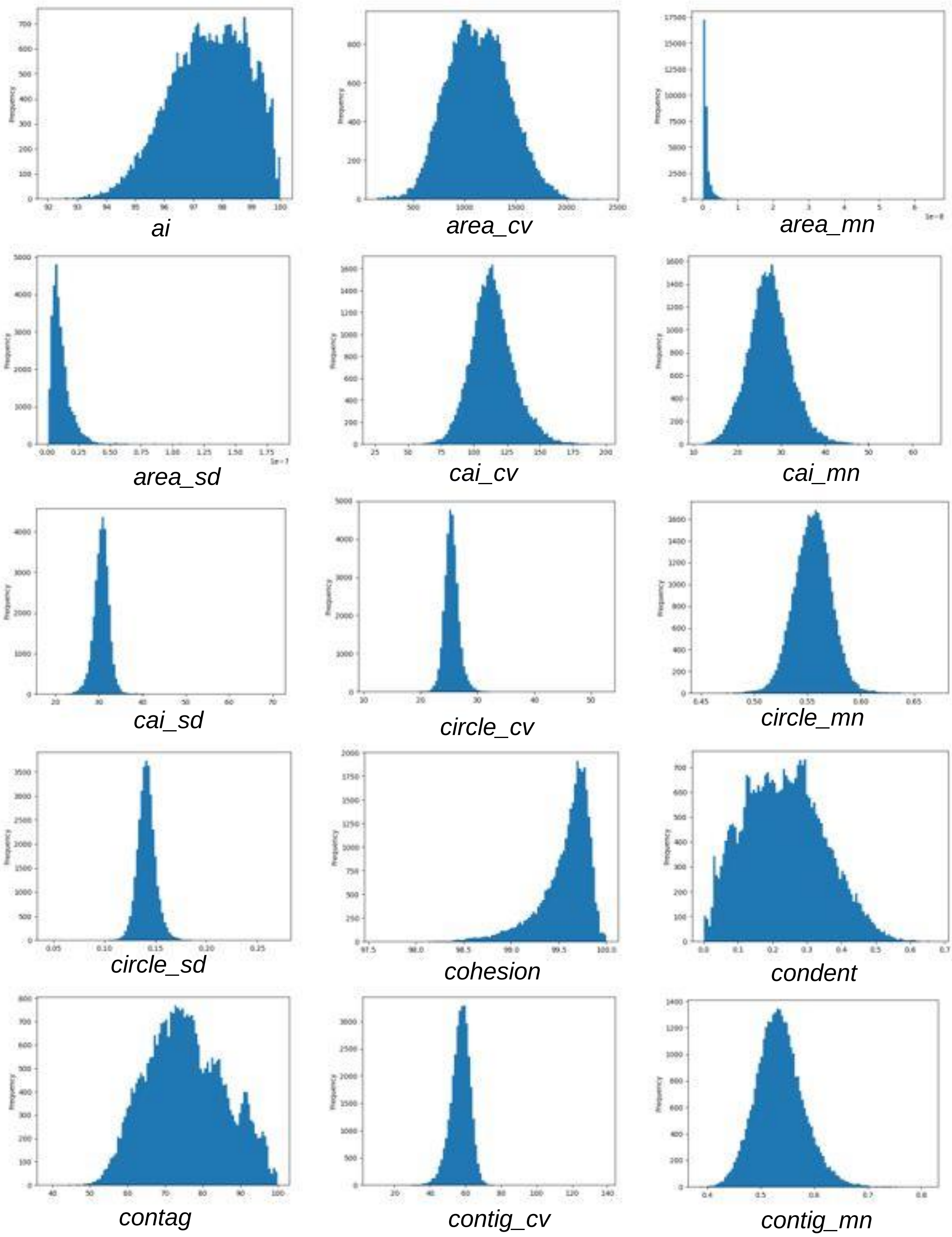
6.1 Procedure to Remove Misclassified Images

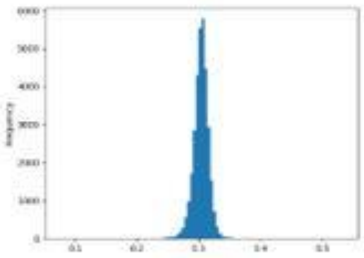
As we visually screened all landscapes, and their image collections, we could see where the land cover classification was abnormal. Upon examination of abnormal instances, the near real time land cover product, Dynamic World (Brown et al. 2022), had misclassified several pixels as snow and ice, even in the middle of a growing season. Firstly, we manually verified the temperature normal for each of these days using climate data from governmental institutions pertaining to each landscape. We subsequently examined the corresponding true-colour Sentinel-2 image on which that land cover map was derived. In all cases, the presence of normal climatology data and the visible presence of clouds suggested these instances were relict clouds cover or haze that was were not removed by (1) Dynamic World's cloud masking algorithm, or (2) our filtering of Sentinel-2's Cloud Probability and Cloud Cover Band ('QA60') metadata.

Methodically, these outliers were removed for each landscape, using the median absolute deviation (MAD). The MAD approach avoids the influence of outliers on the measure of dispersion and does not assume a normal distribution among the data. The MAD identifies outlying observations through calculating the median absolute deviance from the difference of all given values and the median (Rindskopf and Shiyko 2010). For each metric, in each landscape, if observations were greater than or less than three times the median absolute deviation from the median, they were labelled as an outlier. These instances were all manually verified as instances where the scene consisted of snow and ice land cover and were subsequently removed from the time series.

6.2 Supplemental Figures

Figure 6.1 Aggregate frequency distributions for all landscape-level metrics.





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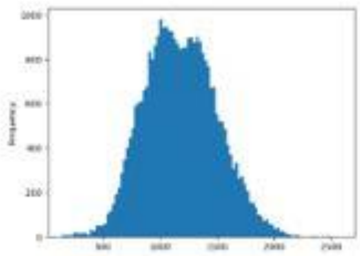

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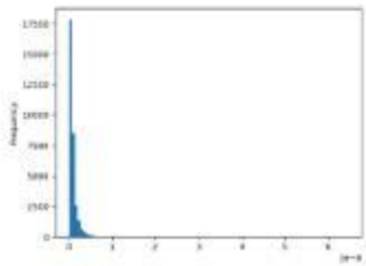

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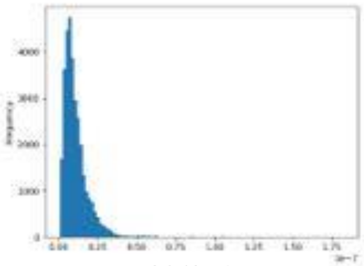

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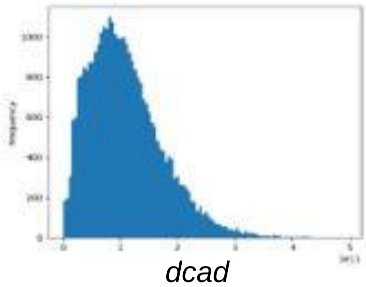

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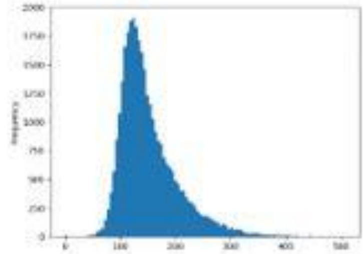

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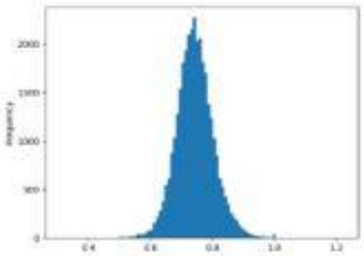

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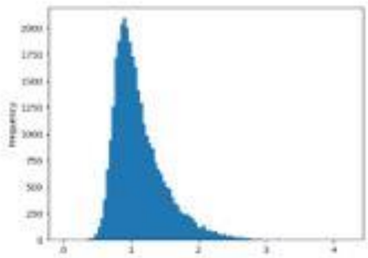

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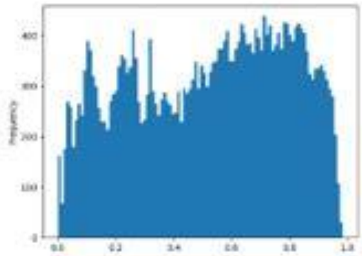

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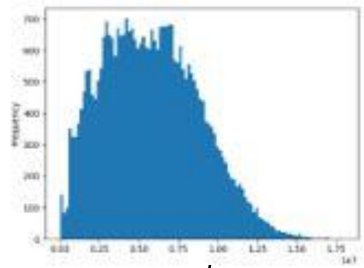

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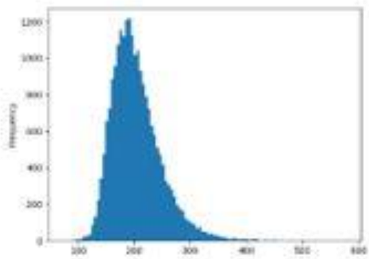

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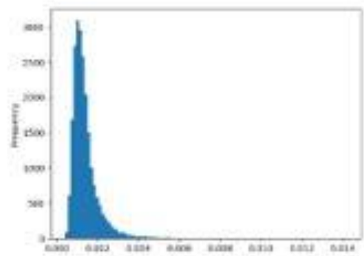

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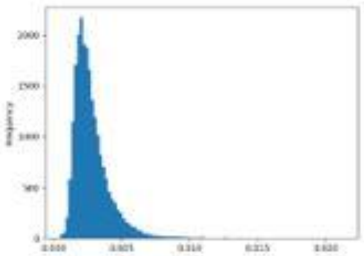

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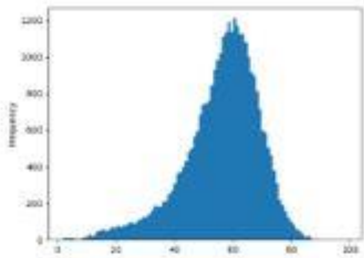

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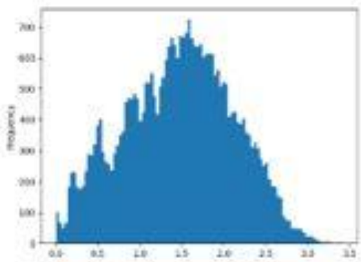

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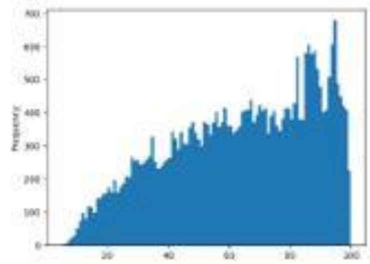

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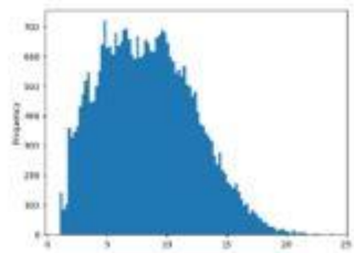

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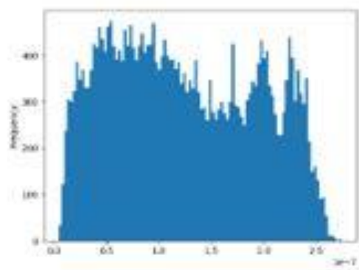

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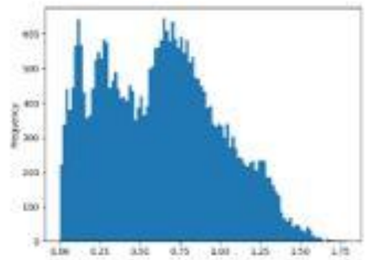

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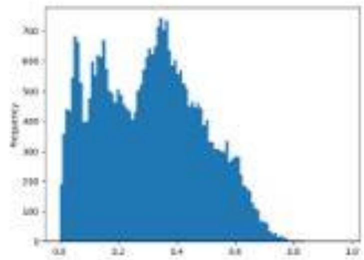

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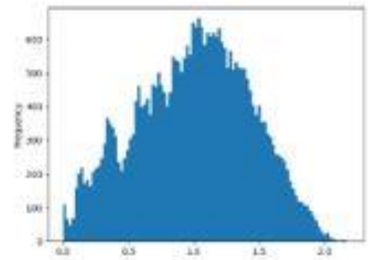

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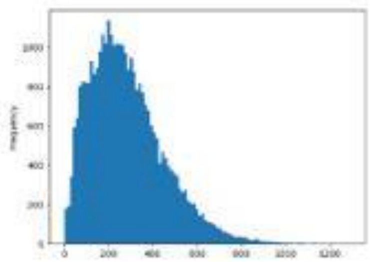

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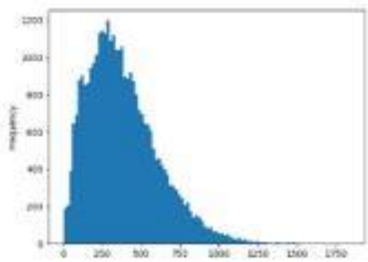

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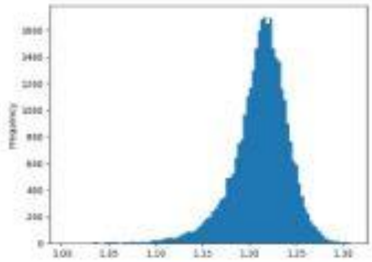

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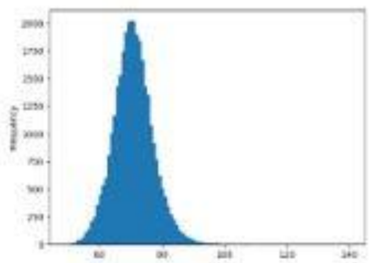

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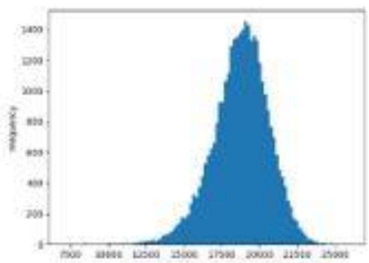

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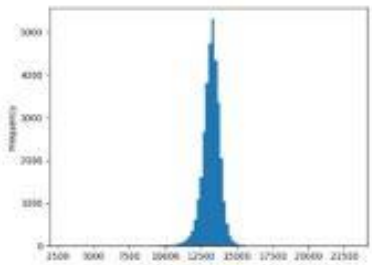

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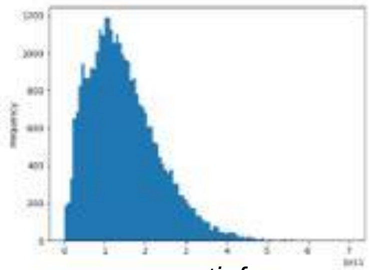
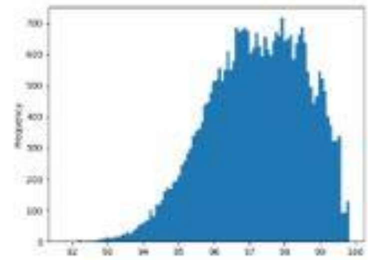


mutinf



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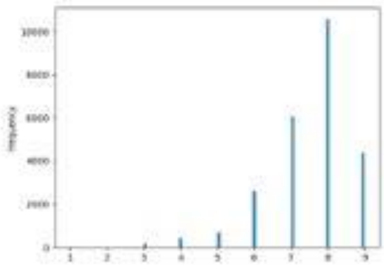
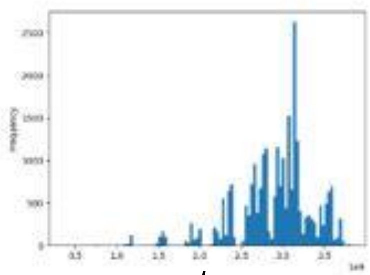
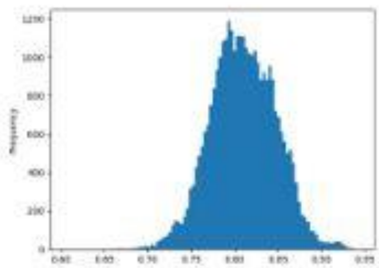


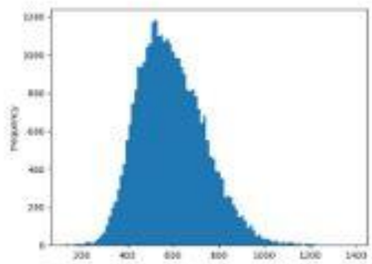
np



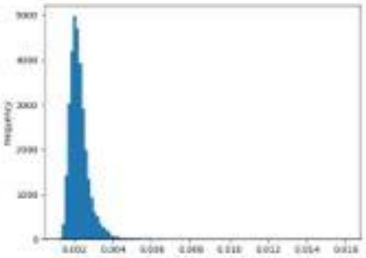
prd

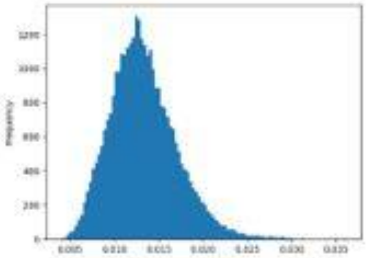


relmutinf



shape_cv


shape_mn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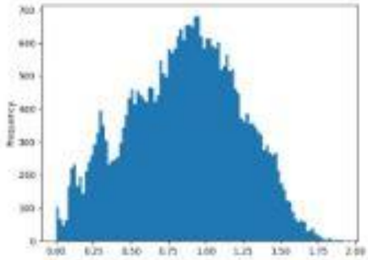
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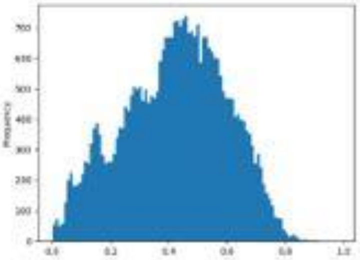
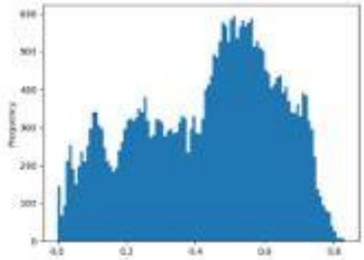

shei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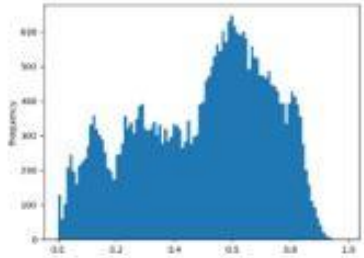
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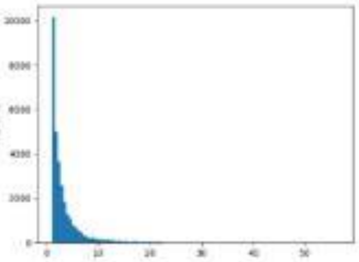
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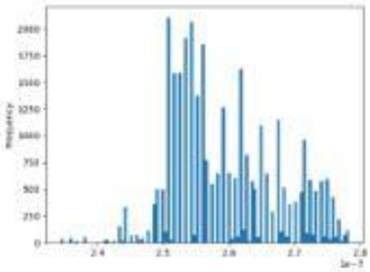
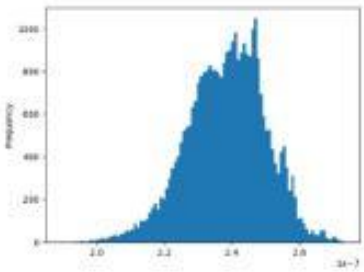

ta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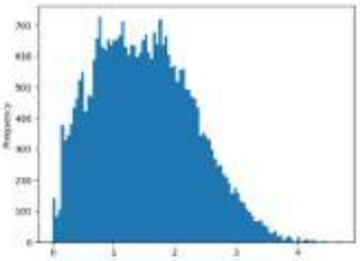
te

6.3 Supplemental Tables

Table 6.1 Landscape metrics' aggregate central tendency, range, variance for all observations (*n* = 108, 922).

Landscape-level metric	**Summary Statistics**				
	Minimum	Maximum	Median	Median absolute deviation (MAD)	Coefficient of variation (CV)
ai	91.03	100.00	97.59	1.01	72.18
area_cv	141.18	2.40E+03	1.13E+03	213.07	3.75
area_mn	0.00	0.00	0.00	0.00	0.22
area_sd	0.00	0.00	0.00	0.00	1.17
cai_cv	19.36	198.36	113.22	10.08	6.92
cai_mn	11.45	99.31	27.28	3.08	5.20
cai_sd	16.91	70.22	30.67	1.07	15.83
circle_cv	11.10	52.04	25.42	0.77	18.91
circle_mn	0.37	0.70	0.56	0.01	29.58
circle_sd	0.05	0.27	0.14	0.01	15.13
cohesion	97.58	100.00	99.64	0.14	357.52
condent	0.00	0.68	0.23	0.09	2.02
contag	38.80	99.99	74.80	7.55	7.27
contig_cv	7.53	137.70	57.49	3.47	10.00
contig_mn	0.37	1.00	0.53	0.03	11.49
contig_sd	0.07	0.55	0.30	0.01	21.87
core_cv	141.24	2.63E+03	1.17E+03	222.90	3.70
core_mn	0.00	0.00	0.00	0.00	0.22
core_sd	0.00	0.00	0.00	0.00	1.13
dcad	3.64E+08	5.54E+11	1.01E+11	4.25E+10	1.67
dcore_cv	0.00	583.76	139.56	27.72	2.83
dcore_mn	0.31	2.00	0.74	0.04	11.77
dcore_sd	0.00	4.44	1.04	0.21	2.84
division	0.00	0.98	0.55	0.23	1.94
ed	0.00	2.04E+07	5.68E+06	2.31E+06	1.89
enn_cv	72.35	578.16	196.90	26.59	4.64
enn_mn	0.00	0.01	0.00	0.00	2.06
enn_sd	0.00	0.02	0.00	0.00	2.08
ent	0.00	2.77	1.26	0.39	2.27
frac_cv	0.21	9.07	5.49	0.35	8.25
frac_mn	0.90	1.00	0.96	0.00	221.90
frac_sd	0.00	0.09	0.05	0.00	8.40
gyrate_cv	132.73	545.83	293.82	33.29	5.92
gyrate_mn	0.00	0.02	0.00	0.00	1.01
gyrate_sd	0.00	0.01	0.00	0.00	2.17
iji	1.76	98.92	58.15	7.65	4.34
joinent	0.00	3.42	1.50	0.47	2.26

lpi	4.93	100.00	65.71	19.54	2.67
lsi	1.00	27.35	8.24	2.95	2.14
mesh	0.00	0.00	0.00	0.00	1.79
msidi	0.00	1.79	0.63	0.29	1.70
msiei	0.00	0.98	0.31	0.14	1.74
mutinf	0.00	2.19	1.02	0.32	2.27
ndca	1.00	1.48E+03	261.00	111.00	1.66
np	1.00	2.07E+03	350.00	149.00	1.65
pafrac	1.00	1.31	1.22	0.02	39.44
para_cv	48.73	163.11	70.68	4.05	10.38
para_mn	76.90	2.62E+04	1.89E+04	1.19E+03	9.59
para_sd	2.79E+03	2.31E+04	1.32E+04	3.56E+02	19.18
pd	3.64E+08	7.99E+11	1.35E+11	5.73E+10	1.66
pladj	90.67	99.83	97.27	1.04	70.08
pr	1.00	9.00	8.00	1.00	6.37
prd	3.64E+08	3.84E+09	2.99E+09	2.55E+08	6.23
relmutinf	0.05	1.00	0.81	0.03	20.58
shape_cv	128.17	1.39E+03	580.06	100.54	4.03
shape_mn	0.00	0.05	0.00	0.00	1.83
shape_sd	0.00	0.04	0.01	0.00	3.47
shdi	0.00	1.92	0.88	0.27	2.28
shei	0.00	0.99	0.43	0.13	2.38
sidi	0.00	0.83	0.47	0.15	2.14
siei	0.00	0.99	0.54	0.17	2.16
split	1.00	61.38	2.23	0.97	0.87
ta	0.00	0.00	0.00	0.00	31.52
tca	0.00	0.00	0.00	0.00	20.39
te	0.00	5.45	1.47	0.60	1.88

Table 6.2 Landscape metrics' variability and the consistency in variability, across all landscapes (N= 680).

Landscape-level metric	**Summary Statistics**			
	Median Coefficient of variation (CV)	Average CV	Standard Deviation (SD)	Coefficient of Quartile Deviation (CQD)
ai	0.01*	0.01	0.00	0.44 t
area_cv	0.14	0.15	0.08	0.36 t
area_mn	0.22	0.40	0.75	0.37 t
area_sd	0.22	0.28	0.28	0.44 t
cai_cv	0.07*	0.08	0.03	0.23 t
cai_mn	0.09*	0.11	0.06	0.23 t
cai_sd	0.03*	0.04	0.02	0.26 t
circle_cv	0.03*	0.03	0.01	0.21 t
circle_mn	0.02*	0.02	0.01	0.20 t
circle_sd	0.03*	0.04	0.02	0.21 t
cohesion	0.00*	0.00	0.00	0.57
condent	0.15	0.21	0.18	0.46 t
contag	0.04*	0.05	0.03	0.45 t
contig_cv	0.06*	0.06	0.03	0.23 t
contig_mn	0.04*	0.05	0.02	0.21 t
contig_sd	0.03*	0.03	0.02	0.24 t
core_cv	0.14	0.15	0.08	0.35 t
core_mn	0.24	0.41	0.77	0.38 t
core_sd	0.23	0.28	0.29	0.45 t
dcad	0.23	0.28	0.21	0.38 t
dcore_cv	0.16	0.18	0.09	0.32 t
dcore_mn	0.06*	0.06	0.02	0.19 t
dcore_sd	0.17	0.19	0.09	0.30 t
division	0.16	0.22	0.23	0.53
ed	0.17	0.23	0.20	0.45 t
enn_cv	0.14	0.15	0.05	0.20 t
enn_mn	0.17	0.20	0.12	0.30 t
enn_sd	0.23	0.25	0.10	0.21 t
ent	0.12	0.17	0.16	0.48 t
frac_cv	0.05*	0.06	0.03	0.28 t
frac_mn	0.00*	0.00	0.00	0.22 t
frac_sd	0.05*	0.06	0.03	0.29 t
gyrate_cv	0.06*	0.07	0.03	0.30 t
gyrate_mn	0.10*	0.17	0.36	0.28 t
gyrate_sd	0.11	0.14	0.14	0.32 t
iji	0.10*	0.12	0.08	0.32 t
joinent	0.13	0.17	0.16	0.48 t
lpi	0.15	0.18	0.14	0.61
lsi	0.15	0.19	0.14	0.45 t

mesh	0.24	0.27	0.20	0.55
msidi	0.18	0.25	0.25	0.52
msiei	0.17	0.25	0.24	0.51
mutinf	0.12	0.16	0.16	0.49[t]
ndca	0.23	0.28	0.21	0.38[t]
np	0.23	0.29	0.21	0.36[t]
pafrac	0.01*****	0.01	0.01	0.29[t]
para_cv	0.05*****	0.05	0.02	0.23[t]
para_mn	0.05*****	0.06	0.03	0.25[t]
para_sd	0.03*****	0.04	0.02	0.23[t]
pd	0.23	0.29	0.21	0.36[t]
pladj	0.01*****	0.01	0.00	0.44[t]
pr	0.08*****	0.09	0.04	0.26[t]
prd	0.08*****	0.09	0.04	0.26[t]
relmutinf	0.02*****	0.02	0.01	0.35[t]
shape_cv	0.13	0.13	0.07	0.36[t]
shape_mn	0.11	0.15	0.23	0.26[t]
shape_sd	0.14	0.15	0.07	0.31[t]
shdi	0.12	0.17	0.16	0.48[t]
shei	0.12	0.16	0.15	0.46[t]
sidi	0.13	0.19	0.20	0.58
siei	0.12	0.19	0.20	0.58
split	0.31	0.38	0.30	0.59
ta	0.00*****	0.00	0.00	0.53
tca	0.02*****	0.02	0.01	0.44[t]
te	0.17	0.23	0.20	0.45[t]

***** Metrics with a median CV less than 0.1 are considered low variability, on aggregate
[t] Metrics with a Coefficient of Quartile Deviation (CQD) less than 0.5 are considered consistent in their variability across landscapes.

Table 6.3 Landscape metrics arranged according to how often they were best predicted by different frequency distribution types (N= 680).

Landscape-level metric	**Distribution Type**							
	Binomial	Gamma	Gaussian	Inverse gaussian	Negative binomial	Poisson	Tweedie	% Fit
ai	-	-	-	680	-	-	-	*100*
area_cv	-	-	-	679	1	-	-	*100*
area_mn	-	-	3	-	-	-	-	*0.44*
area_sd	-	-	54	2	-	-	1	*8.38*
cai_cv	-	-	-	679	1	-	-	*100*
cai_mn	-	-	-	680	-	-	-	*100*
cai_sd	-	-	-	679	1	-	-	*100*
circle_cv	-	-	-	679	1	-	-	*100*
circle_mn	-	-	680	-	-	-	-	*100*
circle_sd	-	-	680	-	-	-	-	*100*
cohesion	-	-	-	680	-	-	-	*100*
condent	-	-	680	-	-	-	-	*100*
contag	-	-	-	679	1	-	-	*100*
contig_cv	-	-	-	680	-	-	-	*100*
contig_mn	-	-	673	-	7	-	-	*100*
contig_sd	-	-	680	-	-	-	-	*100*
core_cv	-	-	-	680	-	-	-	*100*
core_mn	-	-	3	-	-	-	-	*0.44*
core_sd	-	-	55	2	-	-	1	*8.53*
dcad	-	-	-	678	-	2	-	*100*
dcore_cv	-	-	-	676	4	-	-	*100*
dcore_mn	-	-	3	-	677	-	-	*100*
dcore_sd	-	-	2	33	645	-	-	*100*
division	-	-	375	-	305	-	-	*100*
ed	-	-	-	674	5	1	-	*100*
enn_cv	-	-	-	676	3	-	-	*99.85*
enn_mn	-	-	678	-	-	1	-	*99.85*
enn_sd	1	-	677	-	-	-	-	*99.71*
ent	-	-	67	180	433	-	-	*100*
frac_cv	-	-	-	680	-	-	-	*100*
frac_mn	-	-	3	-	677	-	-	*100*
frac_sd	-	-	680	-	-	-	-	*100*
gyrate_cv	-	-	-	680	-	-	-	*100*
gyrate_mn	-	-	680	-	-	-	-	*100*
gyrate_sd	-	-	680	-	-	-	-	*100*
iji	-	-	-	679	1	-	-	*100*

joinent	-	-	48	317	315	-	-	*100*
lpi	-	-	-	680	-	-	-	*100*
lsi	-	-	-	678	2	-	-	*100*
mesh	18	1	595	-	-	-	-	*90.2 9*
msidi	-	-	312	-	368	-	-	*100*
msiei	-	-	664	-	16	-	-	*100*
mutinf	-	-	105	44	530	-	1	*100*
ndca	-	-	-	680	-	-	-	*100*
np	-	-	-	679	1	-	-	*100*
pafrac	-	-	-	2	678	-	-	*100*
para_cv	-	-	-	680	-	-	-	*100*
para_mn	-	-	-	679	1	-	-	*100*
para_sd	-	-	-	679	1	-	-	*100*
pd	-	-	-	678	-	2	-	*100*
pladj	-	-	-	680	-	-	-	*100*
pr	2	-	-	185	493	-	-	*100*
prd	-	-	-	381	297	2	-	*100*
relmutinf	-	-	4	-	676	-	-	*100*
shape_cv	-	-	-	679	1	-	-	*100*
shape_mn	-	-	680	-	-	-	-	*100*
shape_sd	-	-	680	-	-	-	-	*100*
shdi	-	-	141	6	533	-	-	*100*
shei	-	-	599	-	81	-	-	*100*
sidi	-	-	562	-	118	-	-	*100*
siei	-	-	450	-	230	-	-	*100*
split	-	-	-	500	180	-	-	*100*
ta	-	-	-	-	-	-	-	*0*
tca	114	-	260	-	-	-	-	*55*
te	-	-	49	348	283	-	-	*100*

Table 6.4 Landscape metrics according to their model fit, derived from the lowest Bayesian Information Criterion value per the Generalised Linear Models for all landscapes (N= 680). Studentized residuals are computed at a >=1.96 threshold.

Landscape-level metric	**Best-fit Function Types**							
	CDF Link	Log	Identity	Inverse -power	Inverse-squared	Power	%fit	Average % obs. as studentized residuals
ai	-	72	-	4	297	11	*56*	*1.50*
area_cv	-	361	-	-	204	-	*83*	*14.29**
area_mn	-	1	1	-	-	1	*0*	*3.44*
area_sd	-	2	22	-	2	2	*4*	*3.60*
cai_cv	-	119	-	3	165	-	*42*	*2.60*
cai_mn	-	187	-	-	115	-	*44*	*2.96*
cai_sd	-	147	-	1	168	-	*46*	*2.16*
circle_cv	-	94	-	5	135	-	*34*	*2.20*
circle_mn	-	30	146	145	-	-	*47*	*2.41*
circle_sd	-	127	114	59	-	3	*45*	*2.39*
cohesion	-	28	-	8	281	32	*51*	*1.36*
condent	-	78	131	165	-	4	*56*	*3.06*
contag	-	184	-	1	145	-	*49*	*1.89*
contig_cv	-	77	-	5	138	1	*33*	*2.15*
contig_mn	-	46	145	82	-	1	*40*	*2.87*
contig_sd	-	59	62	28	-	-	*22*	*2.11*
core_cv	-	363	-	-	200	-	*83*	*14.63**
core_mn	-	1	1	-	-	1	*0*	*3.44*
core_sd	-	2	22	-	2	2	*4*	*3.66*
dcad	-	106	-	13	230	-	*51*	*3.65*
dcore_cv	-	248	-	-	114	-	*53*	*10.21**
dcore_mn	-	20	82	53	-	2	*23*	*2.55*
dcore_sd	-	99	29	49	39	1	*32*	*3.55*
division	-	51	180	142	-	6	*56*	*2.31*
ed	-	184	1	11	212	-	*60*	*6.26**
enn_cv	-	256	-	-	84	-	*50*	*10.94**
enn_mn	-	51	113	72	1	10	*36*	*2.81*
enn_sd	-	34	82	79	-	8	*30*	*3.05*
ent	-	105	57	46	166	2	*55*	*2.84*
frac_cv	-	173	-	1	122	-	*44*	*2.45*
frac_mn	-	126	73	62	2	-	*39*	*2.16*
frac_sd	-	113	158	30	-	5	*45*	*2.53*
gyrate_cv	-	212	-	2	135	1	*51*	*3.90*
gyrate_mn	-	106	135	51	-	6	*44*	*3.04*
gyrate_sd	-	95	200	61	-	6	*53*	*2.50*

iji	-	123	-	11	189	-	*48*	*2.94*
joinent	-	122	37	28	187	6	*56*	*2.98*
lpi	-	231	-	4	159	-	*58*	*3.42*
lsi	-	176	-	16	186	-	*56*	*3.41*
mesh	-	22	312	1	-	12	*51*	*2.42*
msidi	-	65	127	132	39	8	*55*	*2.69*
msiei	-	73	155	135	-	6	*54*	*2.62*
mutinf	-	78	84	65	140	4	*55*	*2.56*
ndca	-	337	-	-	186	-	*77*	*12.08**
np	-	352	-	1	204	-	*82*	*13.38**
pafrac	-	145	-	2	192	2	*50*	*2.75*
para_cv	-	148	-	1	144	-	*43*	*2.81*
para_mn	-	411	-	-	180	1	*87*	*22.51**
para_sd	-	389	-	-	100	1	*72*	*22.78**
pd	-	97	-	21	254	1	*55*	*3.19*
pladj	-	74	-	3	297	13	*57*	*1.51*
pr	-	20	-	5	60	-	*13*	*2.41*
prd	2	32	-	5	93	-	*19*	*7.33*
relmutinf	-	33	166	152	-	1	*52*	*1.75*
shape_cv	-	340	-	-	151	-	*72*	*12.70**
shape_mn	-	96	181	37	-	9	*48*	*2.97*
shape_sd	-	89	204	40	-	11	*51*	*2.74*
shdi	-	64	98	102	107	6	*55*	*2.82*
shei	-	55	138	148	-	3	*51*	*2.62*
sidi	-	63	145	160	-	7	*55*	*2.34*
siei	-	59	157	148	-	6	*54*	*2.22*
split	-	189	-	8	166	1	*54*	*3.35*
tca	-	21	97	1	-	-	*18*	*1.18*
te	-	125	53	35	161	5	*56*	*3.27*

* Metrics with greater than 5% of observations as significant studentized residuals, on average, invalidate the 95% confidence interval of a Student’s t-test.