Impacts of land use on Ugandan rainforest streams:

From fish physiology to ecosystem functioning

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Abstract

The main objective of this PhD thesis is to document impacts of deforestation and agricultural land use on afrotropical streams at the organismal, community, and ecosystem levels. Using a meta-analysis and systematic literature review comparing global distributions of current deforestation, freshwater fish diversity, consumption and trade of freshwater fishes by human populations, and research effort on deforestation impacts on inland waters, I first demonstrate that tropical Africa is the only region of the world that has rapid deforestation, high biodiversity, and a high reliance of human populations on inland waters for income and food security, and yet a low research effort. In the remainder of the dissertation, I present an empirical case study comparing rainforest and agricultural streams in and around Kibale National Park, Uganda. I first quantified alpha and beta diversity of invertebrates in 34 farm and forest stream sites in and around Kibale, and showed that deforestation reduces alpha diversity but increases beta diversity of Kibale streams. I then focused in on one forest-farm stream pair in each of two watersheds in the Kibale region to measure various ecosystem stocks and functions. Farm streams, compared to forested streams, had lower standing stock biomass of invertebrates despite abundant basal resources, as well as higher primary production, slower invertebrate-mediated litter decomposition, and lower secondary production of invertebrates. Finally, I adopted an evolutionary and eco-physiological perspective to examine adaptive divergence in various populations of a cyprinid fish occurring in both forest and farm streams. I asked whether deforestation-associated stream warming influences the metabolism, growth, and top-down trophic interactions of fish populations in farm streams, which was tested using a combination of acclimation experiments, respirometry, a mark-recapture study, and bioenergetics modeling. I

showed that the metabolic costs of warming had little impact on either fish growth or trophic interactions, and that other effects of land use such as changes in predator and prey density have a much stronger impact on energy flow in these food webs. Overall, this thesis demonstrates strong effects of deforestation and agricultural land use on afrotropical streams at different levels of biological organization (organism, community, and ecosystem), but also identifies important knowledge gaps currently limiting the development of a fully global picture of the impacts of deforestation on the structure and function of stream ecosystems.

Résumé

L'objectif principal de cette thèse est de documenter les impacts de la déforestation et de l'utilisation agricole des terres sur les ruisseaux d'Afrique tropicale, aux niveaux de l'individu, de la communauté et de l'écosystème. Dans un premier temps, j'ai effectué une méta-analyse et une revue de littérature systématique comparant les distributions globales de la déforestation actuelle, la diversité de poissons, le commerce et la consommation de poissons d'eau douce par les populations humaines, de même que l'effort de recherche sur les impacts de la déforestation sur les eaux continentales. J'ai ainsi pu démontrer que l'Afrique tropicale est la seule région au monde qui présente une déforestation rapide, une forte biodiversité et où les populations humaines dépendent grandement des eaux continentales en termes de revenu monétaire et de sécurité alimentaire, avec pourtant un faible effort de recherche. Dans les autres chapitres de cette thèse, je présente une étude de cas comparant les ruisseaux de milieux agricoles et de forêts tropicales humides situés au sein, ou près, du parc national de Kibale, Ouganda. J'ai d'abord quantifié la diversité alpha et bêta des invertébrés dans 34 ruisseaux de fermes et forêts à l'intérieur ou aux alentours de Kibale, ce qui m'a permis de montrer que la déforestation réduit la diversité alpha, mais augmente la diversité bêta des ruisseaux de Kibale. Par la suite, j'ai focalisé sur une paire de ruisseaux forêt-ferme dans deux bassins versants de la région de Kibale afin de mesurer divers lots ('stocks') et fonctions écosystémiques. Comparativement aux ruisseaux de forêt, les ruisseaux agricoles avaient une biomasse d'invertébrés plus faible, malgré les ressources de base abondantes, ainsi qu'une plus grande production primaire, une décomposition plus lente par les invertébrés et une plus faible production secondaire d'invertébrés. Finalement, j'ai adopté une perspective évolutive et écophysiologique pour examiner la divergence

adaptative de plusieurs populations de poissons cyprin présents dans les ruisseaux de ferme et de forêt. J'ai cherché à savoir si le réchauffement des ruisseaux induit par la déforestation influençait le métabolisme, la croissance et/ou les interactions trophiques de type "top-down" des populations de poissons des ruisseaux de ferme, ce qui a été testé par le biais d'une combinaison d'expériences d'acclimatation, de respirométrie, une étude de marquage-recapture ainsi que de la modélisation bioénergétique. J'ai montré que les coûts métaboliques du réchauffement avaient un faible impact sur la croissance des poissons et sur les interactions trophiques, mais que les autres effets liés à l'utilisation des terres, tel un changement dans la densité de prédateurs et de proies, ont un impact bien plus fort sur le flux d'énergie dans ces réseaux trophiques. Dans son ensemble, cette thèse démontre que la déforestation et l'utilisation agricole des terres affectent fortement les ruisseaux afro-tropicaux à différents niveaux d'organisation biologique (organisme, communauté et écosystème), tout en identifiant d'importantes lacunes dans nos connaissances limitant actuellement notre possibilité d'atteindre une compréhension réelement globale des impacts de la déforestation sur la structure et le fonctionnement des écosytèmes de ruisseaux.

Preface

Thesis format

This thesis is written in a manuscript-based format. Chapters 1 to 4 consist of a set of four manuscripts that were or will be submitted for publication in peer-reviewed journals, on which I am the lead author. For Chapters 2 to 4, short prefaces (i.e., linking statements) are included to review the main findings of the previous chapter that led to the key questions explored in the coming chapter. Appendices at the end of thesis provide supplementary information included as online-only material in the manuscripts submitted to peer-reviewed journals. The referencing style of all chapters follows the scientific journal *Ecological Applications*.

<u>Chapter 1</u>: Fugère, V., Nyboer, E. A., Bleecker, J. C. and Chapman, L. J. (in revision). Impacts of forest loss on inland waters: A global mismatch among deforestation rates, ecosystem services, and research effort. *Biological Conservation*.

<u>Chapter 2</u>: Fugère, V., Kasangaki, A. and Chapman, L. J. (in press). Land use changes in an afrotropical biodiversity hotspot affect stream alpha and beta diversity. *Ecosphere*.

<u>Chapter 3</u>: Fugère, V., Jacobsen, D., Finestone, E. H. and Chapman, L. J. (in preparation for *Freshwater Biology*). Deforestation alters stream ecosystem structure and function around an afrotropical rainforest.

<u>Chapter 4</u>: Fugère, V., Mehner, T. and Chapman, L. J. (in preparation for *Functional Ecology*). Impacts of deforestation-induced warming on the growth and trophic interactions of a stream fish: do increased metabolic costs matter in nature?

Contribution of authors

For all manuscripts included in this thesis, I was the main person in charge of hypothesis development, data analysis, and manuscript writing. Therefore, this thesis is primarily the product of my own work. However, all manuscripts benefited greatly from the guidance and logistical support that I received from my advisor, Lauren Chapman. A number of other collaborators also contributed ideas, data, or major feedback, and are thus included as co-author on specific manuscripts. Skilled Ugandan personnel employed by the Kibale Fish and Monkey Project, coordinated by Lauren and Colin Chapman, contributed to data collection in and around Kibale National Park.

<u>Chapter 1</u>: This manuscript is co-authored with Elizabeth Nyboer, Johanna Bleecker, and Lauren Chapman. Elizabeth Nyboer is a PhD student in Lauren Chapman's laboratory. She read and sorted abstracts for the systematic literature review and provided comments on multiple versions of the manuscript. Johanna Bleecker was a research assistant in Lauren Chapman's laboratory. She produced the first version of the maps included in the manuscript. Lauren Chapman assisted with manuscript development. I conceived of the project, gathered data on online databases, conducted all statistical analyses, made final versions of the figures, and wrote the manuscript. <u>Chapter 2</u>: This manuscript is co-authored with Aventino Kasangaki and Lauren Chapman. Aventino Kasangaki was responsible for field sampling and later identification of invertebrates. Lauren Chapman designed and coordinated the sampling campaign, and contributed to manuscript development. I generated the theoretical context for the manuscript, conducted all analyses, and wrote the manuscript.

<u>Chapter 3</u>: This manuscript will be co-authored with Dean Jacobsen, Erin Finestone, and Lauren Chapman. Dean Jacobsen served as my host during a research stay at the University of Copenhagen, where I identified invertebrate samples and developed a functional feeding group classification under his supervision. He also provided advice on analytical approaches, study design, and manuscript preparation. Erin Finestone was an undergraduate student in Lauren Chapman's laboratory working under my supervision. She contributed valuable laboratory assistance and ideas regarding laboratory protocols. Lauren Chapman contributed to manuscript development and provided essential logistical support for both the field and laboratory components of the project. I conceived of the project, developed sampling methodology, collected all field data with the help of field assistants employed by Lauren Chapman, conducted all analyses, and wrote the manuscript.

<u>Chapter 4</u>: This manuscript will be co-authored with Thomas Mehner and Lauren Chapman. Thomas Mehner served as my host during a research stay at the Leibniz Institute of Freshwater Ecology and Inland Fisheries. He offered guidance on bioenergetics modeling, as well as advice on data analysis and interpretation. He also contributed to manuscript preparation and provided comments on previous versions of the manuscript. Lauren Chapman contributed to manuscript development, offered advice on study design and analytical approaches, and provided essential logistical support for both the field and laboratory components of the project. I conceived of the research project, developed sampling methodology and experimental procedures, collected all field and laboratory data, conducted all analyses, and wrote the manuscript.

Statement of originality

This thesis takes a highly integrative approach blending meta-analyses, field survey, field and laboratory experiments, and bioenergetics modeling to explore the impacts of deforestation on afrotropical streams across multiple levels of biological organization, from organismal physiology to community interactions, biodiversity, and ecosystem functioning.

Chapter 1 provides the first systematic (quantitative) review of the literature on deforestation impacts on freshwater ecosystems, as well as the first combined analysis of global datasets (collected from various sources) on countries' deforestation rates, fish biodiversity, water scarcity, trade value of inland fisheries, and consumption of freshwater fish. This analysis allowed me to conclude with quantitative support that impacts of deforestation on afrotropical inland waters are understudied despite being (most likely) strong, such that future research on terrestrial-aquatic linkages should focus on this region.

In Chapter 2, I provide one of the rare descriptions of land use impacts on stream water chemistry and invertebrate communities in the afrotropics; such information is essential for river conservation and management but is only available for a very limited number of other afrotropical sites (Benstead et al. 2003, Masese et al. 2014b, Wronski et al. 2015). This chapter also contributes one of the few (and the first tropical) recent case studies of land use impacts on stream beta diversity, a topic currently widely discussed in the stream community ecology literature (Johnson and Angeler 2014, Hawkins et al. 2015). To my knowledge, this study is also the first to apply to stream communities new (recently published) statistical methods that decompose beta diversity into richness differences and taxa replacement among sites (Podani and Schmera 2011, Podani et al. 2013, Legendre 2014). This analysis reaches the controversial conclusion that deforestation increases among-stream beta diversity, which is likely to stimulate much future research and discussion.

Chapter 3 constitutes one of two existing studies investigating land use impacts on afrotropical stream ecosystem functioning (the other being Masese et al. 2014a). In this chapter, I also provide the first estimates of whole-stream metabolism and invertebrate secondary production for the afrotropics. Yet another novel aspect of this study is its comprehensive characterization of land use impacts on stream functioning, quantifying effects on ecosystem stocks, litter decomposition rates, whole-stream metabolism, and secondary production of invertebrates within the same streams, in a single study.

Chapter 4 is, to my knowledge, one of two existing studies testing for contemporary adaptation to deforested conditions in a stream fish (the other being Schwartz and Hendry 2010). Chapter 4 is also unusually integrative among ecophysiological studies investigating responses of ectotherms to global change, in that it documents impacts of warming not only on metabolic and growth rates, but also on prey production and consequently trophic interactions. This highly integrative approach, combining multiple methods from all of evolutionary ecology, ecophysiology, and community and ecosystem ecology, allowed me to demonstrate that several degrees of environmental warming can have strong impacts on metabolic and growth rates of ectotherms in the laboratory, but that effects in nature can be much more modest and relatively weak compared to effects of habitat degradation. This conclusion is likely to be controversial and thus of strong interest to a large community of ecologists and physiologists studying global change.

Ethics statement

All research included in this thesis was conducted following approval of the Uganda National Council for Science and Technology, the Uganda Wildlife Authority, and the Animal Care and Use Committee of McGill University. The Ugandan Commissioner for Fisheries approved export of fish samples from Uganda.

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I would like to thank first and foremost my advisor, Lauren Chapman, for her steady support and encouragement throughout my entire graduate studies, first as a member of my M.Sc. supervisory committee, and then as my Ph.D. advisor over the past five years. I am especially grateful for her enthusiasm, patience, and generosity, as well as for all the inspiring conversations that we had, for helping me develop the ideas contained within this thesis, for essential logistical and financial support, and for providing me with the opportunity to complete several trips to Uganda, which were truly life changing experiences. The work contained in this thesis relied heavily on Lauren's incredible knowledge of Uganda and its inland waters, as well as on her connections and long-term field projects in Kibale. Lauren, thank you for everything, working under your supervision was an absolute pleasure. I would also like to extend my gratitude to all of my collaborators and previous academic mentors, who provided me with endless advice, support, and, most importantly, encouragement and kind words that helped me develop my confidence as a scientist. Special thanks to Ed Ruthazer and Rüdiger Krahe, my

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Introduction

Lotic ecosystems (henceforth 'streams') harbor a large fraction of global aquatic biodiversity and provide essential ecosystem services for human well-being, but they are also among the most threatened of all ecosystems (Sala et al. 2000, Dudgeon et al. 2006, Vörösmarty et al. 2010). Streams are affected by several anthropogenic disturbances such as dam construction, water extraction, invasive species, global climate change, over-exploitation of harvested species, and anthropogenic land use/land cover changes (Malmqvist and Rundle 2002, Allan et al. 2005, Dudgeon et al. 2006, Strayer and Dudgeon 2010, Vörösmarty et al. 2010). The latter, whereby natural land cover within watersheds (e.g., forests) is converted to human-altered landscapes such as pastures, agricultural fields, or urban areas, is a particularly pervasive and widespread threat to stream ecosystems (Vörösmarty et al. 2010). Terrestrial and aquatic ecosystems are strongly linked, such that land cover modifications induce profound biotic and abiotic changes in streams draining that land (Likens and Bormann 1974, Naiman and Décamps 1997, Allan 2004).

This thesis focuses on the response of streams to one particular type of land cover change, namely the conversion of tropical rainforests to pastures and agricultural fields. Deforestation and agricultural expansion are still proceeding at alarming rates in many regions of the world (FAO 2010). For example, a recent analysis of satellite imagery data revealed that between the years 2000 and 2012, a total of 2.3 million km² of forest was lost globally (Hansen et al. 2013). With the global human population expected to reach 11 billion by the end of the century, it is very unlikely that rates of forest conversion will slow down in the near future. Tilman et al. (2001) calculated rates of agricultural expansion during the second half of the 20th

century as the global human population was expanding to 7 billion, and then extrapolated these rates over the next half-century to predict the amount of land that will be required to sustain global food production in 2050. They concluded that an additional 1 billion hectares of natural ecosystems have to be converted to agriculture by 2050, which is an area roughly the size of Canada. A large fraction of this new agricultural land will certainly come from forest conversion at tropical latitudes. Indeed, future agricultural expansion is expected to occur mainly in the large areas of land with unexploited agricultural potential in South America and Sub-Saharan Africa (Laurance et al. 2014), and agricultural expansion in the tropics is usually achieved via clearing of intact forests (Gibbs et al. 2010). Large-scale tropical deforestation will have important effects on stream ecosystems: already in the late 1990s, when rates of tropical deforestation were lower at the global scale than they are today, Benstead et al. (2003) estimated that *ca*. 500 000 km of stream channel per year were affected by tropical deforestation.

Our understanding of the impacts of deforestation and agricultural expansion on stream ecosystems comes primarily from research conducted in temperate areas. Over the past 50 years, a large number of field surveys in North America, Europe, Australia, and New Zealand have documented differences between forested and agricultural streams in terms of water chemistry, hydrology, geomorphology, and/or biological assemblages (reviewed by Allan 2004). These surveys have revealed that deforestation and agriculture usually lead to higher sediment loads, less stable flow regimes, nutrient enrichment, increased irradiance and water temperature, pollution by various contaminants, a loss of large woody debris, and a reduction in inputs of allochthonous (terrestrial) detritus, an important food source in headwater streams (Hynes 1963, Allan 2004). These changes in the stream abiotic environment have such profound and welldocumented effects on stream biological communities that many countries have national biomonitoring programs measuring stream water quality based on community composition of algae, invertebrates, and/or fishes (e.g., Barbour et al. 1999). Impacts on stream macroinvertebrates (invertebrates larger than 500 µm) have been especially well studied, with agricultural land use usually leading to a loss of many taxa that are sensitive to habitat degradation (elevated water temperature, benthic siltation, etc.), for example mayflies (Ephemeroptera), stoneflies (Plecoptera), and caddisflies (Trichoptera; for more information, see Rosenberg and Resh 1993, Carter et al. 2011, and references therein). Loss of these sensitive taxa often leads to lower species richness and alpha diversity in agricultural streams than in forest streams, as well as changes in the relative representation of various invertebrate trophic guilds, referred to as 'functional feeding groups' (Cummins 1973, 1974).

Agricultural land use can also have dramatic effects on stream ecosystem functioning (i.e., material and energy flow within stream ecosystems). The 'River Continuum Concept', a very influential model of lotic ecosystems developed 35 years ago, suggests that low order streams (headwaters) are net heterotrophic, deriving most of their carbon from allochthonous (terrestrial, detrital) sources rather than in-stream photosynthesis (Vannote et al. 1980). The loss of riparian vegetation reduces those terrestrial carbon inputs, but at the same time canopy clearance increases the amount of photosynthetically active radiation reaching the stream surface, thus allowing for greater in-stream primary production by periphytic algae. This can lead to a switch from heterotrophy to autotrophy (and consequently a shift from detritus-based to periphyton-based food webs), with associated changes in consumer communities (e.g., Benstead and Pringle 2004, Hladyz et al. 2011). Studies confirming impacts of agricultural land use on stream ecosystem functioning became commonplace in the literature in the late 1990s (although some pioneering studies were conducted much earlier, e.g., Haefner and Wallace 1981), focusing

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on important ecosystem functions such as leaf litter decomposition, whole-stream metabolic parameters (primary production, community respiration, and the ratio between the two), and secondary production of macroinvertebrates (e.g., Bunn et al. 1999, Young and Huryn 1999). This then led several authors to suggest that biomonitoring programs should include functional indicators in conjunction with structural indicators (e.g., community composition) to get a more complete assessment of stream integrity (Gessner and Chauvet 2002, Young et al. 2008), which motivated a large number of recent studies on stream functional responses to land use (e.g., Clapcott et al. 2010, Hladyz et al. 2011, Clapcott et al. 2012, Silva-Junior et al. 2014). Finally, several large-scale stream manipulations confirmed experimentally that key variables influenced by riparian deforestation (e.g., water temperature, leaf litter inputs, presence of woody debris, or nutrient concentrations) have important effects on stream ecosystem functioning (Hogg and Williams 1996, Wallace et al. 1997, Nakano et al. 1999, Wright and Flecker 2004, Benstead et al. 2009, Piggott et al. 2015a, Rosemond et al. 2015, Wallace et al. 2015).

Despite significant improvements over the years in our understanding of land use impacts on stream ecosystems, several important gaps remain in the literature. One of those gaps is geographical: many stream ecologists working in tropical countries argue that much less is known about the ecology of tropical than temperate streams, including information on how streams respond to major anthropogenic disturbances such as land use (e.g., Dudgeon 2008 and most contributions therein). Because of important differences in stream communities and functional organization across latitudes (e.g., Boyero et al. 2011a), temperate-derived models of stream response to deforestation might not transfer well to tropical streams, such that the relative lack of information on tropical streams constitutes a major hindrance to freshwater management in what is paradoxically the area of the world experiencing the fastest rates of deforestation and agricultural expansion, as described above. This geographical bias seems especially severe for tropical Africa. For example, in a book chapter reviewing impacts of deforestation on African inland waters, Chapman and Chapman (2003) wrote: 'The paucity of African studies cited in this chapter clearly illustrates that more research is needed to determine the impacts that various forms of human modification to terrestrial habitats will have on African aquatic systems' (p. 242). In another book chapter reviewing studies on tropical stream invertebrates, four wellknown stream ecologists concluded the following: 'While there are manifest benefits to be gained from improving our knowledge of stream macroinvertebrates and their ecology throughout the tropics, in the prevailing context of limited research funds and resources, there is a compelling case for prioritizing research in Africa' (Jacobsen et al. 2008, p. 96). Even basic information on stream ecosystem functioning is lacking for the afrotropics. For example, secondary production of invertebrates and whole-stream metabolic parameters (e.g., primary production and community respiration), which are among the most routinely measured stream ecosystem functions and which are even included in national biomonitoring programs in some countries, have, to my knowledge, never been measured in an afrotropical stream. As such, influential reviews and meta-analyses describing variables that influence these ecosystem functions do not list a single study from the afrotropics (e.g., Davies et al. 2008, Jacobsen et al. 2008, Benke and Huryn 2010, Tank et al. 2010, Finlay 2011).

A second important knowledge gap stems from the traditional focus of stream biodiversity studies on alpha (local) diversity, largely ignoring other aspects of biodiversity such as beta, functional, or phylogenetic diversity until recently (e.g., Poff et al. 2006). Land use impacts on beta diversity, or site variation in community composition over a landscape (Whittaker 1960, 1972), have started to garner much attention in the stream ecology literature in the past few years (Passy and Blanchet 2007, Gutiérrez-Cánovas et al. 2013, Astorga et al. 2014, Bini et al. 2014, Johnson and Angeler 2014, Larsen and Ormerod 2014, Hawkins et al. 2015, Heino et al. 2015). This is due in part to the recent development of multivariate statistical methods allowing for a more standardized quantification of beta diversity (Anderson et al. 2006, Anderson et al. 2011). However, one important factor that still limits our understanding of land use impacts on stream beta diversity is the methodological difficulties associated with distinguishing between the two main components of beta diversity, namely species replacement, or substitution of species between sites, and richness differences caused by species gain and loss, also known as community nestedness (Wright and Reeves 1992, Baselga 2010, Anderson et al. 2011, Podani and Schmera 2011). Distinguishing between these two components of beta diversity is necessary to ensure that different studies compare the same source of site variation in community composition, but also to inform conservation planning (Wright and Reeves 1992). For example, if stream beta diversity within a natural landscape (e.g., a forest) is dominated by taxa replacement, then deforestation of only a small area might lead to species loss at the regional scale (i.e., lower gamma diversity). In contrast, if richness differences underlie a large fraction of among-stream beta diversity in the forest, then ensuring that a few species-rich streams remain forested should be sufficient to conserve the regional pool of forest species (Angeler 2013, Gutiérrez-Cánovas et al. 2013). Novel statistical methods that partition total beta diversity into taxa replacement and richness differences among sites have just recently been published (Podani and Schmera 2011, Podani et al. 2013, Legendre 2014), and applying these methods should allow a much better characterization of stream beta diversity and its response to deforestation and agricultural expansion.

A third important aspect of land use impacts on stream ecosystems that remains largely unexplored is effects on the evolutionary and physiological ecology of individual species, at the organismal level. For example, it is now widely recognized that anthropogenic disturbances can induce rapid phenotypic change in many species by altering local fitness landscapes, leading to adaptive trait divergence between populations living in natural vs. human-altered environments (Palumbi 2001, Hendry et al. 2008, Darimont et al. 2009). Severe changes in the stream environment linked to land use should place strong selective pressures on stream organisms, yet the potential for such deforestation-induced evolution in aquatic taxa remains virtually unstudied (but see Smith et al. 2008 for a terrestrial example). For example, I know of only one study asking whether stream fishes can adapt to riparian deforestation, which linked changes in guppy nuptial coloration to land use-induced variation in water turbidity and light levels (Schwartz and Hendry 2010). In addition to evolutionary change, land use-associated modification of stream habitats could also trigger acute physiological effects in stream organisms. For example, at tropical latitudes, deforestation can lead to an increase of several degrees in mean stream water temperature (e.g., Macedo et al. 2013, Masese et al. 2014a). Such warming should have profound impacts on the energetics of ectothermic organisms living in deforested streams; for example if we assume a standard Q_{10} of 2.4 for the resting metabolic rate of fishes (Clarke and Johnston 1999, Clarke 2004), stream warming of 4 degrees (Macedo et al. 2013) would lead to roughly 1.4 times greater energy requirements just to sustain the basic costs of metabolism. Such increases in metabolic costs may not only impact the fitness of ectotherms living in deforested streams, it could also influence their consumption/energy intake and, by extension, their top-down effects on lower trophic levels in stream food webs. Effects of environmental warming on the metabolism, growth, and trophic interactions of ectotherms have recently been the focus of

intensive research in the literature on global climate change (e.g., Hoekman 2010, Eliason et al. 2011, Vucic-Pestic et al. 2011, Kratina et al. 2012, Shurin et al. 2012, Barneche et al. 2014, Gilbert et al. 2014, Robertsen et al. 2014, Rummer et al. 2014, Sandblom et al. 2014, Sentis et al. 2015) but these questions remain to be explored in the context of land use-associated stream warming.

In this thesis, I address some of the key knowledge gaps outlined above by documenting impacts of deforestation and agricultural land use on afrotropical streams. In Chapter 1, I use a meta-analytical approach to confirm quantitatively that land use impacts on streams are indeed poorly studied in tropical relative to temperate areas. I identify critical areas for future research on terrestrial-aquatic linkages by mapping the global distribution of both past research effort as well as relative research need, the latter estimated from rates of recent deforestation, aquatic biodiversity, and freshwater ecosystem services. In the remainder of the thesis, I use an empirical case study approach comparing forested and agricultural streams located in and around an afrotropical rainforest (Kibale National Park, Uganda) to quantitatively explore the impacts of deforestation on afrotropical streams across multiple levels of biological organization, from organismal physiology to community interactions, biodiversity, and ecosystem functioning. In Chapter 2, I compare the environmental parameters, invertebrate community composition, alpha diversity, and beta diversity of 34 farm and forest stream sites in the Kibale region. I employ new methods of beta diversity decomposition to uncover which component of beta diversity is affected by land use. In Chapter 3, I measure several ecosystem stocks and functions in both forested and deforested streams, and by doing so provide the first estimates of whole-stream metabolism and invertebrate secondary production calculated in the afrotropics. In my final chapter, I then adopt an evolutionary and eco-physiological perspective to investigate impacts of

stream warming on a species of fish occurring in both forested and deforested streams. I combine acclimation experiments, respirometry, a mark-recapture study, and bioenergetics modeling to quantify impacts of warming-associated increases in metabolic rate on the growth and top-down trophic interactions of those fish. I also compare those metabolic impacts with temperature-unrelated effects of land use on fish-invertebrate interactions to assess the relative importance of warming in determining trophic interactions in human-altered food webs. Finally, I conclude the thesis by reviewing major empirical findings from each chapter, and then suggest promising avenues for future research to expand on those findings.

Impacts of forest loss on inland waters: A global mismatch among deforestation rates, ecosystem services, and research effort

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1.1 Abstract

Deforestation is a major threat to global aquatic biodiversity and ecosystem services. Regional studies are needed to understand and mitigate impacts of deforestation on local inland waters, yet such studies remain unavailable in many regions of the world where the risks of impact are high, for example in the tropics. Our goal was to identify such understudied regions by quantifying and mapping the global research need and effort on deforestation impacts on inland waters. We defined research need based on countries' deforestation rate, fish diversity, and vulnerability of human populations to freshwater ecosystem degradation, the latter estimated from water scarcity and consumption and trade of local freshwater fish. We quantified research effort by reviewing 1347 publications on deforestation and freshwater ecosystems, thereby providing the first quantitative literature review on this important conservation problem. We found that tropical countries exhibited strong overlap among deforestation, freshwater fish diversity, and vulnerability of human populations to freshwater ecosystem degradation, and therefore have high research need relative to temperate regions. However, we found that the best predictor of research effort on deforestation and aquatic systems was the size of a country's economy (indicated by gross domestic product), not research need. Finally, we uncovered a strong research bias against tropical Africa, the only extensive region of the world that has a high research need and a low research effort. This global analysis suggests that future research effort on deforestation impacts on inland waters should try to alleviate existing biases by increasing interregional cooperation and transfer of research resources to regions of high research need and/or low research effort, with a particular focus on the critical research zone that is tropical Africa.

1.2 Introduction

Inland waters are among the most threatened of all ecosystems (Sala et al. 2000, Millennium Ecosystem Assessment 2005, Dudgeon et al. 2006, Strayer and Dudgeon 2010). Globally, one of the primary anthropogenic drivers of freshwater ecosystem degradation is land use intensification via deforestation and agricultural expansion (Sala et al. 2000, Dudgeon et al. 2006, Vörösmarty et al. 2010, Collen et al. 2014), which can lead to altered hydrology, increased sediment load, warming, and nutrient enrichment (Allan 2004, Nielsen et al. 2012, Woodward et al. 2014). These impacts not only threaten aquatic biodiversity but also affect many essential ecosystem services provided by freshwater ecosystems, for example fish stocks and provisioning of clean water (Foley et al. 2005, Millennium Ecosystem Assessment 2005, Dugan et al. 2010, WWAP 2015). Although land use impacts on inland waters are relatively well-understood in some watersheds, discrepancies in responses of aquatic systems to deforestation suggests that limnological knowledge is only partially transferable across regions, and thus that studies from a variety of regions are needed (see also Lewis 1987). For instance, even within the tropics, the species richness of fish in tropical rivers from different sites can be increased (Lorion and Kennedy 2009b), reduced (Toham and Teugels 1999), or unaffected (Bojsen and Barriga 2002) by deforestation. Regional studies are thus needed to uncover local impacts of land use on inland waters, as well as to understand potential interactions with other stressors specific to certain regions (e.g., Macedo et al. 2013) or to design optimal management strategies that explicitly consider features of the local landscape (e.g., Iñiguez–Armijos et al. 2014). Despite the need for more regional studies, limited resources evidently restrict the number of watersheds that can be studied. As such, we need to identify critical areas for future research based on a consideration of both current research need and past research effort. Our objective in this study was to detect such areas by identifying regions where deforestation is most likely to cause biodiversity loss and/or affect peoples' livelihoods via aquatic ecosystem degradation (i.e., regions with a high research need), but where little research on land use impacts on inland waters has been conducted (i.e., regions with a low research effort).

We hypothesized that critical research areas are more likely to be located in tropical than temperate regions. Many tropical countries are characterized by rapid deforestation rates, high freshwater biodiversity, and human populations that are strongly reliant on local freshwater ecosystem services. Indeed, in recent years, deforestation has been most intensive and extensive at tropical latitudes (FAO 2010, Hansen et al. 2013), and the tropics are also expected to be hotspots of agricultural intensification and expansion in the near future (Laurance et al. 2014). Studies mapping the biodiversity of freshwater taxa for which global distribution data are available suggest that biodiversity is also greater in the tropics (Abell et al. 2008, Collen et al. 2014), as can be the reliance of human populations on freshwater resources; for example, inland fisheries constitute a much more important source of employment and food for human populations in Latin America, Africa, and Asia than in Europe and North America (Allan et al. 2005, Dugan et al. 2010). Infrastructure for water management is also limited in many tropical countries, and investment in water-related technology to improve human water security is low in most tropical regions with a high population density (Vörösmarty et al. 2010). All of these trends suggest that it is critical to monitor impacts of land use changes on tropical inland waters, and that a large fraction of the global research effort on this conservation problem should target tropical watersheds.

Unfortunately, many bibliometric analyses indicate that research effort in environmental sciences is often determined by economic development rather than by research need (e.g., Pasgaard and Strange 2013). Gross domestic product (GDP) is often the best predictor of the number of research articles published on a given environmental issue in a country (Karlsson et al. 2007, Moustakas and Karakassis 2009, Pasgaard and Strange 2013). As such, less-developed regions tend to receive a smaller fraction of the global research effort on a specific ecological topic. For example, much less research has been conducted on invasive species and climate change in tropical Africa than in other regions of the world (Pyšek et al. 2008, Pasgaard and Strange 2013). Such geographical biases in research effort lead to what has been described as a 'north-south divide' in knowledge availability on ecological issues, whereby 'southern' countries (developing countries of the southern hemisphere) often generate and possess less knowledge about local ecosystems and environmental problems than developed countries in the northern hemisphere (Karlsson et al. 2007). It is likely that research on deforestation and inland waters is

no exception to this pattern, which would be paradoxical given the potentially higher research need in tropical (less-developed) countries, as argued above (see also Ramirez et al. 2008). Surprisingly, to our knowledge no quantitative synthesis of the literature on land use impacts on inland waters has been undertaken, such that it remains unknown whether the geographical distribution of research effort on this problem is indeed biased.

Our study aimed to identify areas that should be prioritized for future research on deforestation impacts on inland waters. We assembled a global database of countries' deforestation rates, freshwater fish diversity, and vulnerability of human populations to freshwater ecosystem degradation, the latter being estimated from the relative reliance on key provisioning services supplied by local inland water ecosystems. Our premise is that countries where those variables overlap strongly have a relatively higher research need. Then, we performed a quantitative literature review on deforestation effects on inland waters to determine predictors of research effort and to identify areas where little research has been conducted. More specifically, our study addressed the following three questions: (1) which countries and/or regions have the strongest overlap among recent deforestation, freshwater fish diversity, and vulnerable human populations? i.e., where is research need highest? (2) Can deforestation rate, freshwater fish diversity, vulnerability of human populations, and/or an indicator of economic development such as GDP predict research effort on effects of deforestation on inland waters? (3) Which countries and/or regions have both a high research need and a low research effort, and should therefore be the focus of future research?

1.3 Materials and methods

1.3.1 Data collection

We combined numerous online databases to obtain country-specific information on rates of recent deforestation, freshwater fish biodiversity, vulnerability of human populations to freshwater ecosystem degradation, and research effort (see Table 1.1 for a description of all variables). We conducted our analysis at the country scale because that was the smallest scale at which inland fisheries data were available for most countries of the world. We first collected basic country information from the Statistics Division of the Food and Agriculture Organization of the United Nations (FAOSTAT; FAO 2013), including total country area, total human population (in 2012), GDP (also in 2012), and GDP per capita (henceforth GDPpc). For rates of recent deforestation, we used two data sources: (1) the 2010 edition of the 'Global Forest Resources Assessment' published by the FAO, which provides forest cover estimates for all countries between 2005 and 2010 (FAO 2010); and (2) an analysis of global Landsat data conducted by Hansen et al. (2013) that reports forest cover change between 2000 and 2012. With both datasets, we calculated relative forest loss as: 1 - (forest cover at the end of the interval \times forest cover at the beginning of the interval⁻¹). Negative values for forest loss represent an increase in forest cover during the interval (due to reforestation, for example). The FAO data are based on official reports from countries that provide information on the area of land allotted to some form of forest land use (parks, tree plantations, etc.). This method can lead to biased estimates of forest cover because of inconsistent land use definitions among countries, inaccurate reporting of land use changes, and because forest land use does not equate to forest cover when land allotted for forest is deforested, e.g., when there is illegal logging or when logging lots are not reforested as planned. The analysis of Landsat data by Hansen et al. (2013) circumvents

these limitations to some degree by employing a biophysical definition of forest cover, i.e., forest is defined as land covered with trees, regardless of how the land is used. However, forest cover can also be altered by natural, periodic perturbations such as fire or insect pest outbreaks. Such natural forest loss may have different effects on aquatic ecosystems than anthropogenic deforestation, which often leads to long-lasting land use change and intensification. Given the different limitations of the two datasets, we included both in our analysis to derive an estimate of relative deforestation based on both land use change and physical reduction in forest cover (Table 1.1).

We quantified freshwater fish biodiversity using fish species checklists available for all countries on Fishbase (Froese and Pauly 2013). We focused our biodiversity analysis on fishes as they appeared to be the freshwater taxon for which global distribution data at the species-level was most accurate and readily available, and because fishes had been used in previous efforts to map global freshwater biodiversity (Abell et al. 2008). We recognize, however, that fish diversity only captures part of the total variation in overall freshwater biodiversity, as was demonstrated recently by Collen et al. (2014). We used two measures of freshwater fish diversity: species richness and the number of endemic species. Both measures were strongly correlated with country area (Pearson's *r* for richness = 0.5397; both correlation coefficients were calculated with untransformed data). To remove the influence of area on fish diversity (as deforestation variables were area-standardized), we performed linear regressions between diversity (richness or number of endemic species) and country area after log-transforming variables. We used the residuals of these linear regressions as our two measures of diversity for all analyses (Table 1.1).

We estimated the vulnerability of human populations to freshwater ecosystem degradation based on the assumption that vulnerability results from a high relative usage of provisioning services delivered by local inland waters. We quantified ecosystem usage based on three provisioning services for which there were sufficient global data: supply of freshwater, and inland fisheries as a source of both protein and income. We assumed that the inhabitants of a country would be relatively more vulnerable to freshwater ecosystem degradation when: (1) water scarcity is high (i.e., when supply of freshwater is limited); (2) freshwater fish contribute an important percentage of animal protein supply in the local diet; and (3) trade of freshwater **fish** constitutes a large fraction of the country's GDP (Table 1.1). Online databases provided by FAOSTAT (FAO 2013) were used to measure all three ecosystem usage variables. Water scarcity was defined as the additive inverse of renewable freshwater supply per capita (m^3 inhabitant⁻¹ year⁻¹), which the FAO calculates for all countries using estimates of average yearly precipitation. For the relative importance of freshwater fish in local **protein supply**, we divided the availability of freshwater fish protein (g capita⁻¹ day⁻¹) by the total availability of animal protein. For trade of freshwater fish, we used estimates of the total export value (in US\$ year⁻¹) of freshwater and diadromous fish (i.e., all species that complete at least part of their life cycle in freshwater) and quantified their relative economic importance by dividing total exports by the country's GDP. Ideally, we would have used the total monetary value of fish production rather than fish exports, but monetary values for production are not provided in FAOSTAT (all fisheries production statistics are in units of mass). The % of GDP comprised of fish exports should be a better indicator of potential negative impacts of ecosystem degradation on people's income than fish production in units of mass, which largely depends on the species of fish that are harvested and which does not necessarily reflect the economic importance of freshwater

fisheries to local livelihoods (Dugan et al. 2010). We included diadromous fish because stocks of many diadromous species can be affected by freshwater habitat degradation (e.g., Bradford and Irvine 2000). We used the most recent year of data provided for all statistics, which ranged from 2009 to 2012 depending on countries and variables.

To estimate research effort, we performed a literature search in 2013 for studies that measured how deforestation affects at least one biotic or abiotic variable in a freshwater ecosystem (either lotic or lentic). We used Web of Science (Thomson Reuters 2013) to find articles in the 'core collection' using the search terms: deforestation OR logging OR clearcut* OR clear-cut* AND lake OR river OR stream OR freshwater OR riparian OR swamp OR marsh OR wetland OR catchment. We used 'logging', 'clear-cut', and 'deforestation' as search terms, because papers from different regions and time periods tend to employ different terms. For example, older papers from North America use 'logging' more often than 'deforestation', while the converse is true for recent papers on tropical countries. Our search yielded 10 396 publications. We read all abstracts and retained 1347 relevant publications from 96 countries spanning the years 1968 to 2012. We only included articles where direct effects of deforestation were used as predictor variables (e.g., loss of canopy cover, sedimentation due to logging activity, etc.), or where explicit spatial (forested vs. deforested) or temporal (before vs. after) comparisons were made. We categorized and tallied papers by country, to obtain the total number of publications per country as our measure of research effort. Articles covering more than one country (e.g., studies on transnational river basins) were included in the publication count of all countries described in the study.

1.3.2 Analyses

All analyses were performed in R version 3.0.2 (R Core Team 2013). We first excluded all countries for which data were missing for one of the target variables: deforestation, fish diversity, or vulnerability, i.e., a few African and Asian countries and most Pacific and Caribbean island countries. We then explored relationships among deforestation, fish diversity, and vulnerability variables to identify redundant variables that could be combined to minimize collinearity in subsequent analyses. All variables were first log-transformed and standardized (mean of zero, unit variance). We then: (1) calculated Pearson's correlation coefficients among all variables, and (2) performed a Principal Components Analysis (PCA) to produce a correlation biplot illustrating correlations among variables. The R package 'vegan' was used for PCA (Oksanen et al. 2013).

Our first objective was to identify countries where deforestation overlaps with both high fish diversity and vulnerability. To that end, we created two new variables: 'forest loss' and 'potential repercussions of ecosystem degradation', hereafter referred to as PRED (Table 1.1). For 'forest loss', we combined both deforestation variables ('Forest loss: FAO' and 'Forest loss: Hansen') to create a single deforestation variable that incorporates both land use changes and forest cover changes (Table 1.1). This was done by calculating the mean of the standardized scores of both deforestation variables, and then re-standardizing the resulting variable. For PRED, we needed to combine vulnerability and fish diversity variables. The two fish diversity variables (richness and endemism) were highly correlated (Pearson's r = 0.79) and thus contained redundant information. Therefore, we first combined both fish diversity variables into a single 'fish diversity' variable, again taking the mean value of standardized scores for both variables and then re-standardizing the resulting scores (Table 1.1). PRED was then calculated as the mean
value from standardized scores for 'fish diversity', 'water scarcity', 'fish in diet', and 'fish exports' (Table 1.1). We used all three vulnerability scores for PRED calculation instead of a single 'vulnerability' score because correlations among the three vulnerability variables were quite low, i.e., each variable contained unique information (maximum Pearson's *r* among the three variables = -0.19; Table A1 in Appendix A). PRED represents the potential (relative) impact of freshwater ecosystem degradation in a country; however, the index was not linked to a particular disturbance. To identify where PRED overlaps geographically with high deforestation rates, we produced a bivariate map with blending color scales for PRED and 'forest loss'. Each country was assigned an integer score for each color scale ranging from 1 to 10 based on deciles (1/10th of samples) calculated from the two variables.

Our second objective was to determine whether research effort can be predicted from deforestation rates, fish diversity, vulnerability, and/or economic development. We performed a negative binomial generalized linear model (GLM) with number of publications as the response variable and forest loss, vulnerability, fish diversity, GDPpc, and total population of the country as predictor variables (refer to Table 1.1 for a description of variables). Population size and GDPpc were also standardized before the analysis. We included population size as a covariate to control for size effects on research effort, assuming that more populous countries would tend to have a greater number of freshwater ecologists and thus a higher publication count (Karlsson et al. 2007, Pasgaard and Strange 2013), and because all of our deforestation, fish diversity, and vulnerability metrics were size-standardized using some measure of country size or economic importance (country area, total forested area, population, or GDP). Collinearity among predictor variables was low, with all variance inflation factors < 1.3. The statistical significance of predictor variables was assessed using likelihood ratio tests, and the pseudo R^2 of the full model

was calculated as 1 - (residual deviance / null deviance). We used the function 'glm.nb' in package 'MASS' to fit the GLM.

Our third and final objective was to identify countries and regions where both forest loss and PRED are high, but where publication number is low; these countries should be the focus of future research. We created a new variable by multiplying the standardized scores for PRED and 'forest loss', and then taking the square root of the product to reduce variance. Multiplying PRED and 'forest loss' effectively combines the two color scales on the PRED vs. 'forest loss' map: countries that score high for the multiplied variable have a high score for both constituent variables. We called this variable 'risk of deforestation impacts' (RDI), which is a measure of overlap among deforestation, fish diversity, and vulnerability. We calculated deciles and country scores (1 to 10) for RDI and publication number and made a second bivariate map.

1.4 Results

At the global scale, the two deforestation metrics were weakly correlated, indicating that changes in land use only partly correspond to actual changes in tree cover (see Appendix A; Table A1; Figure A1). The only strong correlation (r > 0.7) among all deforestation, fish diversity, and vulnerability variables was between the two fish diversity variables (Table A1). Deforestation and fish diversity metrics correlated weakly with importance of freshwater fish as a protein source (positive correlation) and with water scarcity (negative correlation; Table A1; Figure A1). Overall, countries from the same region only showed moderate clustering in multivariate space, indicating considerable intra-regional variation for many variables (Figure A1). Most countries that showed a strong overlap between forest loss and PRED were located in tropical regions of Central and South America, Africa, and Southeast Asia (Figure 1.1). A few

other countries outside of these regions also had a high score (≥ 8) for both deforestation and PRED, namely Sweden, Estonia, and Latvia in Europe, and Pakistan in South Asia (Figure 1.1).

A negative binomial GLM indicated that by far the best predictor of research effort (number of publications) was country GDPpc, after controlling for effects of country population (Table 1.2). Countries with a higher GDPpc produced more publications on deforestation impacts on inland waters. Forest loss and fish diversity were also significant positive predictors of publication number, but vulnerability was not (Table 1.2). Much of the variance in publication number was explained by the combination of predictor variables included in the GLM (model pseudo $R^2 = 0.6157$). With respect to the spatial overlap between research effort and RDI, the only large region of the world with high RDI (≥ 8) and low research effort (≤ 3) was tropical Africa (Figure 1.2). Most countries with high RDI in tropical America and Asia had a high publication count, with the exception of El Salvador, Panama, Paraguay, and the Philippines (Figure 1.2). A few additional countries in other regions also had high RDI and low research effort, namely Estonia, Latvia, and Pakistan (Figure 1.2).

1.5 Discussion

Our study sought to identify critical areas for future research on deforestation impacts on inland waters by considering the global distribution of both research effort and relative research need, which was defined here as strong overlap among deforestation intensity, biodiversity, and reliance of human populations on ecosystem services provided by local inland waters. We combined and analyzed country-specific data on recent deforestation rates, freshwater fish diversity, water scarcity, importance of local inland fisheries for food security and economic production, and research effort, the latter quantified with a literature survey that included 1347

papers on deforestation and freshwater ecosystems. This quantitative review allowed us to reach three main conclusions that answer the questions outlined in the introduction. First, tropical countries exhibit the strongest overlap among deforestation, fish diversity, and vulnerability of human populations to freshwater ecosystem degradation, and therefore have a relatively higher research need. Second, GDPpc is the best predictor of research effort on deforestation and aquatic systems. Fish diversity and deforestation rates, two variables linked to research need, are also positive predictors of research effort, but vulnerability of human populations to freshwater ecosystem degradation is not. Third, tropical Africa is the only extensive region of the world with a high research need but a low research effort, and therefore constitutes a critical area for research on deforestation impacts on inland waters. We now discuss in turn each of these main conclusions.

Our finding that research need is highest for tropical countries is consistent with several studies on other ecosystems that have also reported strong coupling among threat intensity, biodiversity, and/or human vulnerability in the tropics. For instance, the majority of biodiversity 'hotspots', i.e. 'areas featuring exceptional concentrations of endemic (plant) species and experiencing exceptional loss of habitat' (Myers et al. 2000, p. 853), are located at tropical latitudes. Globally, tropical regions exhibit the strongest overlap between poverty and potential loss of terrestrial vertebrate biodiversity (Sachs et al. 2009). At smaller spatial scales within tropical regions, disturbance intensity, biodiversity, and human vulnerability can also correlate spatially. For example, in tropical Africa, Darwall et al. (2011b) reported a positive correlation at the watershed scale between freshwater biodiversity and human poverty, and Balmford et al. (2001) found strong spatial coincidence among terrestrial biodiversity, human population density, and intensity of land/habitat conversion. The tight coupling between deforestation and

PRED in tropical countries will probably continue to intensify, as it is expected that most future deforestation and agricultural expansion will occur in the tropics (Laurance et al. 2014). Tropical deforestation could in turn interact with other anthropogenic disturbances that also tend to be most extensive and/or acute in the tropics, for example overfishing of inland waters (Allan et al. 2005). Our data add to the general conclusion that tropical countries constitute a central arena for conservation action if global objectives of biodiversity conservation are to be met, and should thus be the focus of much conservation research.

Our second important finding was that GDPpc was the best predictor of research effort, even more than total population of a country. This is not surprising given that high-GDP countries (i.e., members of the Organisation for Economic Cooperation and Development) contribute the bulk of global gross expenditure on research and development, employ more researchers per capita, file more patent applications, and author the majority of highly-cited publications across all disciplines of science (King 2004, Westholm et al. 2004, Karlsson et al. 2007). Many bibliometric analyses of research allocation on other stressors or ecosystems have also found that indicators of economic development such as GDP are the best predictors of publication number (Karlsson et al. 2007, Moustakas and Karakassis 2009, Pasgaard and Strange 2013). A lower research effort in tropical (developing) than temperate countries seems to be a common pattern in ecology and in the environmental sciences as a whole, leading to a northsouth (developed-developing) divide in scientific knowledge (Karlsson et al. 2007). Research effort in this analysis followed a less dramatic divide, as the publication count of several tropical countries in South America and Southeast Asia were among the highest globally (e.g., Brazil, Indonesia, and Malaysia). Indeed, deforestation rate and fish diversity, both of which are generally higher in the tropics, were also positive predictors of research effort, suggesting that

many 'hotspots' with high biodiversity and disturbance intensity are well studied. Vulnerability of human communities to ecosystem degradation was however not related to research effort in this analysis, although our metric for human vulnerability is admittedly simple due to limited data availability on freshwater ecosystem services at the global scale. Analyzing the literature on climate change, Pasgaard and Strange (2013) similarly found that most of the global research effort (also measured by publication number) had focused on a few wealthy countries with low human vulnerability to climate change (determined by risks of exposure to and adaptive capacity towards drought, sea-level rise, and various other extreme climate related events). Assuming that locally derived scientific knowledge can improve management of anthropogenic impacts on ecosystem services, conducting research in areas of high human vulnerability should be as much of a priority as studying systems with high biodiversity.

Our third and perhaps most important finding is that most countries in tropical Africa have a high risk of deforestation impacts and yet a low research effort. Bibliometric analyses in other sub-disciplines of ecology have also identified research biases against Africa, for example in the climate change or invasion ecology literature (Pyšek et al. 2008, Pasgaard and Strange 2013). Karlsson et al. (2007) found that Africa contributed less than 1% of 6 441 papers published in nine leading ecology and environmental science journals during the years 1993, 1998, and 2003. While the causes of this bias are certainly manifold, one factor likely to exert a strong influence is the relatively low development status of most tropical African countries, where long-lasting socioeconomic problems have led to low government investment in science and destitute research infrastructures (Hassan 2001). The potential consequences of this research bias are multifaceted. First, land use impacts on African freshwater biodiversity remain largely unknown, yet these impacts are likely substantial. Indeed, the majority of threatened freshwater crabs, fish, and mollusks in Africa occur in poorly-protected watersheds (Darwall et al. 2011b), and some areas of high dragonfly diversity occur outside of terrestrial biodiversity hotspots that are more likely to receive land protection (Clausnitzer et al. 2012). Second, lack of knowledge on land use impacts on water quality or inland fisheries could also have unrecognized health or economic effects among human populations. For example, deforestation impacts on water temperature and flow regime have been linked to upsurges in malaria vectors in Africa, Asia, and South America (Patz et al. 2000). Finally, the knowledge gap on African freshwaters makes it difficult to predict which management or mitigation strategies might be effective locally. For example, riparian buffer zones are known to successfully reduce impacts of agricultural land use on stream ecosystems in other tropical regions (e.g., Lorion and Kennedy 2009b). Although buffer zone regulations exist in some afrotropical regions, little information is available on, for example, the optimal width of buffer zones to achieve the largest improvement in water quality, or which local riparian tree species are most effective at stabilizing river banks. Such knowledge gaps limit our ability to manage afrotropical inland waters and use limited resources for ecological restoration efficiently (see also Chapman and Chapman 2003).

It is important to acknowledge that we could have underestimated publication number because we could not find papers published in the so-called 'grey literature' with Web of Science, nor could we access publications in a language other than English. This is a (perhaps inevitable) bias present in all bibliometric analyses (e.g., Pyšek et al. 2008, Pasgaard and Strange 2013). It is unclear whether the underestimation of publication number is geographically heterogeneous; some developing countries might have many publications in journals in languages other than English (e.g., Brazil and China), while unpublished government research might on the contrary be most common in high-GDP countries of North America and Europe. Importantly, these biases should not affect the main conclusion that research effort is lower in the afrotropics relative to other regions. For example, we know of no limnology journal published in an African language, and the African Journal of Aquatic Science, one of the main outlets for local, applied research, is in English and indexed on Web of Science. Further, government research is unlikely to be more intensive in Africa than other regions; if anything, it might be less intensive. We thus believe that our finding of low research effort on deforestation impacts on inland waters in tropical Africa is robust and unlikely to change with better access to the grey/non-English literature.

To conclude, the biases that we report in this study should direct future research effort on deforestation impacts on inland waters. Simply put, more research on this important conservation problem is needed in tropical Africa (Chapman and Chapman 2003). In the short term, this could be achieved via increased intercontinental cooperation, whereby more researchers from high-GDP countries would develop collaborations and research programs in Africa (Karlsson et al. 2007, Pyšek et al. 2008, Pasgaard and Strange 2013). Such cooperation has been very useful to tackle other problems in aquatic ecology; for example, recent biodiversity mapping efforts from the International Union for the Conservation of Nature have made Africa the first continent for which there is a comprehensive, continent-wide inventory of fishes, molluscs, odonates, crabs, and aquatic macrophytes (Darwall et al. 2011a, Darwall et al. 2011b, Clausnitzer et al. 2012). Such novel information should facilitate the study of African inland waters and make them more attractive study systems for freshwater ecologists, which we hope will help palliate the current knowledge gap on how these ecosystems are responding to the dramatic land use changes occurring in this region of the world.

1.6 Tables

Variable	Description and data provenance			
Deforestation, fish diversity, vulnerability, and research effort variables				
Forest loss: FAO	% forest cover loss between 2005 and 2010			
	reported by the FAO (2010). Negative values			
	indicate an increase in forest cover.			
Forest loss: Hansen	% forest cover loss between 2000 and 2012			
	reported by Hansen et al. (2013). Negative values			
	indicate an increase in forest cover.			
Fish diversity: fish richness	Number of freshwater fish species (Fishbase),			
	corrected for country area (see methods).			
Fish diversity: fish endemics	Number of endemic freshwater fish species			
	(Fishbase), corrected for country area.			
Vulnerability: water scarcity	Inverse of average annual renewable freshwater			
	supply per capita (FAOSTAT: Aquastats).			
Vulnerability: fish in diet	% of total animal proteins available per capita per			
	day provided by freshwater fish (FAOSTAT:			
	Food balance sheets).			
Vulnerability: fish exports	% of GDP contributed by exports of freshwater			
	and diadromous fish (FAOSTAT: Fisheries).			
Research effort: publications	Total number of publications covering country			
	(Web of Science).			

Table 1.1. Summary table of all variables and metrics used for maps and analyses.

Forest loss	Mean of two forest loss scores.		
Fish diversity	Mean of fish richness and fish endemics.		
Vulnerability	Mean of water scarcity, fish in diet, and fish		
	exports.		
Potential repercussions of ecosystem	Mean of fish diversity, water scarcity, fish in diet,		
degradation (PRED)	and fish exports.		
Risk of deforestation impacts (RDI)	Square root of product of forest loss and PRED.		
	Our metric of research need.		

Metrics combining more than one of the above-listed variables after standardization

Table 1.2. Results of negative binomial GLM with five standardized predictor variables and number of publications as a response variable. For each predictor variable, the slope of the effect is provided (β), along with the standard error estimate for that slope, the increase in residual deviance when the variable is excluded from the full model (Δ deviance), and the *p* value obtained from a likelihood ratio test (LRT) comparing a model missing the variable with the full model. Asterisks indicate *p* values below 0.05. GDPpc: gross domestic product per capita.

ß	standard error	Δ deviance	LRT <i>p</i>
2 6389	1 1334	65 358	< 0.0001*
2.0507	1.1551	00.500	0.0001
2.9140	1.1310	90.659	< 0.0001*
1.6866	1.1407	14.004	0.0002*
1.5127	1.1255	0.228	0.0014*
0.9477	1.1375	10.251	0.6329
	β 2.6389 2.9140 1.6866 1.5127 0.9477	β standard error 2.6389 1.1334 2.9140 1.1310 1.6866 1.1407 1.5127 1.1255 0.9477 1.1375	βstandard errorΔ deviance2.63891.133465.3582.91401.131090.6591.68661.140714.0041.51271.12550.2280.94771.137510.251

1.7 Figure captions

Figure 1.1. Bivariate map showing overlap between recent forest loss and potential repercussions of freshwater ecosystem degradation (PRED). Each color axis is divided in 10 based on deciles, such that country scores for each variable are integers ranging from 1 to 10. Countries in red or purple have a high score for both variables.

Figure 1.2. Bivariate map showing overlap between research effort (number of publications) and RDI (risk of deforestation impacts), a score that includes both recent forest loss and PRED (i.e., the two color axes on Figure 1.1). Countries in red or purple have a high RDI score but a low number of publications.

Figure 1.1



Figure 1.2



Preface to Chapter 2

The main finding of Chapter 1 is that deforestation impacts on afrotropical inland waters have been very poorly studied even though the afrotropics are characterized by rapid rates of current deforestation, high freshwater biodiversity, important water scarcity, and a strong reliance of human populations on inland fisheries for economic production and food security. Deforestation is thus likely to have large impacts on biodiversity and human well being via the degradation of afrotropical inland waters, but many of these impacts remain undocumented. The following two chapters quantify some of these impacts by comparing forested (rainforest) and deforested (agricultural) streams located in and around Kibale National Park, Uganda.

In Chapter 2, I first used multivariate statistics to compare the physico-chemical parameters and macroinvertebrate community composition of 11 forest streams located inside Kibale and 23 farms streams from two agricultural regions outside of the park. Such descriptive information is only available at a few other afrotropical sites (Benstead et al. 2003, Kasangaki et al. 2008, Masese et al. 2014b, Wronski et al. 2015). I then tested whether farm streams have lower alpha diversity than forest streams, as would be predicted from a multitude of previous studies (Allan 2004, Ramirez et al. 2008). Finally, I measured and compared among-stream beta diversity between the forested and agricultural landscapes (Anderson et al. 2011). I employed new statistical methods that partition beta diversity into its two main constituents, namely taxa replacement and site differences in taxa richness (Podani and Schmera 2011, Podani et al. 2013, Legendre 2014) and argued that this approach will help reduce discrepancies among the few recent studies investigating land use impacts on stream beta diversity (Gutiérrez-Cánovas et al. 2013, Johnson and Angeler 2014, Larsen and Ormerod 2014, Hawkins et al. 2015).

Land use changes in an afrotropical biodiversity hotspot affect stream alpha and beta diversity

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2.1 Abstract

Land use changes such as deforestation and agricultural expansion strongly affect stream biodiversity, with several studies demonstrating negative impacts on stream alpha diversity. Effects of forest conversion on stream beta diversity are much harder to predict, both because empirical studies are few and because competing theories suggest opposite responses. Moreover, almost no data exist for tropical Africa, a region that is paradoxically a hotspot of both current deforestation and freshwater biodiversity. Here, we compared environmental variables, invertebrate community composition, and alpha and beta diversity of forested and deforested (agricultural) streams in and around Kibale National Park, Uganda. We found that forest conversion strongly influenced stream environmental variables and invertebrate community composition, and that agricultural land use reduced stream alpha diversity. However, amongstream beta diversity was greater across the agricultural landscape than inside the forest. Decomposing beta diversity into taxa replacement and richness differences demonstrated that replacement contributed a similar proportion to total beta diversity in both land use classes. Because of this greater beta diversity, the agricultural landscape had similar gamma diversity as the forested landscape despite its lower alpha diversity. We discuss conservation implications of these land use-associated biodiversity changes in a highly diverse yet little-studied deforestation hotspot.

2.2 Introduction

Global land use change such as conversion of forests into agricultural fields and pastures is a major driver of biodiversity change in both terrestrial and aquatic systems (Sala et al. 2000, Foley et al. 2005, Millennium Ecosystem Assessment 2005). Although often overlooked in conservation planning and land management schemes, stream ecosystems are especially affected by forest conversion because they receive terrestrial inputs such as sediment, nutrients, and contaminants via runoff in their watershed (Dudgeon et al. 2006, Abell et al. 2007, Strayer and Dudgeon 2010). Common effects of agricultural land use on streams include sedimentation and siltation linked to catchment erosion, increased nutrient and pollutant concentrations associated with fertilizer and pesticide runoff, and decreased habitat quality for stream organisms due to such factors as elevated water temperature and lower dissolved oxygen concentration (Allan 2004). Because of these influences on stream habitat integrity and water quality, land use change is consistently listed as one of the most important threats both to the biodiversity of streams and to the important ecosystem services that they provide (Sala et al. 2000, Dudgeon et al. 2006, Dugan et al. 2010, Vörösmarty et al. 2010, Collen et al. 2014).

Many studies from both temperate and tropical regions have demonstrated that declines in water quality associated with land use often lower stream species richness and/or other indicators of alpha diversity (Allan 2004, Ramirez et al. 2008). Land use changes may also influence beta diversity (i.e., variation in assemblage composition across the landscape; Whittaker 1960, 1972), a component of biodiversity that has received comparatively less attention until recently despite its obvious relevance for conservation planning (Ferrier 2002, McKnight et al. 2007, Anderson et al. 2011). Effects of forest conversion on stream beta diversity are much harder to predict, both because empirical studies are few and because competing theories suggest opposite responses. On one hand, cultural eutrophication (i.e., a rise in nutrient concentration and primary productivity associated with agricultural land use in a watershed) may increase beta diversity by strengthening stochastic processes during community assembly (Chase and Leibold 2002, Chase 2010, Bini et al. 2014). Indeed, if a larger proportion of the regional species pool can persist in more productive than less productive environments, stochasticity in colonization history can lead to 'multiple stable equilibria' of community structure, thereby increasing beta diversity (Chase 2010). On the other hand, deforestation also causes habitat degradation that negatively affects many pollution-intolerant taxa; this should allow a smaller, not larger, fraction of the regional species pool to maintain viable populations at deforested sites, thus lowering beta diversity. Moreover, some abiotic effects of forest conversion on streams such as silt deposition on the stream bed and loss of woody debris could reduce habitat heterogeneity among streams, leading to biotic homogenization and lower beta diversity (e.g., Passy and Blanchet 2007, Donohue et al. 2009 for an example in lakes). Finally,

deforestation could influence the dispersal of aquatic taxa with terrestrial, aerial life stages (e.g., aquatic insects; Petersen et al. 2004, Smith et al. 2009), which would also affect stream beta diversity (Matthiessen and Hillebrand 2006, Heino et al. 2015*a*). Of course, multiple mechanisms could be simultaneously at play, such that their combined effects remain unknown. Indeed, the few recent studies that have examined effects of land use on stream beta diversity have reached contradictory conclusions (Heino et al. 2009, Gutiérrez-Cánovas et al. 2013, Bini et al. 2014, Johnson and Angeler 2014, Larsen and Ormerod 2014, Hawkins et al. 2015).

Understanding anthropogenic impacts on beta diversity is complicated by the fact that beta diversity is multi-faceted and often defined (and measured) differently across studies (Anderson et al. 2011). Two sources of variance among communities can contribute to beta diversity: species replacement, or substitution of species between sites (known as 'taxa turnover' when the substitution occurs along a clearly-defined gradient), and richness differences caused by species gain and loss, where some species-poor assemblages are simply nested subsets of other richer assemblages (Wright and Reeves 1992, Lennon et al. 2001, Baselga 2010, Anderson et al. 2011, Podani and Schmera 2011). Many studies fail to distinguish these two components of beta diversity, yet they have contrasting conservation implications (Wright and Reeves 1992, Angeler 2013, Gutiérrez-Cánovas et al. 2013). For example, if the beta diversity of a landscape is dominated by replacement, then many sites (i.e., a large area) should be protected to conserve regional (gamma) diversity. In contrast, when richness differences underlie beta diversity, protecting a few species-rich sites would suffice to preserve gamma diversity. Novel methods have recently been developed to decompose beta diversity indices into separate replacement and richness difference (or abundance difference) components (Baselga 2010, Podani and Schmera 2011, Baselga 2013, Podani et al. 2013). The two components of beta diversity can then be

analyzed separately, for example, to explore how they vary along environmental gradients or disturbance classes (Marini et al. 2013, Podani et al. 2013, Legendre 2014). Although decomposition of beta diversity into replacement and richness/abundance differences could provide a common 'beta diversity currency' that would make comparisons across studies easier and more informative, this method has yet to be broadly applied.

In this study we employed methods of beta diversity decomposition to examine land use effects on the biodiversity of streams inside and outside of an African rainforest. Afrotropical inland waters are highly diverse ecosystems (Clausnitzer et al. 2012, Collen et al. 2014) that, paradoxically, remain very poorly studied (Chapman and Chapman 2003, Jacobsen et al. 2008). For example, to our knowledge not a single study has measured the beta diversity of afrotropical streams (although the analysis of Heino et al. 2015b included a sub-tropical dataset from South Africa), let alone how it varies with anthropogenic land use. Moreover, many afrotropical regions also experience high rates of deforestation and agricultural expansion, both currently (FAO 2010, Hansen et al. 2013) and expected over the next century (Laurance et al. 2014). This strong spatial overlap among forest conversion, biodiversity, and low research effort highlights the critical need for quantifying effects of deforestation on aquatic communities in tropical Africa (Chapman and Chapman 2003). We measured the invertebrate community composition, environmental variables, and alpha and beta diversity of forested and deforested (agricultural) streams in and around a protected area located in an afrotropical biodiversity hotspot: the Albertine Rift Valley (Plumptre et al. 2007). We focused our analysis on invertebrates because they are highly diverse, functionally important in stream food webs, and extremely responsive to changes in water quality (Wallace and Webster 1996, Barbour et al. 1999, Jacobsen et al. 2008). We hypothesized that agricultural land use would alter stream communities and water chemistry and lead to a reduction in alpha diversity, as has been observed in many other regions. For beta diversity, we refrained from deriving specific predictions because, as mentioned above, we currently have a limited understanding of land use impacts on stream beta diversity, and existing empirical studies on this topic have reached contradictory conclusions (see also Heino et al. 2015a, b).

2.3 Methods

2.3.1 Study region and site selection

Kibale National Park (hereafter Kibale) is a 795 km²-patch of mid-altitude (1100-1600 m), moist evergreen rainforest located in southwestern Uganda (park geographical range: 0°13' – 0°41' N, 30°19' – 30°32' E; Figure 2.1, left panel). Kibale is one of the last few large forest fragments remaining in Uganda (Figure 2.1, left panel) and one of the few remaining mid-altitude rainforests in East Africa (Wrangham and Ross 2008). The park is located within the Albertine Rift Valley, which forms part of the 'Eastern Afromontane' biodiversity hotspot described by Conservation International (Plumptre et al. 2007, Mittermeier et al. 2011). Kibale was designated as forest reserve (with controlled logging) in 1932 and then as a fully protected national park in 1993 (Struhsaker 1997). Sixty percent of the park area consists of tall forest (canopy >25 m high), with the remainder composed of wetlands, grasslands, timber plantations and regenerating forest that are mostly in the southern half of the park (Chapman and Lambert 2000). The park receives ca. 1691 mm of rain annually, with two distinct wet and dry seasons (drier months = May-August and December-February; data collected between 1990 and 2013 by C. Chapman & L. Chapman). Land use in the area surrounding Kibale is dominated by intensive smallholder agriculture (farms <5 ha including a mix of pasture and small-scale subsistence

agriculture) but also includes a few large tea estates and timber plantations (Hartter 2007, Southworth et al. 2010). Since 1920, a seven-fold increase in population density around the park and the associated surge in demand for farmland have resulted in no large tract of forest outside of the park, and the few remaining (small) forest fragments are being rapidly converted to agricultural land (Southworth et al. 2010).

We compared 11 forested stream sites in the northern half of the park with 23 farm stream sites from two agricultural regions outside of the park (18 stream sites in Kabarole and 5 in Kamwenge districts, west and southeast of Kibale, respectively; see Figure 2.1, right panel). These two agricultural regions were mostly cleared for agriculture prior to 1984 and currently have similar land use consisting of mixed intensive agriculture (Southworth et al. 2010). To pick study streams within accessible areas in each of the three regions, we randomly selected easting and northing coordinates using the Universal Transverse Mercator (UTM) grid system, and then walked from those random points to find the stream closest to each set of coordinates. Access to Kamwenge was harder from the field station where we resided in the northwestern region of the park (Figure 2.1, right panel), limiting the number of sites selected. Within Kibale, access to streams was limited by availability of roads and trails, and therefore most of the sites that we chose were located close to the park border (Figure 2.1, right panel); however, we only sampled streams originating within the park such that all forest sites were located several hundred meters upstream of the park border (and thus of any agricultural land use). In all regions, we only included first or second order streams of similar wetted width (<1 m) and depth (<50 cm mean depth), and we ensured that the same stream was not sampled more than once from two different sets of coordinates. Except for sparse shade trees or exotic eucalypts planted for timber, the riparian zone surrounding all of our farm sites consisted entirely of crops and grass.

2.3.2 Measurement of environmental variables and invertebrate sampling

All forest streams and all Kabarole farm streams were visited once between the summer dry season of 2005 or the winter dry season/early wet season of 2006. Logistical constraints prevented us from sampling all sites during a single season, such that we completed two sampling campaigns separated by a period of 7 months (which included one wet season). After conducting preliminary analyses that indicated strong effects of land use in Kabarole, we subsequently sampled the five Kamwenge sites during the dry seasons of 2007, to verify that land use had similar effects across a larger spatial scale. Temporal variation (i.e., sampling date) had no apparent effect on our results, perhaps due to the coarse taxonomic resolution at which samples where identified (see below). Indeed, analyzing subsets of sites from the same season and/or excluding Kamwenge sites led to qualitatively identical results as when all sites were included in the analysis (see also *Results* section).

At each site, a 20-m reach was sampled at 5-m intervals, resulting in five sampling stations per site. At each station the following environmental variables were measured: benthic substrate composition, dissolved oxygen (DO), water temperature, pH, specific conductance, and water transparency. pH was measured using an Oakton digital pH testr 2 (Model 76072; Forestry Suppliers, Jackson, MS, USA). Conductance (μ S/cm), DO (mg/L), and water temperature were measured with YSI meters (model 76244 and 76390; Forestry Suppliers). The dominant benthic substrate at each station was assessed visually and coded categorically based on particle size (1=silt, 2=sand, 3=gravel, 4=cobbles, 5=boulders). Water transparency was measured by pouring a water sample in a graduated cylinder with a miniature Secchi disc at the bottom and recording the depth at which the disc disappeared (Kasangaki et al. 2008). All measurements of

environmental variables were taken between 12:00 - 14:00 h. The five samples from each site were averaged to get a single mean value per site for each environmental variable.

Macroinvertebrate samples were collected at the same five sampling stations per site using a D-shaped kick net (bottom frame width = 40 cm, mesh size = 1 mm). Macroinvertebrates were sorted and preserved in 10% formalin on site. All individuals were later identified under a dissecting microscope to family level using various taxonomic keys (Day et al. 2001, Day and de Moor 2002*a*, *b*, Day et al. 2002, de Moor et al. 2003*a*, *b*, Stals and de Moor 2007). Some groups were identified to higher taxonomic levels than family (Nematoda: phylum; Oligochaeta: order; Turbellaria: class). Given the limited taxonomic information available for many afrotropical invertebrate taxa, family is the lowest taxonomic level to which almost all taxa could be identified. Such a coarse taxonomic resolution could limit our ability to detect subtle site differences in community composition and/or biodiversity (Jones 2008), or could have influenced our measurements of beta diversity due to the specific mathematical properties of family-level datasets (e.g., fewer variables and zeros than in species-level community matrices; Vanderklift et al. 1996). However, family richness and species richness often correlate strongly in stream invertebrate communities, and the same key environmental variables seem to drive assemblage composition at the species and family levels; thus, family-level identification is sufficient to at least describe the main patterns of biodiversity/assemblage variation among streams in a given region (e.g., Melo 2005, Heino and Soininen 2007, Mueller et al. 2013). Finally, we pooled all five invertebrate samples per site to obtain a single abundance value per taxon per site.

2.3.3 Analysis of environmental variables and community composition

All statistical analyses were conducted in the statistical computing software R version 3.0.2 (R Core Team 2013). We first performed univariate tests to compare regions and land use types for all environmental variables independently. We used one-way ANOVAs to test for an effect of 'region' (Kibale vs. Kabarole vs. Kamwenge) and planned contrasts to test for an effect of 'land use' (Kibale vs. Kabarole + Kamwenge). Then, to detect differences between farm and forest streams when considering all environmental variables together, we performed a series of multivariate analyses using the R packages 'vegan' and 'cluster' (Oksanen et al. 2013, Maechler et al. 2014). We first conducted a cluster analysis using the UPGMA clustering method on a Gower dissimilarity matrix; Gower's coefficient is an appropriate dissimilarity index when the response variables are of different mathematical types (Borcard et al. 2011; in this case, benthic substrate was an ordinal variable). We did not cut the resulting tree in clusters; we simply noted whether sites with a similar land use (farm or forest) clustered together. A principal components analysis (PCA) was then used to reveal the environmental variables that differed most between farm and forest streams. We visualized PCA results with a correlation biplot to optimally represent the relationships among variables rather than site distances (Legendre and Legendre 2012). Finally, to test whether there was an overall difference between farm and forest sites for all environmental variables combined, a permutational multivariate analysis of variance (PERMANOVA; Anderson 2001) was conducted using land use as a predictor variable and the Gower dissimilarity matrix as the response matrix. Since clustering and PCA results showed no difference between Kamwenge and Kabarole sites (see Results section), sites from both regions were grouped (land use = farm) for the PERMANOVA and all subsequent analyses.

We conducted similar analyses with the invertebrate community data to see whether land use types could also be distinguished based on their invertebrate assemblages. We first used a PERMANOVA to test for an overall difference in community composition across land use types, using as the response matrix a Bray-Curtis dissimilarity matrix computed from log-transformed abundances. Then a UPGMA cluster analysis was conducted on this dissimilarity matrix to see whether farm and forest sites clustered together based on invertebrate community composition. Finally, we produced a heat map of relative abundance of abundant taxa (> 20 individuals collected across all sites) to illustrate main differences in community composition between land use types.

2.3.4 Biodiversity analysis

To ensure that we adequately sampled the regional taxon pool, we first drew taxa accumulation curves using the 'specaccum' function in vegan. We created separate curves for forest or farm streams alone, and for both stream types combined, to verify that our sampling of family richness reached an asymptote in each case. We then used the function 'estaccumR' in vegan to estimate the size of the taxon pool in the farm and forest regions and used those extrapolated richness values as measures of gamma diversity in both landscapes. To measure alpha diversity, we calculated taxon (family) richness, Pielou's evenness, and Shannon-Wiener's *H* for each stream. We also measured rarefied richness (using the function 'rarefy' in vegan) to control for potential abundance differences across land use types that could bias our estimates of family richness, using the abundance of the site with the lowest total abundance (77 individuals) as the subsample size. We used Wilcoxon rank sum tests to compare farm and forest sites for richness, rarefied richness, evenness, *H*, and total abundance.

Beta diversity was estimated by calculating the average dissimilarity in invertebrate assemblage between all pairs of sites of a given land use type (Anderson et al. 2006, Anderson et al. 2011). We used the 'vegdist' function in vegan to first convert our community data into two separate distance matrices using the Jaccard dissimilarity index, which only considers taxa occurrences (presence), and the Ružička dissimilarity index (also known as the Marczewski-Steinhaus coefficient of dissimilarity; Podani et al. 2013), which also incorporates abundances when calculating site dissimilarity. We graphically represented Jaccard- or Ružička-based site distances using principal coordinates analysis (PCoA). We then performed a permutation-based test of multivariate homogeneity of group dispersions (PERMDISP) on each distance matrix using the function 'permutest.betadisper' in vegan. This test assesses the mean distance of sites from their group centroid in multivariate space; if one of the groups (in this case a land use type) has a significantly higher mean distance, then this group has more dissimilar assemblages on average and therefore greater beta diversity (Anderson et al. 2006). We used Jaccard and Ružička indices to produce distance matrices, because those are most easily decomposed into replacement and richness/abundance matrices (see following paragraph). These indices, however, can be biased by differences in alpha diversity among groups (Chase et al. 2011), i.e., land use types in this case. To measure beta diversity independently of alpha diversity, we also calculated dissimilarity using the Raup-Crick index computed with the 'raupcrick' function in vegan. This function uses null models to predict the number of shared taxa between two sites based on site richness and the frequency of taxa occurrence, and calculates dissimilarity as the deviation from this predicted number of shared taxa. This approach is useful to compare the beta diversity of regions or experimental treatments that differ in alpha diversity (Chase et al. 2011), which we expected to be the case here. Finally, farm sites may show higher dissimilarity than

forest sites because we sampled more farm sites. To correct for this potential bias, we ran a resampling procedure where we selected 11 farm sites from the 23, computed a new Jaccard or Ružička distance matrix, calculated the median multivariate distance of those 11 sites to their group centroid, and repeated the process 10,000 times. We then used those 10,000 estimates to corroborate the results of the PERMDISP tests by calculating the probability of observing a median distance to centroid with a random collection of 11 farm sites that was greater or lesser than the median distance observed for the 11 forest sites.

To analyze which component of beta diversity was affected by land use, we used the recent method developed by Podani and Schmera (Podani and Schmera 2011, Podani et al. 2013) that decomposes a distance matrix into both a replacement matrix and a difference in richness (for Jaccard) or abundance (for Ružička) matrix. One can then divide the summed dissimilarity of the replacement matrix or changes in richness/abundance matrix by the total dissimilarity calculated in the original Jaccard/Ružička matrix to get an estimate of the relative contribution (percent) of both processes (replacement and changes in richness/abundance) to total beta diversity. We used the R function 'beta.div.comp' provided in a recent publication (Legendre 2014) to perform such a decomposition of our four distance matrices (Jaccard/Ružička, farm/forest). To test whether the percent contribution of replacement to beta diversity (henceforth %CRBD) differed between land use types, we used a similar resampling procedure than described above for distance to group centroid: we randomly selected 11 farm sites from the 23, computed a new Jaccard or Ružička distance matrix, decomposed it to get %CRBD, repeated the process 10,000 times, and used those 10,000 estimates to: (1) build a 95% confidence interval around our estimate of %CRBD for farm sites, and (2) calculate the probability of observing with a random sample of 11 farm sites a %CRBD value similar to what was observed for forest sites.

2.4 Results

All three regions had similar water conductance, pH, and transparency; however regions differed in DO, substrate particle size, and water temperature (Table 2.1). This difference was due to an effect of land use: forest sites had higher DO, a substrate composed of larger particles, and lower maximum water temperature than farm sites (Table 2.1). Kamwenge and Kabarole (farm) streams clustered together based on environmental variables but both agricultural regions differed markedly from the forest sites (Figure 2.2a, left panel). Only one farm stream (stream number 1 from Kabarole region) clustered with the forest streams. A PERMANOVA comparing farm and forest sites confirmed that land use had a strong effect on stream environmental variables ($F_{(1,32)} = 22.693$, p < 0.001). Principal components analysis also showed strong differences between farm and forest sites (Figure 2.2b). With the exception of Kabarole 1, the two types of land use separated completely along principal components (PC) 1 and 2, which explained 67.36% of site variation in environmental variables. Farm and forest sites separated best along PC1; the environmental variables with the highest loadings for this component were DO, water temperature, and mean substrate particle size, confirming the trends described above and seen in Table 2.1. PC2 loaded primarily with pH and conductance, which varied across sites within regions but not between land use categories.

Farm and forest sites also differed strongly in macroinvertebrate community composition (PERMANOVA: $F_{(1,32)} = 15.61$, p < 0.001). Cluster analysis revealed that forest sites had a community composition more similar to other forest sites than to farm sites (Figure 2.2a, right panel), with the exception of two farm sites that had forest-like assemblages (Kabarole 18 & 19; interestingly, those two sites do not include Kabarole 1, which had environmental variables similar to forest sites). Forest assemblages were characterized by many mayfly and caddisfly

taxa such as Calamoceratidae, Hydropsychidae, Lepidostomatidae, and Leptophlebiidae (Figure B1). Elmidae (Coleoptera), Tipulidae (Diptera), and Turbellaria were also abundant at many forest sites. Farm sites, on the other hand, had a very high abundance of dragonfly larvae (Libellulidae) and air-breathing planorbid snails. Chironomidae (Diptera) and Caenidae (Ephemeroptera) were the only two taxa abundant across both land use types, although Caenidae were much more abundant in farm than forest streams (Figure B1).

Taxa accumulation curves indicated that we sampled enough streams to characterize the taxon pool of both landscapes (Figure 2.3a). The size of the taxon pool estimated for the forest and farm landscapes was 46 and 50 taxa, respectively, while that of both land use types combined was 57. Total invertebrate abundance was similar across land use types (Figure 2.3b). However, family richness was much lower for farm sites than forest sites, with median richness being eight families or 40% lower at farm than forest sites (Figure 2.3c). Farm sites also had lower values for all other measures of alpha diversity, namely rarefied family richness, Pielou's evenness, and Shannon-Wiener's *H* (Figure 2.3d-f).

Total beta diversity was higher for farm sites than forest sites both when dissimilarity among sites was calculated based on taxa occurrence (PERMDISP for Jaccard distance: $F_{(1,32)} =$ 29.17, p < 0.001; Figure 2.4a) or abundance (PERMDISP for Ružička distance: $F_{(1,32)} = 15.51$, p < 0.001; Figure 2.4c), although the difference was more pronounced for taxa occurrence. This result was not due to differences in alpha diversity between land use types: farm sites also had greater Raup-Crick dissimilarity than forest sites (PERMDISP $F_{(1,32)} = 13.75$, p < 0.001; Figure B2). No combination of 11 farm sites out of 10,000 random samples produced a median distance to group centroid that was as low as what was observed for forest sites, neither for Jaccard- nor Ružička-based distances (see distribution of 10,000 medians in red next to boxplots of Figure 2.4a,c). Decomposition of Jaccard distance matrices showed that %CRBD was similar for farm sites (70%) and forest sites (74%; Figure 2.4b). This difference of 4% is likely due to sampling error because: (1) the value of 74% observed for forest sites was well within the confidence interval calculated for farm %CRBD based on 10,000 random combinations of 11 farm sites (Figure 2.4b), and (2) the probability that one of those random samples had a %CRBD value higher than 74% was 0.35. In contrast, decomposition of Ružička distance matrices showed that %CRBD was higher for farm sites (54%) than forest sites (39%; Figure 2.4d). None of 10,000 combinations of 11 farm sites yielded a %CRBD value as low as what was observed for forest sites, and the forest %CRBD was 5% lower than the lower limit of the confidence interval calculated for farm %CRBD (Figure 2.4d). In summary, total dissimilarity in taxa occurrence, and hence beta diversity, is much greater among farm sites than forest sites, with a similar relative contribution of taxa replacement in both land use categories. The smaller difference in beta diversity between land use classes when using Ružička distance instead of Jaccard distance is due to large abundance differences among forest sites.

2.5 Discussion

Our comparison of environmental variables and invertebrate assemblages of forested streams inside Kibale National Park with nearby streams that were deforested over the past century demonstrated that forest conversion strongly modifies the habitat, community composition, and biodiversity of streams from a region that has been largely under-studied by stream ecologists. Compared to forest streams, farm streams had higher water temperature, a finer benthic substrate, and lower DO. Invertebrate assemblages of farm and forest streams were markedly distinct, and farm streams had a much lower alpha diversity than forest streams. However, beta diversity was greater over the agricultural landscape than in the park, with similar relative contribution of replacement to beta diversity in both types of land use. We now examine in turn each of these findings in more detail, and then conclude by briefly discussing the general conservation implications of our results.

Increases in water temperature, stream bed siltation, and decreased DO are well-known effects of shade removal, catchment erosion, and increases in biological oxygen demand that can accompany riparian deforestation and agricultural land use (Allan 2004, Ramirez et al. 2008). Similar abiotic effects of forest conversion have been observed in high-altitude regions of Uganda (Kasangaki et al. 2008), at dryer sites in East Africa (Masese et al. 2014), and around rainforests in other tropical regions (e.g., Iwata et al. 2003, Lorion and Kennedy 2009). These modifications of the stream habitat most likely contributed to the lower alpha diversity observed in deforested streams; many studies at other tropical sites have linked deforestation-induced habitat degradation to a decrease in stream alpha diversity (Benstead et al. 2003, Bojsen and Jacobsen 2003, Lorion and Kennedy 2009, but see Encalada et al. 2010 for greater richness in pasture than forest streams). Benthic siltation could be a major driver of such declines in richness, as this disturbance can in itself lower invertebrate alpha diversity in both tropical and temperate streams (Wantzen 2006, Larsen and Ormerod 2014). In other systems, the negative effects of agricultural land use on species richness was linked to insecticide use (Schulz and Liess 1999). No data is available on pesticide use in this region, but it is possible that insecticides also contribute to the decline in alpha diversity that we observed in the agricultural landscape.

The lower invertebrate richness of agricultural sites is likely to have negative impacts on stream ecosystem processes such as decomposition of leaf litter and benthic primary production (Jonsson and Malmqvist 2000, Cardinale and Palmer 2002, Lecerf and Richardson 2010). Some

taxa that were absent from agricultural streams have been described as functionally important in other tropical streams. For example, the abundance of leaf-shredding calamoceratid caddisflies has been reported as a good predictor of litter decomposition rate in Ecuadorian streams (Encalada et al. 2010). We observed a very high abundance of calamoceratid caddisflies in forested streams but not in agricultural streams. Other caddisfly families described as important decomposers/shredders in tropical streams (e.g., Lepidostomatidae; Masese et al. 2014) were also absent from agricultural streams adjacent to Kibale. The loss of these detritivorous taxa is very likely to reduce rates of organic matter processing in agricultural streams, a hypothesis currently being addressed with a litterbag experiment in a subset of our study streams.

Although alpha diversity was much lower in farm streams, we observed greater beta diversity over the deforested landscape than inside the park. This result may be a consequence of variation in other biodiversity components, as beta diversity is simply a product of alpha and gamma diversity (Chase et al. 2011, Kraft et al. 2011). For example, the lower alpha diversity of farm sites could lead to a greater mean Jaccard dissimilarity simply because of a sampling effect (Chase et al. 2011). This alpha-dependence of many beta diversity indices prompted the development of null modeling approaches that calculate the probability that two sites share a given number of species based on both site richness and the frequency of occurrence of each taxon across the landscape. We employed one such null model-based dissimilarity index (the modified Raup-Crick index; Chase et al. 2011) and confirmed that farm communities are more dissimilar than forest communities even when accounting for differences in alpha diversity between land use types. Gamma diversity, in this case the total number of taxa sampled in a given land use type, was similar for forest sites (46 taxa) and farm sites (50 taxa). The fact that we sampled more sites and over a larger geographical area in the agricultural landscape than

inside the park could have overestimated the apparent gamma diversity of farm sites, which would effectively overestimate their relative beta diversity as well. However, this explanation is unlikely for four reasons: (1) species accumulation curves showed that sampling effort was sufficient to appropriately estimate gamma diversity in both land use classes; (2) only four taxa occurred in the Kamwenge sites but not in the Kabarole sites, such that including five sites from Kamwenge only had a modest effect on farm gamma diversity; (3) although we did not conduct formal spatial analyses, community composition was not apparently linked to site proximity. For example, the two farm sites with unusual (forest-like) assemblages, Kabarole 18 and 19, were located in the center of the Kabarole area close to sites that had no forest taxa; and (4) our resampling procedure showed that all random combinations of 11 farm sites had greater beta diversity than the 11 forest sites (and many of those combinations excluded all Kamwenge sites and the two outliers from Kabarole). Therefore, farm communities do have greater beta diversity than forest communities, which leads to similar gamma diversity between land use types despite the lower alpha diversity of farm sites. Decomposition of beta diversity confirmed that taxa replacement/turnover contributed an equally large fraction to beta diversity in both landscapes (70% vs. 74%), such that **absolute** taxa replacement (i.e., total dissimilarity \times %CRBD) was higher over the agricultural landscape.

This finding contrasts with results obtained in other studies of stream invertebrate beta diversity. Some authors working in temperate regions found a negative relationship between invertebrate beta diversity and forest degradation (Heino et al. 2009) or proxies of land use intensity such as nutrient concentration (Johnson and Angeler 2014) or percent crop cover in the watershed (Maloney et al. 2011). The only other tropical study that we are aware of also found a negative impact of deforestation on stream invertebrate beta diversity, although the authors used

an entirely different statistical approach (Bojsen and Jacobsen 2003). Studies on other stream taxa (e.g., algae: Passy and Blanchet 2007) or other freshwater ecosystems (e.g., lake invertebrates: Donohue et al. 2009) also report a decrease in beta diversity in impacted landscapes. In contrast, Larsen and Ormerod (2014) found no difference in beta diversity among pasture and semi-natural streams. Bini et al. (2014) reported a hump-shaped response of stream beta diversity to nutrient concentration linked in part to agricultural land use, but the geographical extent of the study was so large that land use effects cannot be distinguished unambiguously from broad-scale spatial variation in environmental variables. Aside from results reported here, only two other studies have found greater stream beta diversity in human-altered landscapes at the regional scale (Gutiérrez-Cánovas et al. 2013, Hawkins et al. 2015). Interestingly, one of these studies found that land use affected richness differences but not taxa turnover/replacement, which is inconsistent with what we report (Gutiérrez-Cánovas et al. 2013). Our results for afrotropical streams, therefore, only agree with one other study (Hawkins et al. 2015).

Resolving these discrepancies will require many additional empirical studies, but also a common method for measuring beta diversity. Some studies have measured beta diversity using dissimilarity indices that include abundance differences across sites, which could inflate the apparent beta diversity of undisturbed sites (e.g., Maloney et al. 2011, Johnson and Angeler 2014). Indeed, when we used abundance data to calculate dissimilarity, we also observed less difference in beta diversity between farm and forest communities, but beta diversity decomposition demonstrated that this effect was due to an increase in abundance differences among forest sites, rather than actual taxa replacement. Other studies that did decompose beta diversity (Gutiérrez-Cánovas et al. 2013, Bini et al. 2014, Hawkins et al. 2015) all: (1) employed

a slightly different method that partitions beta diversity into 'nestedness' and turnover instead of richness differences and replacement (Baselga 2010), and (2) used presence-absence data only for decomposition. We opted for the decomposition method of Podani and Schmera (Podani and Schmera 2011, Podani et al. 2013) because the interpretation of richness/abundance differences is perhaps simpler than that of nestedness, which only includes a fraction of total richness differences (Legendre 2014), and because the decomposition method for abundance data is a simple logical extension of decomposition based on presence-absence data (Podani et al. 2013). Regardless of the choice of decomposition method, we believe that distinguishing replacement from richness differences is important in understanding which component of beta diversity is affected by anthropogenic disturbances and propose that such analytical approaches be more commonly integrated into studies evaluating effects of landscape change on aquatic communities. General responses of stream beta diversity to anthropogenic land use will most likely only be detectable if various studies compare the same component(s) of beta diversity.

Our results indicate greater beta diversity among agricultural than forest sites, with equal contribution of taxa replacement in both land use categories; the obvious question that follows is what metacommunity processes underlie this pattern. Three commonly invoked mechanisms could explain the greater beta diversity of agricultural sites: increased productivity, decreased dispersal, and/or increased habitat heterogeneity. Chase (2010) demonstrated experimentally that landscape productivity can correlate positively with beta diversity due to stronger priority effects during community assembly in more productive environments, and proposed that cultural eutrophication of water bodies could lead to increased beta diversity (see also Bini et al. 2014). Our results would be consistent with this hypothesis if our agricultural streams were more productive than forest streams. However, we measured nutrient concentrations, periphyton
biomass, algal accrual on artificial substrates, and whole-stream primary production from a subset of farm streams for another study (V. Fugère and L. Chapman, *unpublished manuscript*) and observed low primary production and nutrient concentrations (e.g., orthophosphate < 10 μ g/L, which would be equivalent to nutrient-poor, undisturbed streams in other regions). In addition, heterotrophic production should be lower at farm sites due to reduced canopy cover/litter inputs, making it even less likely that whole-stream productivity would be considerably higher at farm than forest sites. We therefore speculate that increased productivity is unlikely to explain our results, but this hypothesis remains to be disproved.

If among-stream dispersal of aquatic taxa was more limited in the agricultural than forested landscape, greater beta diversity of farm communities would be expected (Matthiessen and Hillebrand 2006). The limited data available on effects of land use on the dispersal of adult (flying) stream insects indicate that riparian deforestation can hinder, facilitate, or have no impact on dispersal, depending on which taxa are considered (Briers et al. 2002, Petersen et al. 2004, Smith et al. 2009). Shifts in community composition associated with changes in water quality could also influence the mean dispersal rate and/or distance of farm and forest communities, regardless of land use impacts on adult flight activity. These hypotheses require further study given the current paucity of data on land use impacts on stream invertebrate dispersal (Smith et al. 2009).

Increased habitat heterogeneity across streams could also account for the greater beta diversity of farm communities if deforestation and agricultural land use created a diversity of stream habitats from what was otherwise fairly homogeneous stream conditions inside the forest. We did observe greater variance in environmental variables for farm than forest streams, for example in our PCA results. The only other study of stream beta diversity in agreement with ours (Hawkins et al. 2015) also found greater habitat heterogeneity among disturbed than pristine sites and concluded that this was the likely cause of the higher beta diversity observed at disturbed sites. Numerous other studies have looked at the relationship between stream habitat heterogeneity and invertebrate beta diversity, but results are mixed, possibly because of variation in the spatial scale at which beta diversity is measured (Astorga et al. 2014, Bini et al. 2014, Heino et al. 2015*a*, *b*). Based on a recent conceptual framework, regional-scale, among-stream beta diversity would be expected to be most strongly related to habitat heterogeneity (followed by species sorting) rather than dispersal rates (Heino et al. 2015*a*). We therefore believe that increased habitat heterogeneity across streams is the most likely explanation for the greater beta diversity of farm streams, but a more precise characterization of stream habitats would be required to test this hypothesis, including for example hydrological variables (current velocity, bed shear stress, etc.) in addition to water chemistry. Such data could be obtained in the future; however, given that experimental approaches are more likely to unambiguously expose processes regulating beta diversity (Anderson et al. 2011), we are instead planning manipulative experiments to test some hypotheses that emerge from our results.

Regardless of the metacommunity processes that underlie the differences in biodiversity patterns that we observed between farm and forested landscapes, these differences have important implications for biodiversity conservation in this region. Although the total number of taxa present in both land use types was similar, the community composition of farm and forest streams was strikingly different. Many taxa only occurred inside the park, indicating that forests are key contributors to regional diversity. Yet, except for Kibale and a few other protected areas, a large fraction of previously-forested areas of the Albertine Rift has already been cleared, and the small forest fragments that remain are rapidly being converted to agricultural land as human population density continues to increase (Plumptre 2002, Southworth et al. 2010). Protected forests therefore seem essential to safeguard the diversity of aquatic invertebrates in the Albertine Rift (see also Plumptre et al. 2007 for a similar argument based on terrestrial taxa). The high contribution of replacement to beta diversity inside the park (74% when based on presenceabsence data) indicates that community composition varies considerably even within Kibale, such that any reduction in park area could drive biodiversity loss. Fortunately, although agricultural encroachment in Kibale was common in the past (Chapman and Lambert 2000), forest cover within the park boundaries has been quite stable in recent years (Southworth et al. 2010), suggesting that this protected area should be effective at preserving forest-specific taxa in this region. Such protection is unfortunately not standard across the afrotropics, as the majority of threatened freshwater species in sub-Saharan Africa occur in watersheds with insufficient protected land cover to avoid potential declines in water quality (Darwall et al. 2011). Interestingly, farm sites also had many taxa absent from the park, and deforested streams had high landscape-scale diversity. Even if farm streams have environmental variables indicating a degraded habitat (lower DO, higher temperature, more silt on the stream bed), they most likely provide favorable conditions for taxa adapted to more open habitats, such as gastropods grazing on algae. This suggests that a mosaic of forested and open habitats (not necessarily disturbed) is likely optimal to conserve the regional species pool. At the watershed scale, species diversity of African dragonflies also seems to correlate with landscape heterogeneity (Clausnitzer et al. 2012), although in this case the greatest regional diversity is observed in watersheds containing a mixture of natural (not degraded) habitats.

In conclusion, this study clearly demonstrates impacts of deforestation and agricultural land use on stream biodiversity in the afrotropics, a region that has received little attention from stream ecologists (Chapman and Chapman 2003, Jacobsen et al. 2008). The effects that we observed were quite strong, such that further investigation aiming to reveal the metacommunity mechanisms responsible for such effects is a promising avenue for future research. It would also be important to examine whether deforestation also increases stream beta diversity at other tropical sites, using recent methods to measure and decompose beta diversity. Finally, additional studies documenting land use impacts on afrotropical streams are critically needed given the vast agricultural expansion that is expected for this region over the course of the 21st century (Laurance et al. 2014); monitoring how such anthropogenic land cover changes affect highly diverse afrotropical inland waters is vital for the conservation of global freshwater biodiversity.

2.6	
Tables	

bold. DO: dissolved oxygen. SPS: mean substrate particle size. ANOVAs and contrasts respectively testing for differences across regions or land use types. p values lower than 0.05 are indicated in Table 2.1. Mean (+/- standard deviation) for environmental variables of streams from the three study regions, and results of one-way

$y = 0.434 F = 0.99; \ p = 0.326$ $y < 0.001 F = 120.4; \ p < 0.001$ $y < 0.001 F = 60.3; \ p < 0.001$ $p = 0.013 F = 9.87; \ p = 0.002$	F = 60.3; p F = 30.2; p F = 5.06; p	3.29 +/- 1.36 20.42 +/- 1.40	20.02 +/- 1.88	18.32 +/- 0.84	
y = 0.434 F = 0.99; p = 0.3 y < 0.001 F = 120.4; p < 0.001 p < 0.001 F = 60.3; p < 0.000	F = 60.3; p F = 30.2; p	3.29 +/- 1.36			Tomporatura (OC)
p = 0.434 $F = 0.99; p = 0.3p < 0.001$ $F = 120.4; p < 0.001$	F = 60.3; p		3.12 +/- 1.65	7.05 +/- 0.68	DO (mg/L)
$\overline{y} = 0.434$ $F = 0.99; p = 0.3$		1.06 +/- 0.13	1.18 +/- 0.38	3.00 +/- 0.63	SdS
	F = 0.86; p	60.46 +/- 29.83	49.36 +/- 27.17	61.24 +/- 21.66	Transparency (cm)
p = 0.185 $F = 4.21; p = 0.00$	F = 2.11; p	6.19 +/- 0.12	6.26 +/- 0.73	6.74 +/- 0.50	pH
p = 0.677 $F = 0.70; p = 0.40$	F = 0.39; p	182.33 +/- 20.95	203.37 +/- 182.49	156.04 +/- 57.77	Conductance (µS)
		farm	farm	forest	Land use
ion) land use)	regio	(mean +/- s.d.)	(mean +/- s.d.)	(mean +/- s.d.)	variable
(effect of Contrast (effect	ANOVA (Kamwenge (n=5)	Kabarole (n=18)	Kibale (n=11)	Environmental

2.7 Figure captions

Figure 2.1. Study site. Left, map of Uganda showing the location of Kibale National Park (NP) and other large forested areas. Right, map of Kibale and surrounding area indicating the position of sampling sites in the three study regions. MUBFS: Makerere University Biological Field Station.

Figure 2.2. Results of multivariate analyses of site environmental parameters and invertebrate community composition. (a) Cluster analyses of site environmental parameters (left) and invertebrate community composition (right). Site codes include the study area and the site number within that region (Kab = Kabarole farm streams, Kam = Kamwenge farm streams, For = forested streams inside the park). Forest sites and their associated branches are highlighted in red for illustrative purposes. (b) Correlation biplot showing relationships among environmental variables (arrows) and principal components (PC) 1 and 2 (dotted lines). Sites are represented by different symbols based on their respective region. The variance represented by PC 1 and 2 is indicated in parentheses. DO: dissolved oxygen. SPS: mean substrate particle size.

Figure 2.3. Alpha diversity of forest and farm streams. (a) Taxa accumulation curves showing cumulative family richness as a function of the number of sites sampled in the forest (red line), in the farms (blue line), or when combining both types of sites (black line). The light grey polygon indicates 95% confidence intervals for the black line (both land use types combined). Dotted lines extrapolate farm and forest accumulation curves to their respective estimated richness if 34 streams had been sampled in each region. (b-f) Boxplots showing the medians (thick black line),

quartiles (box outline), and range (vertical lines) of forest and farm streams for total abundance (b), family richness (c), rarefied richness (d), Pielou's evenness (e), and Shannon-Wiener's H (f). Outliers are represented as circles. p values indicate the results of Wilcoxon rank sum tests comparing both land use types for each response variable.

Figure 2.4. Beta diversity of forest and farm streams. (a,c) Left: principal coordinates biplots showing Jaccard (a) or Ružička (c) distance between assemblages within each land use type. Large red circles indicate group centroids, while dotted lines represent the minimum convex hulls around each group. Right: Boxplots showing the distance of forest and farm streams to their respective group centroid in multivariate space. The meaning of lines, boxes, and circles is the same as in Figure 2.3. Red bars on the right represent the range of medians obtained from 10,000 random subsamples of 11 farm streams. (b,d) Stacked bar graph illustrating the % contribution of replacement (%CRBD) and richness or abundance differences to total Jaccard (b) or Ružička (d) dissimilarity for both land use types. Dotted lines indicate the 95% confidence interval calculated for farm %CRBD from 10,000 random subsamples of 11 farm streams.





Figure 2.2











Preface to Chapter 3

Chapter 2 documented important impacts of agricultural land use on the physicochemical parameters, invertebrate community composition, and alpha and beta diversity of Kibale streams. These impacts are likely to have important repercussions on stream ecosystem structure and function. For example, farm streams were warmer than forest streams, and water temperature is known to be one of the main factors influencing key ecosystem functions such as ecosystem metabolism, detritus decomposition, and secondary production of consumers (Morin and Dumont 1994, Bernot et al. 2010, Boyero et al. 2011b). Changes in invertebrate community composition could also lead to changes in the relative abundance or biomass of invertebrate trophic guilds, known as functional feeding groups, which exert important influences on various stream ecosystem functions (Wallace and Webster 1996). For example, I hypothesized in the discussion of Chapter 2 that the loss of detritivorous caddisflies belonging to the 'shredder' functional feeding group would result in slower rates of detritus decomposition at farm sites.

In Chapter 3, I tested these hypotheses and investigated consequences of land useassociated changes in water chemistry and invertebrate assemblages for the functioning of Kibale streams. I measured several ecosystem stocks and functions in two forest streams inside Kibale and two nearby farm sites immediately outside of the park. I also re-analyzed the invertebrate abundance dataset presented in Chapter 2, applying a functional feeding group classification of all invertebrate taxa sampled in Kibale streams, to test whether the abundance of different functional feeding groups differed between farm and forest sites. This Chapter provides, to my knowledge, the first study documenting multiple ecosystem stocks and functions in afrotropical streams, as well as how those respond to land use.

Deforestation alters stream ecosystem structure and function around an afrotropical rainforest

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3.1 Summary

1. Land use is known to strongly influence the structure and function of stream ecosystems, yet studies on such impacts remain scarce in many hotspots of deforestation, most notably tropical Africa. Moreover, very few studies document impacts of land use on multiple structural and functional ecosystem properties related to both allochthonous and autochthonous energy pathways, which is necessary to reveal effects of land use on overall stream functioning. This study directly addresses these knowledge gaps by quantifying land use impacts on several ecosystem stocks and functions of afrotropical streams.

2. We sampled rainforest and recently deforested (agricultural) streams in and around Kibale National Park, Uganda. In both stream types, we measured the biomass of benthic algae, detritus, and invertebrate functional feeding groups, as well as invertebrate secondary production, rates of litter decomposition (microbial and shredder-mediated), and whole-stream metabolic parameters (gross primary production, ecosystem respiration, and production to respiration ratio) over several months spanning one wet and two dry seasons. To test the regional generality of these results, we also analysed a previously published dataset of invertebrate abundance in many farm and forest streams in the Kibale region using the functional feeding group classification developed for the focal streams in which ecosystem functions were measured.

3. We found that deforested streams, although still strongly heterotrophic, had higher stocks of benthic algae as well as greater gross primary production and production to respiration ratios than forested streams. Invertebrate shredders were almost entirely absent from deforested streams, which resulted in much slower litter decomposition rates at these sites despite comparable rates of microbial decomposition. Abundance data from many farm and forest streams around Kibale confirmed the low abundance of all shredder taxa at farm sites. Finally, the biomass of invertebrate functional feeding groups at farm and forest sites did not match resource availability: in addition to low shredder biomass, deforested streams also had a lower biomass of scrapers and collectors despite their higher algal stocks and comparable biomass of fine detritus. The low invertebrate biomass at farm sites led to a 41 to 66 % reduction in invertebrate production despite the higher water temperature of deforested streams.
4. In summary, this study documents strong effects of deforestation and agricultural land use on stream ecosystem structure and function around an afrotropical rainforest. Whole-stream productivity appeared depressed at farm sites despite somewhat higher primary production,

suggesting that deforestation impairs stream functional integrity in this region. Our results highlight the need for additional research on land use impacts on afrotropical streams, and stress the importance of management options such as the maintenance of riparian buffer zones.

3.2 Introduction

Land use changes such as deforestation and agricultural expansion are major threats to stream ecosystems (Dudgeon et al. 2006, Ramirez et al. 2008, Vörösmarty et al. 2010). Common effects of agricultural land use on streams include increased sedimentation, nutrient enrichment, loss of riparian shading and associated increases in irradiance and water temperature, and lower inputs of allochthonous detritus, all of which can impact stream biodiversity and ecosystem functioning (Likens and Bormann 1974, Allan 2004). Although land use impacts on streams have been studied for several decades, many questions remain open. For example, research on stream responses to land use has traditionally focused on structural variables related to water chemistry and community composition, providing little information on functional aspects of stream integrity (Bunn et al. 1999, Gessner and Chauvet 2002). Important stream ecosystem functions such as litter decomposition, ecosystem respiration, and primary and secondary production, all of which are key components of energy and material flow in stream ecosystems, can all be affected by land use (Young and Huryn 1999, Young et al. 2008, Benke and Huryn 2010, Tank et al. 2010). A second important knowledge gap stems from the biased geographical distribution of the global research effort on land use impacts on freshwater ecosystems (see Chapter 1). Some areas of the world exhibiting rapid deforestation rates remain very poorly studied, most prominent among which are tropical regions of Africa (Chapman and Chapman 2003, Jacobsen et al. 2008; see also Chapter 1). For example, we are aware of no publication

reporting estimates of whole-stream metabolism or secondary production for an afrotropical stream, and meta-analyses on these important ecosystem functions do not include a single case study from the afrotropics (e.g., Davies et al. 2008, Jacobsen et al. 2008, Finlay 2011). Our main objective in this study is to address these knowledge gaps by documenting land use impacts on multiple ecosystem stocks and functions in streams located within an afrotropical deforestation hotspot.

There are two main pathways for energy and material flow in stream ecosystems: a detritus-based (allochthonous) pathway and an algal-based (autochthonous) pathway, the former supporting the bulk of consumer production in low-order streams characterized by high litter inputs but low light availability (Vannote et al. 1980, Wallace et al. 2015). These two pathways can have either distinct or similar responses to land use. For example, some authors have found that increased irradiance and reduced litter inputs associated with deforestation stimulate primary production but depress detritus decomposition (e.g., Hladyz et al. 2011, Silva-Junior et al. 2014), a response that is comparable to the downstream switch in ecosystem functioning that normally occurs along the river continuum (Vannote et al. 1980). In contrast, both detrital and autotrophic energy pathways can sometimes benefit from nutrient enrichment and/or increased irradiance at agricultural sites (Young et al. 2008, Woodward et al. 2012). Distinguishing among these responses requires measuring multiple ecosystem stocks and functions related to both allochthonous and autochthonous energy pathways, an integrative approach which is rarely applied to tropical streams (Silva-Junior et al. 2014) and which has, to our knowledge, never been adapted in the afrotropics.

From a conservation perspective, land use impacts on afrotropical stream functioning require immediate attention as many afrotropical regions currently exhibit rapid deforestation

rates (FAO 2010, Hansen et al. 2013), and this area is expected to be a hotspot of agricultural expansion over the next century (Laurance et al. 2014). In addition, studies of afrotropical streams may reveal mechanisms that underlie geographical variation in responses to land use. For example, one the main mechanisms through which agricultural land use can affect stream functioning is nutrient enrichment linked to increased soil erosion and/or fertilizer runoff (Young et al. 2008, Bernot et al. 2010). Such nutrient enrichment could be much more modest in the afrotropics, where soils are often nutrient-depleted due to low fertilizer usage (Sanchez 2002). There are also important differences in stream faunal composition and diversity across latitudes as well as within tropical regions (Boulton et al. 2008, Jacobsen et al. 2008, Boyero et al. 2011a, Boyero et al. 2012), which may influence land use effects on stream functioning. For example, geographical variation in the diversity and/or taxonomic composition of invertebrate functional feeding groups (FFGs: i.e., collector-filterers, collector-gatherers, predators, scrapers, and shredders; Merritt and Cummins 2011) may affect the sensitivity of particular FFGs to land useassociated changes in water quality, which could then have cascading effects on rates of herbivory (by scrapers) and detritivory (by collectors and shredders; Wallace and Webster 1996, Boyero et al. 2012). Such impacts are currently very challenging to predict, because we lack fundamental information on the response of invertebrate FFGs to land use in the afrotropics (but see Benstead and Pringle 2004, Masese et al. 2014b).

In this study, we measured multiple stream ecosystem stocks and functions in and around a protected rainforest located in the 'Albertine Rift Valley', an area that has been described as one of Africa's most important regions for conservation based on its biodiversity and threat intensity (Plumptre et al. 2007). Streams outside of the protected area were deforested *ca*. 50 years ago and are now subjected to agricultural land use. In each stream, we measured stocks of basal

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resources and invertebrate FFGs, as well as secondary production of invertebrates, litter decomposition by microbes and shredders, and whole-stream metabolism during both dry and wet months. To generalize our results to a larger area, we also performed a functional feeding group analysis on a previously published dataset of aquatic invertebrate abundance in a larger number of forested and deforested streams in the region (Chapter 2). We aimed to test which of the responses described above best describes land use impacts on afrotropical stream functioning, and by doing so provide the first study measuring multiple ecosystem functions in streams from this poorly studied yet increasingly perturbed area of the world (Chapter 1).

3.3 Methods

3.3.1 Study area

This work was conducted in and around Kibale National Park (hereafter Kibale), a 795 km^2 mid-altitude (1100-1600 m), moist evergreen rainforest located in southwestern Uganda (park geographical range: 0°13' – 0°41' N, 30°19' – 30°32' E; Figure 3.1). Kibale is one of the few large forest fragments in the Albertine Rift, which forms part of the 'Eastern Afromontane biodiversity hotspot' described by Conservation International (Plumptre et al. 2007, Mittermeier et al. 2011). Kibale receives ca. 1691 mm of rain annually, with two distinct wet and dry seasons (dry months = May-August and December-February; data collected between 1990 and 2013 by C. Chapman & L. Chapman). The park comprises two main watersheds, the Mpanga and Dura watersheds (Figure 3.1), both of which are subwatersheds of the Nile Basin. Kibale was gazetted as a forest reserve with controlled logging in 1932 and then as a fully protected national park in 1993 (Struhsaker 1997). Since 1920, population density in the area surrounding the park has increased seven-fold (reaching 270 people km⁻² along the western edge of the park), which led to

rapid conversion of forest to agricultural land (Southworth et al. 2010). Although some forest patches remain outside of the park, land use in the vicinity of Kibale is dominated by intensive smallholder agriculture (farms <5 ha with a mixture of food crops, pastures, and occasionally cash crops such as coffee or tea), a few larger tea estates, and some monocultures of exotic pines and eucalypts planted for timber (Hartter 2007, Southworth et al. 2010).

We studied two forested and two agricultural (farm) first-order streams nearby a field station located in the northwestern area of the park (Figure 3.1). We selected one forest-farm stream pair from each watershed (Mpanga and Dura, hereafter referred to as watershed 1 and 2, respectively). The forest streams inside Kibale were situated in areas of tall forest with canopy > 25 m high, while farm streams outside of the park were located in agricultural land that was deforested in the 1960s. The entire area drained by the two farm streams consisted of pastures and crops, with the exception of a few dispersed eucalyptus and shade trees (*Neoboutonia* spp. or *Macaranga schweinfurthii* Pax). Farm streams were thus mostly open, although grasses and emergent macrophytes shaded part of the stream surface. In each stream, we delineated a 100-m reach over which all measurements were taken. All fieldwork took place between June and August 2011 unless stated otherwise.

3.3.2 Stream physico-chemical parameters

We measured altitude range and slope (m m⁻¹) by recording altitude with a GPS (Garmin: Olathe, KS, USA) at the upstream and downstream ends of each study reach. Channel width, mean depth, canopy cover, photosynthetically active radiation (PAR), and benthic substrate composition were measured at 5-m intervals along each reach. Mean depth was calculated by averaging depth measured at 1/4, 1/2, and 3/4 of the stream cross-section. We measured canopy

cover in the middle of the stream cross-section, using a spherical densiometer placed 30 cm above the stream surface. PAR was measured on a cloudless day between 10 am and 12 pm with a photometer (Li-Cor Biosciences: Lincoln, NE, USA) placed 10 cm above the stream surface. Benthic substrate was sampled at three locations along the stream cross-section at each 5-m interval, totalizing 60 sampling locations. The dominant substrate at each sampling location was determined following the Wentworth particle size scale. The % cover of each substrate type was calculated by calculating the proportion of sampling locations where a particular substrate type was dominant. To measure nutrient concentrations, we collected four water samples at each site using acid-washed bottles pre-conditioned with stream water. Two of the samples were filtered on site using syringe filters with a pore size of $0.45 \,\mu\text{m}$ (Sarstedt: Nümbrecht, Germany). Samples were kept on ice after collection and then frozen until analysis. Unfiltered samples were used to measure total nitrogen (TN) and total phosphorus (TP) concentrations, while filtered samples were analyzed for ammonium (NH_4^+) , nitrite + nitrate $(NO_2^- + NO_3^-)$, and soluble reactive phosphorus (SRP). Nitrogen concentrations were determined with a Lachat spectrophotometer (Lachat Instruments: Milwaukee, WI, USA), using the phenol-hypochlorite method for NH_4^+ and the cadmium reduction method for TN and $NO_2^- + NO_3^-$, with alkaline persulfate digestion prior to cadmium reduction for TN (Wetzel and Likens 2000). TP and SRP were measured with the molybdenum blue method using an Astoria analyzer (Astoria-Pacific: Clackamas, OR, USA). Water turbidity, pH, and electrical conductivity were estimated using a subset of data collected for a long-term stream monitoring project initiated by L. Chapman. All three water chemistry parameters are measured monthly at each site; we used values recorded between February 2011 and January 2013 to calculate mean values. Water turbidity is measured with a LaMotte 2020e portable turbidimeter (LaMotte Company: Chestertown, MD, USA), pH

with an Oakton pHTestr 1 (Oakton Instruments: Vernon Hills, IL, USA), and conductivity with a YSI Model 30 probe (YSI: Yellow Springs, OH, USA). Stream discharge, water temperature, and dissolved oxygen were measured weekly between June and August 2011 and between January and May 2012, at the same time as stream metabolic measurements were taken (see below). Diel variation in temperature and dissolved oxygen was measured using Handy Polaris 2 oxygen/temperature probes with data logging capacities (Oxyguard: Farum, Denmark). Two probes were placed at the upstream (0 m) and downstream (100 m) ends of the reach for 24 hours; values from both probes were averaged to obtain diel mean, maximum, and minimum temperature and dissolved oxygen concentration. We measured stream discharge by calculating the time required for a conservative tracer (NaCl) to travel through the 100-m reach (Webster and Valett 2011). This method was most appropriate given the shallow depth and abundant structure that characterized the study streams. No statistical analysis of physico-chemical parameters was performed given the low (or absence of) replication for many variables; we only used these data to provide site descriptions and to aid with interpretation of ecosystem structure and function data.

3.3.3 Stocks of basal resources and invertebrate FFGs

Stocks of benthic algae were assessed by measuring area-specific biomass of chlorophyll *a* in periphyton samples (Steinman et al. 2011). Periphyton was sampled at 10-m intervals along the study reach (totalizing 10 samples per stream) from the dominant substrate present at a sampling station, using either a Loeb sampler (for rocky substrates) or a syringe of similar diameter (for silt). Periphyton samples were stored on site in dark bottles with 30 ml of stream water, and then immediately transported to the field station where they were filtered (Whatman

GF/C glass filter paper), covered in tin foil, and frozen until analysis. Pigments were later extracted from filter papers with buffered acetone in the laboratory, where pigment concentration was measured spectrophotometrically and then converted to area-specific units (Steinman et al. 2011). To measure stocks of fine particulate organic matter (FPOM; organic detritus with a particle size range of $> 0.45 \,\mu\text{m}$ to $< 1 \,\text{mm}$), coarse particulate organic matter (CPOM; organic detritus larger than 1 mm), and invertebrate functional feeding groups (FFGs), we collected 10 benthic samples in each stream at 10-m intervals, in the middle of the stream cross-section. We used a quantitative Surber sampler with a quadrat area of 929 cm^2 and a mesh size of 500 μ m (Rickly Hydrological Company: Colombus, OH, USA). In forest streams, this sampling protocol resulted in 5 pool and 5 riffle samples; in farm streams, there was no apparent riffle-pool sequence. Samples were preserved in formalin on site and then sorted under a dissecting microscope in the laboratory. Invertebrates were separated from detritus and stored in smaller sample jars for later identification. The remaining material (detritus) was sorted into CPOM and FPOM samples using nested sieves with mesh sizes of 1 mm and 45 µm. Detritus samples were dried to constant-mass at 60 °C for 48 hours and then weighed to obtain dry mass. Samples were later combusted at 550 °C for 4 hours, after which the remaining material was weighed again to obtain ash weight. Ash weight was subtracted from dry mass to obtain ash-free dry mass (AFDM) of organic matter, which was then converted to area-specific units.

Invertebrates were identified using a variety of taxonomic keys (Day et al. 2001b, Thorp and Covich 2001, Day and de Moor 2002a, b, Day et al. 2002, de Moor et al. 2003a, b, Stals and de Moor 2007, Merritt et al. 2008). Given the lack of taxonomic information for many afrotropical invertebrates, we identified taxa to the family level, which was the most precise taxonomic level at which almost all taxa could be identified. The only exceptions were the family 'Chironomidae', which we split into major subfamilies or tribes to account for the large variation in feeding ecology present in this family, and water mites, springtails, turbellarians, and ostracods, which we identified to either class or order. Each individual was measured for body length using an optical micrometer. We then used published length-mass relationships to convert length to individual dry mass (see Table C1 for length-mass coefficients and references). To validate our method, we dried two samples with contrasting invertebrate communities to constant mass and then directly measured sample biomass. Measured invertebrate dry mass (DM) in these two samples was within 14% and 16% of the DM estimated using length-mass equations. Each invertebrate taxon was then assigned one or two FFGs, namely collector-filterer, collectorgatherer, predator, scraper or shredder. Most FFGs were assigned based on a recent study of invertebrate stomach contents conducted in and around a Kenyan rainforest (Masese et al. 2014b). We found a few taxa (14 out of 79 taxa) that were not present at the Kenyan site; we assigned FFGs to these taxa based on ecological information contained in taxonomic keys (see Table C1 for all FFG classifications and references). We then calculated the total dry mass of each FFG in each sample, and divided the resulting value by the Surber sampler area to obtain area-specific biomass. We also calculated the density of each FFG in each sample (number of individuals m⁻²) to examine whether abundance and biomass data led to similar patterns. Some taxa with flexible diets and more ambiguous FFG classification (e.g., mayfly taxa such as Baetidae, Caenidae, and Leptophlebiidae) were assigned two FFGs, and their biomass/density was split between the two FFGs. The biomass/density of collector-filterers and collectorgatherers were combined to get total 'collectors' biomass, given that these two FFGs feed on the same resource (FPOM).

Land use effects on the area-specific biomass of chlorophyll *a*, FPOM, CPOM, and all FFGs were tested with nested ANOVAs with the factor 'stream' (one of four sites) nested within 'land use' (forest or farm), using periphyton or benthic samples as replicates. Response variables were log-transformed to improve the normality of model residuals. We also used stacked bar charts to illustrate the relative contribution of various taxa to the biomass of each FFG at each site. Finally, we tested for land use effects on the density of each FFG with generalized linear models (GLMs), again using 'stream' as a factor nested within 'land use'. GLMs were fitted with a gamma error distribution to accommodate the skewed distribution of our density data, which could not be improved by common data transformations. Statistical significance of the 'land use' effect in GLMs was assessed with likelihood ratio tests. These as well as all subsequent statistical analyses were conducted in R version 3.0.2 (R Core Team 2013).

3.3.4 Stream ecosystem function

In all study streams, we measured whole-stream metabolism (gross primary production, ecosystem respiration, and production to respiration ratio), litter decomposition (microbial and invertebrate-mediated), and secondary production of invertebrates. Stream metabolic measurements were obtained using the two-stations open-channel diel-oxygen change method (Bott 2011). Oxygen concentration, oxygen percent saturation, and temperature in the middle of the water column were logged every 15 minutes at the upstream (0 m) and downstream (100 m) ends of the study reach for 24 hrs using the Handy Polaris 2 probes described above. Probes were calibrated to within \pm 0.1 mg L⁻¹ of one another before each deployment, and no drift was detectable during the measurement periods. Oxygen production time series were adjusted for reaeration rate using the energy dissipation model (Tsivoglou and Neal 1976, Bott 2011), which was found to accurately predict reaeration rate in streams with similar morphological and hydrological properties as our Kibale streams (Riley and Dodds 2012). Mean water velocity was estimated by dividing reach length (100 m) by the time required for 50% of a conservative tracer (NaCl) to travel from the upstream to the downstream end of the reach (using the same procedure described above for discharge measurements). Ecosystem respiration (ER) was estimated based on reaeration-corrected nighttime changes in oxygen saturation and then extrapolated throughout the entire 24-hr period (Bott 2011). Because of the large diel variation in temperature at the two farm sites, we temperature-corrected ER to a common temperature of 20 °C following the method outlined by Riley and Dodds (2012). Gross primary production (GPP) was calculated as the net difference between daytime changes in oxygen saturation and extrapolated rates of daytime ER (Bott 2011). We also calculated the production to respiration ratio (P/R ratio) by dividing GPP by ER. Metabolic parameters were measured once per week at each stream during two sampling periods, namely the summer dry season of 2011 (5 weeks from June to July) and the winter dry and wet seasons of 2012 (10 weeks from February to May). This sampling design led to roughly 15 temporal replicates for all metabolic parameters for each stream during both dry and wet months, although some replicates had to be discarded due to occasional equipment malfunction or when elephants or cattle disturbed the probes. Land use effects on each metabolic parameter were tested using separate nested ANOVAs with 'site' nested within 'land use' (GPP values were log-transformed prior to the analysis, but ER and P/R values were not).

To measure litter decomposition rates, we conducted a litterbag experiment (Graça et al. 2005) using leaves from *Neoboutonia macrocalyx* Pax (Euphorbiaceae), the only species of tree present in the riparian zone of all of our study reaches (i.e., at least one tree within 5 m of the reach). We also chose to use this tree species because shredders were often associated with *N*.

macrocalyx leaves in benthic samples, and because feeding observations in laboratory aquaria confirmed that two shredder taxa (Calamoceratidae and Lepidostomatidae) readily consumed N. *macrocalyx* leaves (V. Fugère, unpublished data). Leaves were collected near trees located close to each study reach by gently shaking branches and gathering fallen leaves, which were then brought to the laboratory and air-dried in a food dehydrator. A subset of air-dried leaves were weighed, then oven-dried to constant mass at 60 °C for 48 hrs and then weighed again to obtain an air-dried to oven-dried (i.e., DM) conversion equation (DM = $-0.0118 + 0.86 \times air$ -dried mass; R = 0.9988). A subsample of these dried leaves was combusted at 550 °C to estimate mean ash content (10.2 %) and to convert DM to AFDM. Another subset of air-dried leaves was immersed in water for 72 hrs, and then oven-dried and weighed to estimate a correction factor for leaching (leaching-corrected AFDM = $-0.008 + 0.8 \times AFDM$; R = 0.9769). The remainder of air-dried leaves was weighed, rehydrated, and placed in either fine- or coarse-mesh litterbags (mesh sizes = 0.5 and 10 mm). Fine-mesh and coarse-mesh bags, respectively, prevent and allow macroinvertebrate shredders from accessing the leaf that they contain, and can thus be used to compare rates of microbial decomposition (fine-mesh bags) vs. microbial + shredder-mediated decomposition (coarse-mesh bags). A total of 320 bags were constructed, allowing 40 bags of each type to be deployed in each stream. Sites of leaf collection were standardized, such that an equal number of leaves from all four collection sites were used for each stream. Before deployment, the leaching-corrected AFDM of each litterbag was calculated (AFDM_{t0}). Bags were then anchored to the stream bottom at random locations in each study reach using stones and twist ties. Ten bags of each type were subsequently retrieved from all streams at weekly intervals over a 1-month period. The litter content remaining in each bag was dried to constant mass, weighed, and combusted to calculate AFDM of litter retrieved from the stream (AFDM_{t1}).

Leaf mass loss (i.e., decomposition) was then calculated as: $1 - (AFDM_{t1} \times AFDM_{t0}^{-1})$. Land use effects on leaf mass loss (arcsine-transformed) in fine- and coarse-mesh bags were tested using separate nested ANOVAs with 'site' nested within 'land use', including as covariates the number of weeks in-stream and its interaction with land use and site.

To measure secondary production of macroinvertebrates, we used a published empirical model of stream invertebrate instantaneous growth rate (Morin and Dumont 1994). This model provides taxon-specific equations (for Diptera, Ephemeroptera, Plecoptera, and Trichoptera; for other taxa a general growth model is provided) predicting growth rate based on mean individual body mass (heavier invertebrates grow less) and mean water temperature at a site (faster growth in warmer conditions; Morin and Dumont 1994). We used these equations to estimate the growth rate of all taxa in all samples, using our individual dry mass and temperature measurements to calculate mean body mass and mean water temperature. To estimate production, we then multiplied the instantaneous growth rate of a taxon in a sample by its area-specific biomass to obtain area-specific instantaneous production (mg dry mass $\times m^{-2} \times y^{-1}$). Finally, we summed production estimates of all taxa from all samples from the same site to obtain a single value of total area-specific invertebrate production in the study reach. Pooling multiple benthic samples provides a more reliable estimate of stream secondary production (Morin and Dumont 1994), but this procedure also resulted in a lack of replication. As such, no statistical analysis of secondary production was conducted.

3.3.5 FFG abundance in a larger number of Kibale streams

We measured several ecosystem functions within the same streams, sometimes including multiple temporal replicates, which limited the number of streams that we could study. To test

whether our results for invertebrate FFGs were valid at a spatial scale larger than the area in the vicinity of the field station, we re-analysed a stream invertebrate dataset collected as part of a large biodiversity survey in the Kibale region (see Chapter 2). Briefly, this dataset includes macroinvertebrate abundance sampled once in 11 forest streams inside Kibale (dispersed throughout the northern half of the park) and 23 farm streams outside of Kibale (from areas both west and east of the park), the latter having similar watershed land use than the farm streams included in this study. Five invertebrate samples were collected at each site with a D-shaped kick net with a mesh size of 1 mm and then grouped to get a single pooled sample per site. Individuals were identified to the same taxonomic level and with the same taxonomic keys as described above. However, individuals were not measured for body length, such that only abundance (and not biomass) was calculated (see Chapter 2 for more details). We assigned one or two FFG to each invertebrate taxon present in this abundance dataset using the same literature sources as above (see Table C1 for FFG classification). We calculated total abundance of each FFG at each stream, splitting abundance for taxa with two FFGs. We compared the abundance of each FFG between land use classes (farm vs. forest) using separate Wilcoxon rank sum tests. Finally, when the abundance of a given FFG differed between land use classes, we also compared the median abundance at farm and forest sites of all taxa forming that FFG, also using separate Wilcoxon rank sum tests.

3.4 Results

Although trends were not confirmed statistically, farm and forest sites differed on many physico-chemical parameters measured (Table 3.1). Farm streams had notably lower canopy cover and nutrient concentrations, as well as higher PAR, water temperature, and turbidity (Table

3.1). Benthic substrate composition also seemed to vary with land use, with the percentage of silt on the streambed being much higher at farm sites (Table 3.1). Compared to forest sites, the two farm sites had slightly lower pH and conductivity. Slope, width, depth, discharge, and dissolved oxygen varied among sites but these differences were not linked to land use (Table 3.1).

In terms of ecosystem stocks, the most notable differences between farm and forest streams were in stocks of periphyton and FFGs. Farm streams had a higher area-specific biomass of periphyton than forest streams (ANOVA, effect of 'land use': $F_{1,36} = 31.76$, p < 0.0001; Figure 3.2a). Land use had no effect on FPOM biomass (ANOVA, effect of 'land use': $F_{1,36} = 0.34$, p =0.5639; Figure 3.2b), while farm streams had a marginally lower biomass of CPOM than forest streams (ANOVA, effect of 'land use': $F_{1,36} = 3.13$, p = 0.0852; Figure 3.2c). Stocks of invertebrate FFGs did not track changes in stocks of basal resources: compared to forest streams, farm streams had a lower biomass of scrapers (ANOVA, effect of 'land use': $F_{1,36} = 25.22$, $p < 10^{-10}$ 0.0001; Figure 3.2d), collectors (ANOVA, effect of 'land use': $F_{1,36} = 5.64$, p = 0.0229; Figure 3.2e), and shredders (ANOVA, effect of 'land use': $F_{1,36} = 43.83$, p < 0.0001; Figure 3.2f). However, land use had no effect on area-specific predator biomass (ANOVA, effect of 'land use': $F_{1,36} = 0.05$, p = 0.8207; Figure 3.2g). Density followed a slightly different pattern: farm streams had a lower density of both scrapers (GLM, effect of 'land use': $\chi^2 = 16.87$, p < 0.0001; Figure 3.2d) and shredders (GLM, effect of 'land use': $\chi^2 = 67.59$, p < 0.0001; Figure 3.2f), but land use had no effect on collector (GLM, effect of 'land use': $\chi^2 = 0.05$, p = 0.7364; Figure 3.2e) or predator density (GLM, effect of 'land use': $\chi^2 = 0.27$, p = 0.3371; Figure 3.2g). The lower biomass of three invertebrate FFGs at farm sites was due to reductions in the biomass of a few taxa with a high biomass at forest sites: Leptophlebiidae and Elmidae (scrapers, Figure 3.2d), Hydropsychidae (collectors, Figure 3.2e), and Calamoceratidae, Lepidostomatidae, and

Tipulidae (shredders, Figure 3.2f). Predator assemblages also differed between land use classes despite the overall similarity in total biomass. For example, farm sites had a greater biomass of Libellulidae than forest sites (Figure 3.2g).

In terms of ecosystem functioning, measurements of whole-stream metabolism indicated higher GPP at farm sites than at forest sites (ANOVA, effect of 'land use': $F_{1,47} = 60.82$, p < 1000.0001) but only a marginally-significant difference in ER between land use classes (ANOVA, effect of 'land use': $F_{1,47} = 3.88$, p = 0.0548; Figure 3.3a). Hence, the P/R ratio of farm sites was higher than that of forest sites ($F_{1,47} = 111.3$, p < 0.0001), although all streams were still strongly heterotrophic with P/R ratios well below 1 throughout the entire sampling period (Figure 3.3a). Decomposition of N. macrocalyx leaves also differed between land use classes. In fine-mesh bags, land use showed complex interactions with time and site effects (ANOVA, three-way interaction between 'land use', 'site', and 'weeks': $F_{8,143} = 6.16$, p < 0.0001); leaf mass remaining differed between the farm and forest streams in only one of the two watersheds at two time points (Figure 3.3b). In coarse-mesh bags, however, land use had a strong effect on leaf mass loss in both watersheds (ANOVA, three-way interaction: $F_{8,139} = 1.44$, p = 0.18; main effect of 'land use': $F_{1,139} = 184.7$, p < 0.0001), with leaf mass remaining approaching 0% after 4 weeks of decomposition in both forest streams (Figure 3.3b). Interestingly, rates of leaf mass loss at farm sites were similar for fine-mesh and coarse-mesh bags (Figure 3.3b). Finally, land use also had an impact on secondary production of invertebrates (Figure 3.3c). Our one-time, pooled estimate of production indicated that area-specific invertebrate production was 66% lower at the farm than forest stream in watershed 1 (2.5 vs. 7.4 g m⁻² y⁻¹) and 41% lower in watershed 2 (3.2 vs. 5.5 g m⁻² y⁻¹; Figure 3.3c).

By conducting a FFG-based analysis of invertebrate abundance recorded in a previous survey of 11 forest streams and 23 farm streams in the Kibale area (Chapter 2), we found that farm and forest streams had a similar abundance of scrapers (W = 119, p = 0.7966), collectors (W = 107, p = 0.4842), and predators (W = 136, p = 0.7404; Figure 3.4). However, farm streams had a lower median abundance of shredders relative to forest streams (W = 16, p < 0.0001; Figure 3.4), in line with the trends reported above for biomass and density in the four focal streams where ecosystem functions were measured. Farm streams had a lower abundance of all shredder taxa occurring in and around Kibale, namely Calamoceratidae (W = 20.5, p < 0.0001), Lepidostomatidae (W = 34.5, p = 0.0002), Pisuliidae (W = 28, p = 0.0001), and Tipulidae (W = 18, p < 0.0001; Figure 3.4b).

3.5 Discussion

The primary objective of our study was to document land use impacts on stream ecosystem structure and functioning in the afrotropics, a region of the world that remains poorly studied despite exhibiting high rates of current deforestation (Chapter 1). We measured multiple ecosystem stocks and functions in four focal streams in and around Kibale National Park, Uganda, and performed a functional feeding group analysis on a previously published dataset of aquatic invertebrate abundance in a larger number of regional streams (Chapter 2). Our main findings for the four focal streams were that: 1) agricultural streams had a greater biomass of benthic algae and higher whole-stream GPP and P/R ratio than forested streams, yet were still strongly heterotrophic; 2) shredders had a very low biomass in agricultural streams, which led to much slower detritus decomposition rates at farm sites despite no change in microbial decomposition rates; and 3) stocks of invertebrates did not match stocks of basal resources, as

agricultural streams had, relative to forest streams, a lower biomass of scrapers and collectors despite their higher algal biomass and comparable FPOM biomass. The lower biomass of all FFGs except predators at farm sites led to lower overall secondary production of invertebrates. Then, our functional feeding group analysis of invertebrate abundance in 34 farm and forest streams around Kibale confirmed that all shredder taxa were virtually extirpated from agricultural sites, suggesting that at least some of our results for the four focal streams apply to the entire agricultural area around Kibale. As a whole, this study reveals strong but complex responses of afrotropical streams to land use, which was only possible by measuring multiple ecosystem stocks and functions within the same set of streams.

Agricultural land use stimulated autochthonous production in our study streams, as shown by the higher algal biomass, GPP, and P/R ratio of farm streams. This finding is consistent with conclusions of meta-analyses revealing generally positive effects of agricultural land use on stream GPP and P/R ratios (Young et al. 2008, Bernot et al. 2010, Finlay 2011). This increase is likely due to greater irradiance (PAR) at farm sites (Mulholland et al. 2001, Bernot et al. 2010). The two farm streams, however, were still strongly heterotrophic, with P/R ratios well below 1 (maximum P/R ratio including all sites and sampling weeks was 0.19). GPP and P/R values of the two forest sites corresponded to what has been reported for other pristine tropical sites (e.g., Ortiz-Zayas et al. 2005), but GPP and P/R values of the two farm sites were lower than that of other tropical, agricultural streams (e.g., Gücker et al. 2009, Silva-Junior et al. 2014). This relatively modest increase in primary production at farm sites relative to forest sites is likely due to nutrient limitation, as the concentration of nutrients such as SRP is the second most important factor determining GPP levels after PAR (Mulholland et al. 2001). Indeed, farm streams had lower nutrient concentrations than forested streams, which is opposite to what is

usually reported (Allan 2004, Bernot et al. 2010, see Masese et al. 2014a, for an afrotropical example). Additional sampling would be required to distinguish the cause of these low nutrient concentrations, but we speculate that one important factor could be the high biomass of emergent macrophytes at farm sites, which can strongly influence stream nutrient dynamics (e.g., Levi et al. 2015). Low fertilizer usage leading to nutrient-depleted soils, as is common throughout the afrotropics (Sanchez 2002), could also be a key factor, but data on fertilizer usage in the region are currently unavailable. Finally, higher water turbidity at farm sites likely contributed further to limit GPP despite high PAR on the stream surface (Young and Huryn 1999). Regardless of what limited the increase in primary production at farm sites, the small increase that we did observe was not transferred to the primary consumer level. While we might have expected higher scraper biomass to align with higher primary production at farm sites, scraper biomass and density was lower at farm sites in our focal study of four streams, and in the broader regional data set, scraper abundance did not differ between farm and forest streams. Some dominant scraper taxa in the Kibale region are sensitive to pollution or habitat degradation (e.g., Leptophlebiidae, Elmidae), which may have prevented increases in scraper abundance at degraded farm sites where water temperature, silt cover on the streambed, and water turbidity were all higher. Alternatively, the higher GPP and algal stocks at farm sites could be based on a shift in algal community composition from palatable diatoms to unpalatable green algae, which could also limit consumer growth (Bunn et al. 1999).

Our second important (and perhaps most striking) result was the almost complete disappearance of shredders at agricultural sites, leading to much slower litter decomposition rates in coarse-mesh bags. This finding seems robust given that all measures of shredder density, biomass, and abundance indicated low abundance (or absence) of shredders in all agricultural streams sampled around Kibale. Other studies from Kenya and Madagascar have also reported negative impacts of deforestation on shredder biomass and/or litter decomposition rates (Benstead and Pringle 2004, Masese et al. 2014b, a), as have studies from other tropical regions (Encalada et al. 2010, Silva-Junior et al. 2014). The large difference in decomposition rates between fine-mesh and coarse-mesh bags at forest sites confirms the functional importance of shredders in afrotropical streams (Masese et al. 2014a, b), which contradicts the prevalent hypothesis that shredders play a less important role in detritus processing in tropical than temperate streams (Boulton et al. 2008, Boyero et al. 2011b). Agricultural land use affected all dominant shredder taxa in Kibale streams, namely Calamoceratidae, Lepidostomatidae, Pisuliidae, and Tipulidae, all of which were reported as important shredders at other tropical sites (Encalada et al. 2010, Boyero et al. 2011a, Masese et al. 2014b). Understanding the causes of this decline would require further experimentation, but it is likely that shifts in both water quality (e.g., higher water temperature) and litter quality and quantity at farm sites contributed to shredder extirpation (Benstead and Pringle 2004, Boyero et al. 2011a, Masese et al. 2014a, Wallace et al. 2015). In contrast, rates of microbial litter breakdown in fine-mesh bags did not differ between land use categories (see also Encalada et al. 2010). Numerous studies from temperate regions report faster microbial decomposition at agricultural sites, with temperature increases and nutrient enrichment usually invoked as causal mechanisms (Young et al. 2008, Woodward et al. 2012). Farm streams in this case had lower nutrient concentrations than forest streams, which, within the range of dissolved nitrogen and phosphorus concentrations observed, would be expected to result in slower microbial decomposition at farm sites (Woodward et al. 2012). However, nutrient-associated decreases in decomposition rate may have been

compensated for by positive effects of higher water temperature at farm sites (Boyero et al. 2011b), resulting in no net change in microbial decomposition rate.

Changes in stocks of basal resources at farm sites did not correspond to changes in stocks of invertebrate FFGs. In our four-stream study, farm sites had a lower biomass and density of scrapers and shredders, as described above, but also a lower biomass of collectors despite no clear difference in FPOM availability between land use categories. Importantly, low standings stocks of three FFGs at farm sites would not have been detectable using only abundance data, as abundance and/or density were poor indicators of biomass (except for shredders, which had very low abundance or were completely absent from farm sites). Low invertebrate biomass at farm streams led to much lower overall invertebrate secondary production despite higher water temperature at these sites. This result could be related to habitat degradation at farm sites (e.g., higher water temperature and turbidity), leading to the extirpation of many sensitive taxa (see Chapter 2), but also to shifts in the availability of basal resources, i.e., reduced litter inputs and lower CPOM availability at farm sites (Benstead and Pringle 2004). Indeed, as demonstrated by a long-term manipulative experiment, a reduction in litter inputs can it itself strongly reduce invertebrate secondary production (Wallace et al. 2015). However, a recent meta-analysis (including mostly temperate sites) has shown that decreases in litter inputs are usually compensated by higher nutrient concentrations (and consequently higher algal biomass) at human-impacted sites, leading to large increases (not decreases) in overall invertebrate secondary production (Finlay 2011). Farm streams around Kibale may exemplify impacts of land use on stream ecosystem functioning in the absence of nutrient enrichment, whereby negative effects of lower detrital inputs and habitat degradation (e.g., siltation) on stream functioning are not compensated for by positive effects of higher nutrient concentrations, thus leading to overall

lower stream productivity. We speculate that this could be a common (and perhaps distinctive) functional response of afrotropical streams to agricultural land use.

In conclusion, our results indicate drastic effects of land use on stream food web structure and ecosystem functioning in the afrotropics. These impacts have important conservation implications given their likely effect on stream ecosystem services. For example, changes in GPP and decomposition rates could affect water quality, while lower secondary production of invertebrates at deforested sites could affect production of exploited invertivorous fishes. All four focal streams include, for example, populations of *Clarias liocephalus* (V. Fugère & L. Chapman, unpublished observation), a catfish species important as a local food fish as well as regionally as baitfish (Yatuha 2015). Finally, given that tropical Africa is expected to be a global hotspot of deforestation and agricultural expansion over the next century (Laurance et al. 2014), additional research is urgently needed to further document land use impacts on afrotropical streams as well as explore potential management strategies. For example, studies from neotropical sites have found that natural vegetation along riparian corridors can mitigate impacts of agricultural land use (elsewhere in the watershed) on invertebrate assemblages (Lorion and Kennedy 2009a, Iñiguez–Armijos et al. 2014) or stream ecosystem functioning (Silva-Junior et al. 2014). Only limited information is currently available on the effectiveness of riparian buffer strips in the afrotropics (Maritz and Alexander 2007, Enanga et al. 2011), such that filling this knowledge gap should be considered a research priority.
was lost during transport.				
Watershed	Mp	anga	Du	ıra
Site	forest 1	farm 1	forest 2	farm 2
altitude range (masl)	1483-1485	1440-1443	1471-1472	1455-1456
slope (m m ⁻¹)	0.02	0.03	0.01	0.01
canopy cover (%)	79.1 ± 1.9	23.19 ± 5	64.6 ± 2.6	17.9 ± 3.5
PAR (μ mol m ⁻² s ⁻¹)	20.5 ± 3.9	952.2 ± 96.3	39 ± 5.2	1053.3 ± 69.5
channel width (m)	0.84 ± 0.05	0.56 ± 0.05	1.48 ± 0.09	0.63 ± 0.05
depth (cm)	6.2 ± 0.6	4.9 ± 0.3	7.8 ± 0.7	8.7 ± 0.5
discharge (m ³ min ⁻¹)	0.19 ± 0.06	0.13 ± 0.01	0.43 ± 0.05	0.35 ± 0.05
substrate composition (%):				
silt (particle diameter < 0.0625 mm)	22.4	84.2	7.6	62.7
sand (0.0625-2 mm)	20.8	15	36.4	23.8
gravel (2-64 mm)	53.4	0.8	29.6	13.4
cobble (64-256 mm)	3.1	0	19	0
boulder (> 256 mm)	0	0	7.1	0
mean water temperature (°C)	17.7 ± 0.2	20.2 ± 0.2	18 ± 0.1	19.2 ± 0.3
minimum water temperature (°C)	16.3 ± 0.3	17 ± 0.4	16.8 ± 0.2	17.1 ± 0.3
maximum water temperature (°C)	18.9 ± 0.2	25 ± 0.3	19.5 ± 0.2	23.6 ± 0.6
mean DO concentration (mg L^{-1})	3.4 ± 0.5	4.1 ± 0.3	7.2 ± 0.1	5 ± 0.2
minimum DO concentration (mg L ⁻¹)	2.6 ± 0.5	3 ± 0.3	6.8 ± 0.1	4.4 ± 0.2

AR: photosynthetically active radiation. *No standard error is reported for that value because one of the two unfiltered water samples	<i>able 3.1.</i> Physico-chemical parameters of the four study streams. \pm indicates standard error of the mean. DO: dissolved oxygen.
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3.6 Tables

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SRP-P 6	TP 18	NO ₂ ⁻ -N+NO ₃ ⁻ -N 79	NH4 ⁺ -N 3	TN 94	utrient concentrations ($\mu g L^{-1}$):	urbidity (NTU) 1	lectrical conductance (µS cm ⁻¹) 16	H	naximum DO concentration (mg L ⁻¹)
2.6 ± 6.4	83.4 ± 5.7	9.6 ± 20.1	8.4 ± 3.1	2.6 ± 23.2		1.5 ± 0.8	3.5 ± 10.3	5.3 ± 0.1	4 ± 0.5
7.1 ± 0.7	30.4 ± 2.9	7.8 ± 0.9	18 ± 1.8	381.8 ± 17.4		22.4 ± 2.3	142.4 ± 7.5	6.1 ± 0.1	5 ± 0.3
59.9 ± 1.6	88.9*	436.4 ± 6	15.5 ± 2.8	977.7		9.4 ± 0.5	202.8 ± 11.8	6.7 ± 0.1	7.5 ± 0.1
7.8 ± 0.9	66.6 ± 0.4	1.9 ± 1.6	11.1 ± 0.5	372.3 ± 17.4		14.6 ± 1.9	150.3 ± 7.7	6.3 ± 0.1	5.6 ± 0.1

3.7 Figure captions

Figure 3.1. Maps of study sites. Left, outline of Kibale (in grey) indicating the location of the field station and the two rivers draining the area. The location of Kibale within Uganda is shown on the inset map. Right, map of area around the field station, indicating the location of the four study sites (circles) and the divide between the two regional watersheds (dotted line).

Figure 3.2. Stocks of basal resources and invertebrate FFGs in forest and farm streams. a-c: areaspecific biomass of periphyton (a), FPOM (b), and CPOM (c) in the four streams. Grey lines connect sites from the same watershed. Error bars = sem. AFDM: ash-free dry mass. Chl. a = chlorophyll a. CPOM: coarse particulate organic matter. FPOM: fine particulate organic matter. d-f: area-specific biomass (top) and density (bottom) of scrapers (d), collectors (e), shredders (f), and predators (g) at all sites. For each FFG, stacked bar graphs indicate the fraction of total sampled biomass contributed by various dominant invertebrate taxa. Symbols and error bars in density plots indicate the mean and standard error of 10 benthic samples. DM: dry mass. ind.: individual.

Figure 3.3. Whole-stream metabolism, litter decomposition rates, and secondary production of forest and farm streams. (a) Whole-stream metabolic parameters measured multiple times between June 2011 and May 2012, including gross primary production (GPP; top panel), ecosystem respiration (ER; middle panel), and production to respiration ratio (P/R ratio; bottom panel). In each panel, the vertical line indicates a time gap on the *x* axis (between August 2011 to January 2012) during which no measurements were taken. In the bottom panel, the dotted line indicates a P/R ratio of 1. (b) Mass loss of *N. macrocalyx* leaves over time at each site in fine-

mesh bags (top) or coarse-mesh bags (bottom). Each symbol (and error bars) represents the mean (and standard error) of 10 replicate mesh bags. The convex hull encircling all data points in the top panel is shown as a grey polygon in the bottom panel to facilitate the comparison of decomposition rates in fine-mesh and coarse-mesh bags. AFDM: ash-free dry mass. (c) Secondary production of invertebrates calculated as the summed production of 10 benthic samples collected at each site. Grey lines connect farm and forest sites from the same watershed.

Figure 3.4. Invertebrate FFG abundance in 11 forest streams inside Kibale National Park and 23 farm streams outside of the park. (a) Mean abundance of all FFGs. (b) Mean abundance of all shredder taxa. error bars = sem. Calamoc.: Calamoceratidae. Lepidost.: Lepidostomatidae. *statistically-significant difference in abundance detected with Wilcoxon rank sum test.

Figure 3.1















Preface to Chapter 4

One of the main knowledge gaps in the literature on land use impacts on streams is the lack of information on effects at the organismal level, on specific stream organisms. For example, Chapters 2 and 3 revealed that farm streams are warmer than forest streams, which could have important eco-physiological and evolutionary implications. Indeed, for ectotherms such as fishes, warmer environmental temperatures leads to increased metabolic rates, which then diverts energy from growth and reproduction. This situation should alter the strength and shape of natural selection operating on metabolic traits, favoring for example the evolution of a lower resting metabolic rate to compensate for the metabolic costs of warming. Alternatively or in addition to such changes in metabolic traits, ectotherms can also increase their prev consumption (and energy intake) to maintain equal energy investment in growth and reproduction despite elevated costs of metabolism. This is then predicted to alter the strength of predator-prey interactions, depending also on the relative effects of warming on prey production. There is an important body of literature discussing these ideas in the context of global climate change (e.g., Gilbert et al. 2014, Merilä and Hendry 2014, Sentis et al. 2015), but impacts of deforestation-associated warming on the metabolic rate and trophic interactions of a stream ectotherm have never been explored. Moreover, metabolic effects of warming are rarely compared with other effects of anthropogenic disturbances on the performance and trophic interactions of ectotherms, yet this is necessary to assess whether predicted warming will indeed be a major force affecting the fitness of organisms (Dillon et al. 2010) and restructuring aquatic food webs (Kratina et al. 2012, Shurin et al. 2012).

In Chapter 4, I asked whether deforestation-associated warming affects the metabolism, growth, and predator-prey interactions of the cyprinid fish *Barbus neumayeri*, found in both forested and deforested streams around Kibale. I used respirometry and a long-term acclimation experiment to measure the temperature-dependence of the metabolic and growth rates of *B. neumayeri* from two farm and two forest populations, testing for local adaption to deforested (warmer) conditions. I also conducted a mark-recapture study in all four streams to measure the natural growth rates of *B. neumayeri* in situ. I then modeled effects of stream warming on the energetic needs of *B. neumayeri* for growth and metabolism in farm and forest streams, as well as on the production of its invertebrate prey items, to ask whether warming has a net weakening or strengthening effect on fish-invertebrate interaction strength (sensu Gilbert et al. 2014). Finally, I compared temperature-related and temperature-unrelated effects of land use on fish-invertebrate interactions, to assess the relative importance of warming in determining food web dynamics in human-altered ecosystems.

Impacts of deforestation-induced warming on the growth and trophic interactions of a stream fish: do increased metabolic costs matter in nature?

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4.1 Abstract

For ectotherms, anthropogenic warming increases energy requirements for metabolism, which should lead to either growth impairment or increased consumption and stronger top-down trophic interactions. However, such consequences may be mitigated by thermal adaptation that compensates for increased metabolic costs, and by higher prey production at warmer temperatures that weakens predator-prey interactions. Moreover, when compared with other drivers of interaction strength also affected by anthropogenic disturbances (e.g., predator and prey density), metabolic effects of warming could have a relatively weak impact on predatorprey interactions. We examined effects of deforestation-associated warming on the metabolism, growth, and top-down trophic interactions of a stream fish occurring both inside and outside of a protected afrotropical rainforest. Using a combination of temperature acclimation experiments, metabolic measurements, and quantification of natural growth rates in both warm (deforested) and cool (forested) streams, we showed that metabolic costs of warming decreased fish growth in the laboratory but not in the field. We found no evidence of thermal adaptation, suggesting that fish in deforested streams must increase consumption to achieve similar growth despite higher metabolic costs. Although this could strengthen fish-prey interactions, we measured invertebrate production in warm and cool streams and found that warming increased prey production more than fish metabolism, and thus had a net weakening effect on interaction strength. Most importantly, impacts of land use on fish and invertebrate density not directly related to temperature had a much stronger influence on fish-invertebrate interaction strength than temperature effects. We conclude that many ectotherms might be able to offset the metabolic costs of warming with a small increase in consumption that has little effect on predator-prey interactions, and that other ecological impacts of anthropogenic disturbances such as changes in population density are likely more important in determining food web interactions.

4.2 Introduction

Many ecosystems worldwide are experiencing anthropogenic increases in temperature associated with land use changes, thermal pollution, and/or global climate change (Burrows et al. 2011, Kirillin et al. 2013, Macedo et al. 2013). For organisms with a body temperature that is a direct function of environmental temperature (ectotherms), a warmer environment can lead to an increase in metabolic rate that diverts energy from growth and reproduction (McNab 2002). When energy is limited, for example in laboratory experiments using restricted food ration or in nature when resource availability is low, ectotherms such as fishes can be unable to offset the metabolic costs of warming and consequently suffer growth impairment and fitness declines (Cui and Wootton 1988, Donelson et al. 2011, Carey and Zimmerman 2014). However, when energy supply is sufficient, and when warming is not severe enough to impair cardiac function (Farrell et al. 2008, Pörtner and Farrell 2008), ectotherms can compensate for metabolic costs of warming by consuming more prey so as to achieve similar (or even higher) growth rates (Cui and Wootton 1988, Neuheimer et al. 2011, e.g., Carey and Zimmerman 2014). Such an increase in energy intake and prey consumption should then lead to stronger trophic interactions (defined here as the fraction of biomass produced by one species that is consumed by another species; Gilbert et al. 2014), suggesting that warming could result in a general strengthening of predator-prey interactions in food webs (Sanford 1999, Hoekman 2010, Rall et al. 2010, Shurin et al. 2012).

Much research on anthropogenic warming has been conducted in experimental settings or via modelling, and when temperature effects on growth, metabolic rate, and/or consumption are detected, it is often speculated that warming will also have an impact on the fitness or trophic interactions of the study species in nature. Experimental or theoretical approaches have been critical in isolating and detecting specific effects of temperature; however, impacts of warming on ectotherms might be more modest in natural settings for several reasons. First, metabolic effects of warming could be buffered in part by thermal adaptation, i.e. phenotypic plasticity or contemporary evolution in thermal physiology in response to warmer conditions (Angilletta 2009, Merilä and Hendry 2014, Sandblom et al. 2014, Sentis et al. 2015). Second, warming might have minimal fitness consequences if individuals can simply consume slightly more prey to offset a rise in metabolic costs. Third, even when warming increases predator metabolism and

prey consumption, this may not result in stronger top-down trophic interactions, as temperature also influences prey production (Rall et al. 2010, Hannesdóttir et al. 2013, Gilbert et al. 2014). If warming stimulates prey production more than prey consumption by predators, it could have a net weakening effect on top-down interactions. Finally, even when warming has an effect on predator-prey interaction strength, it does not necessarily follow that this effect will significantly influence community dynamics. In food webs where there are strong fluctuations in other drivers of interaction strength such as predator and prey density, it is possible that small increases in predator consumption due to warming have a relatively minimal effect on overall energy flow. To answer this question, one would need to compare warming effects on predator metabolism with other influences on interaction strength.

Our aim was to assess whether, and by how much, warming by a few degrees can influence fitness and trophic interactions of an ectotherm in a natural ecosystem experiencing multiple stressors. Our study compared streams subjected to intensive anthropogenic land use to nearby streams in a protected forest. Catchment deforestation is one of the most important threats to stream ecosystems worldwide (Allan 2004, Vörösmarty et al. 2010), with tropical streams currently experiencing particularly fast rates of deforestation and agricultural expansion (Ramirez et al. 2008, Laurance et al. 2014). Loss of riparian tree cover and associated increases in solar energy reaching the stream surface can lead to a rapid and persistent rise in water temperature of several degrees; some authors have found the mean water temperature of tropical agricultural streams to be 4 °C warmer than forested streams from the same region (Macedo et al. 2013, Carlson et al. 2014). Such acute and severe warming should strongly influence metabolic costs in ectotherms inhabiting deforested streams, yet this hypothesis remains largely unexplored. Importantly, other impacts of land use also have strong effects on stream

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communities. For example, decline in habitat quality associated with streambed sedimentation or a loss of woody debris can influence the density of both fish and the invertebrates on which they prey (Wright and Flecker 2004, Wantzen 2006), which should also alter the strength of predatorprey interactions. Streams affected by land use therefore constitute an excellent system to compare the relative importance of warming and other temperature-unrelated anthropogenic influences on the fitness and trophic interactions of ectotherms.

We studied various populations of a stream-dwelling cyprinid fish found inside and outside of a protected rainforest in Uganda, East Africa, surrounded by pastures and agricultural land. We first confirmed that deforested streams are indeed warmer than forested streams, and then assessed the effect of deforestation-associated warming on fish resting metabolic rate (RMR), growth, and top-down trophic interactions. We adopted an integrative approach combining methods and concepts from evolutionary biology, physiology, and community and ecosystem ecology. We used respirometry and an acclimation experiment to isolate temperature effects on fish metabolism and growth, and to reveal any (potentially adaptive) divergence in these traits between populations. Then, we measured natural growth rates in the focal populations to assess whether warming had fitness consequences in situ. To estimate predatorprey interaction strength, we then quantified invertebrate production and calculated the fraction of production required to sustain fish growth and metabolism at each site. Finally, we decomposed land use impacts on interaction strength into temperature-related and unrelated effects. We asked the following questions: (1) do farm populations have a lower metabolic rate than forest populations due to local adaptation or phenotypic plasticity? (2) Do metabolic costs of warming impair growth in the laboratory when food availability is limited and/or in the field where fish can presumably increase their consumption? (3) Do warmer temperatures at farm sites increase benthic prey production, and if so by how much relative to fish metabolism? I.e., does warming weaken or strengthen fish-invertebrate interactions? (4) How important are effects of warming on predator-prey interactions relative to impacts of land use not directly related to temperature, for example changes in fish or invertebrate density associated with habitat degradation?

4.3 Materials and methods

4.3.1 Study location and species

Kibale National Park (hereafter Kibale) is a 795 km² mid-altitude (1100-1600 m), moist evergreen rainforest located in southwestern Uganda (park geographical range: $0^{\circ}13' - 0^{\circ}41'$ N, 30°19' – 30°32' E). Kibale, located in the 'Eastern Afromontane biodiversity hotspot' described by Conservation International, is one of the last large forest fragments in Uganda and one of the few remaining mid-altitude rainforests in East Africa (Plumptre et al. 2007, Wrangham and Ross 2008). The park is drained by two mid-size regional watersheds: the Mpanga and Dura watersheds (hereafter referred to as watershed 1 and 2, respectively). This study was conducted near the Makerere University Biological Field Station (MUBFS), situated in the northwestern section of the park (Figure D1a in Appendix D). MUBFS is conveniently located near the park border and at the divide between watersheds 1 and 2, which allows for easy access to both forested and deforested streams in each watershed. We studied one forest and one farm firstorder stream from each watershed (Figure D1b). Inside Kibale, our study streams were situated in tall forest with canopy > 25 m high. Our study streams outside of the park drained an area dominated by intensive smallholder agriculture, including a mix of pasture and small-scale subsistence agriculture (Southworth et al. 2010). Except for rare shade trees or exotic trees planted for timber, this agricultural area was completely deforested by the 1960s.

In each stream, we delineated a 100-m reach in which we carried out all measurements and sampling (Figure D2 in Appendix D). The four reaches had a roughly similar gradient (range = 0.5 - 3%), mean discharge (range = $0.13 - 0.43 \text{ m}^3 \text{min}^{-1}$), mean wetted width (range = 0.56 -1.47 m), maximum depth (range = 0.12 - 0.43 m), mean pH (range = 6.3 - 6.7), and mean conductivity (range = $142 - 203 \ \mu\text{S cm}^{-1}$). Canopy cover measured with a spherical densiometer placed 30 cm above the stream surface was less than 25% for farm sites (and constituted entirely of emergent macrophytes < 1 m tall) but above 60% at forest sites (Figure D2). On a cloudless day between 10 am and 12 pm, photon flux density 10 cm above the water surface averaged 952 and 1053 μ mol m⁻² s⁻¹ at the two farm sites and 21 and 39 μ mol m⁻² s⁻¹ at the two forest sites (measurement made with a LI-COR 189 photometer; see Chapter 3). Such large differences in canopy cover and solar radiation should induce significant warming in farm streams.

Each stream included a population of *Barbus neumayeri*, a widespread benthivorous cyprinid fish with a maximum (observed) standard length of 82.4 mm at our sites. *B. neumayeri* is the most abundant predatory fish in these streams such that it likely exerts considerable top-down influence on the stream invertebrate community. The only other two (less-abundant) fish species in these streams are introduced guppies (*Poecilia reticulata*) and the catfish *Clarias liocephalus*. In each watershed, the farm and forest fish populations are separated by a hypoxic papyrus swamp with a dissolved oxygen concentration generally < 1 mg O₂ L⁻¹ (watershed 1: Chapman et al. 1999; watershed 2: L. Chapman, unpublished data; Figure D1b). Although swamp-adapted populations of *B. neumayeri* are found in some papyrus swamps, stream-adapted populations lacking traits for hypoxia tolerance (e.g., enlarged gills) very rarely disperse through papyrus swamps, and there is evidence for genetic differentiation between low-oxygen swamp populations and connected high-oxygen stream populations (Chapman et al. 1999, Harniman et

al. 2013). Gene flow and dispersal between farm and forest populations should therefore be low in each watershed, preventing fish migration back into the forest when the two farm streams were deforested. Molecular studies have also established that populations from watersheds 1 and 2 are genetically distinct (Harniman et al. 2013), confirming that each forest-farm population pair constitute an independent replicate to test for potential thermal adaptation to deforested (warmer) conditions.

4.3.2 Stream temperature measurements

We measured water temperature at each site over a 12-week period spanning the end of a dry season and beginning of a wet season. We measured temperature variation over 24 h using two Handy Polaris 2 data loggers (Oxyguard: Farum, Denmark) placed at a depth of 10 cm at the beginning and end of one of the 100-m reaches. Temperature was recorded every 15 min with an accuracy of \pm 0.2 °C. When measurements at a site were completed, the dataloggers were transferred to another stream, such that all streams could be measured once per week. Measurements from the two dataloggers from the same site and day were averaged to get a single temperature value per 15-min interval. As thermal conditions within each stream should be reasonably homogeneous (all streams have a shallow depth, constant flow, fairly uniform canopy cover, and no known groundwater inflow), the mean temperature value taken at two locations of a 100-m reach should be representative of the temperature experienced by *B. neumayeri* at that time/site. We calculated an average diel temperature curve for each site by taking the mean value (\pm 95% confidence intervals) at each time point from all 12 diel temperature time series. We also noted the maximum and minimum temperature by performing ANOVAs with

planned contrasts comparing the two farm sites with the two forest sites. This analysis as well as all subsequent statistical analyses described below were conducted in the statistical computing software R version 3.0.2 (R Core Team 2013).

4.3.3 Temperature acclimation experiment and respirometry

We used minnow traps to catch 6 to 11 fish from the study reach in each stream. A total of 38 fish were captured and transported to our aquatic facility at McGill University, Canada. Each fish was measured (wet mass and standard length) and tagged with visible implant elastomers (Northwest Marine Technology: Shaw Island, WA) to allow for individual recognition. Wet mass of fish ranged from 0.88 to 5.96 g, standard length from 37.1 to 69.2 mm. Fish were housed in 37.5-L aquaria in groups of 3-4 individuals from the same population. Group composition was designed to standardize as best as possible total fish biomass in each aquarium. Aquaria were filled with aged tap water conditioned with NovAqua® (Kordon: Hayward, CA). Underwater pumps (Hagen: Baie d'Urfé, QC) with sponge biofiltration were used to filter water. Aquaria were exposed to a 12h:12h light:dark photoperiod. Conductivity, pH, ammonia concentration, nitrate concentration, and dissolved oxygen were measured weekly to monitor water quality. Aquaria were placed in a room with precise temperature control, at an ambient air temperature of 16 ± 0.2 °C. This air temperature led to a mean water temperature in aquaria of 18 ± 0.3 °C due to the warming effects of the electrical pumps.

Half of the aquaria were maintained at 18 °C while the other half were heated to 23 ± 0.3 °C with submersible heaters (Hagen: Baie d'Urfé, QC). We chose 23 °C as our 'warm treatment' to produce a sufficiently broad temperature range to calculate an activation energy for metabolic rate, and because maximum water temperature is on average 5 °C higher at farm sites than forest

sites during the afternoon (see results). Room and water temperature were recorded daily to ensure that water temperature in each tank was always within 0.3 °C of the target temperature. Fish were kept in their respective temperature treatment for six months. Fish were fed daily with flake food for tropical fish (Tetra: Blacksburg, VA). We fed each aquarium 4 mg (dry mass) of food times the number of fish in the tank, as recommended by the food supplier. Assuming equal food consumption among fish within each aquarium, this feeding regime resulted in 280.4 J fish⁻¹ day⁻¹. During the last two months of treatment, all fish were individually measured once for resting metabolic rate (RMR) using respirometry (see below). Hence, all respiration measurements were taken after at least four months of acclimation. Then, at the end of the six months period, fish were measured again for mass and length, and then moved to a tank with the opposite temperature treatment. The entire experiment was repeated for another six months, and each fish was again measured for RMR in the last two months of this interval. At the end of this second growth interval, fish were measured for final length and mass and then transferred to larger holding aquaria for use in other projects. Growth at each experimental temperature was measured as: (mass at the end of the six months interval - mass at the beginning of the interval) \times day⁻¹.

Fish respiration was measured with an intermittent-flow respirometry system (Loligo Systems: Tjele, Denmark). A 1.45-L respirometer was housed in a larger holding tank with a water temperature of 18 or 23 °C, depending on the acclimation temperature of the fish used in the respirometry trial. Temperature control was achieved via cooling with ice packs or warming with an electrical heater. Water in the holding tank was constantly bubbled to ensure 100% dissolved oxygen saturation. The holding tank was emptied in between trials to avoid accumulation of nitrogenous waste products and to minimize microbial growth. We measured

respiration of a single fish per day, after a 24-h period of food-deprivation to ensure that the fish was post-absorptive. The fish was transferred from its housing aquarium to the respirometer and allowed to acclimate for 2 h, after which oxygen consumption measurement cycles started, alternating between 9 min of measurements and 8 min of flushing/re-aeration. Water temperature was also recorded continuously (every second). Dissolved oxygen saturation never dropped below 90% in the respirometer. Oxygen consumption in the respirometer, measured in mg O_2 h⁻¹, was automatically calculated for each measurement interval with the software Autoresp (Loligo Systems: Tjele, Denmark). Oxygen consumption typically declined in the first one to three hours of measurements, and then reached an asymptote, defined here as five consecutive measurements within 0.5 mg O_2 h⁻¹ of each other (i.e., a stable respiration rate over 85 min). Acclimation and respiration measurements were always performed between 10 AM and 5 PM to minimize circadian effects on RMR. Constant water current was maintained throughout the trial at a very low velocity, enough to ensure proper water mixing in the respirometer without inducing fish swimming. Once every three trials, control measurements were performed after the fish was removed from the respirometer, to estimate oxygen consumption due to microbial respiration. Fish RMR was estimated by averaging five respiration measurements taken after oxygen consumption had reached an asymptote, and then subtracting the microbial respiration rate measured closest in time to the respiration trial (day of the trial ± 1 day). All respiration measurements used for RMR calculations were performed when water temperature was within 0.3 °C of the target temperature.

We analyzed growth and RMR data with linear mixed effects models (LMMs), to account for the repeated-measures structure of the dataset (with one measurement per fish per temperature treatment for each response variable). These models included fish identity as a random intercept, and body mass, watershed of population of origin, land use around population of origin, and temperature treatment as fixed effects. We fit the models using the R package 'lme4' (Bates et al. 2014). Significance of fixed effects was assessed by removing the effect from the full model and testing for a significant change in likelihood with a likelihood ratio test. To test relationships between RMR and growth and verify that energy costs of metabolism can indeed impair growth in laboratory conditions with limited food availability, both rates had to be mass adjusted to account for variation in body size. We first converted rates (growth or RMR) to mass-specific values by dividing rates by fish mass. We then found the allometric mass-scaling exponents for growth and RMR by performing linear regressions between ln(mass-specific rate) and ln(mass). The slope of these linear regressions gives the allometric mass-scaling exponent of the mass-unadjusted rate (given by 1 - slope of regression). The mass scaling exponent of RMR and growth were 0.7958 and -0.7464, respectively. We mass-adjusted rates with the following equation: rate \times mass^{-b}, b being the scaling exponent for that rate. The effects of mass-adjusted RMR and temperature treatment on mass-adjusted growth were tested using a LMM with fish as a random factor. We also modeled maximum mass-adjusted growth as a function of massadjusted RMR using a linear quantile mixed effect model with fish as a random intercept (Geraci 2014). We fit the model to the 0.99 quantile; the R package 'lqmm' was used for the quantile regression. No significant interactions between fixed effects were found in any of the LMMs such that we only report results of models without interaction terms.

4.3.4 Mark-recapture study

Each study stream was sampled over a 5-day period. Fences crossing the stream wetted width and buried 30 cm into the stream bed were placed at the beginning and end of the 100 m

reach before trapping to prevent fish dispersal in and out of the study reach during the marking period (i.e., to create 'closed' populations for abundance measurement). Fish were captured with 10 minnow traps placed randomly within the study reach from 5PM to 8AM the next morning. Each captured fish was measured for mass and length, and then tagged with a unique color combination of 3 visible implant elastomers injected into 5 possible landmarks on the right side of the fish. Trapping and fish marking at each site was performed over three consecutive days. We then waited two days before performing one final night of trapping to estimate fish abundance based on the ratio of marked to unmarked fish. We originally planned to calculate a Petersen-Chapman estimate of population size, but given that all but a few captured fish at all sites on this last day of trapping were marked, we simply used the total number of marked fish at a site as our measure of abundance. Fences were then removed.

Recapture was achieved by trapping at each site monthly over a 10-month period. Any recaptured fish was measured for length and mass and released back into the stream. Length and mass growth within each recapture interval was calculated as: (standard length or mass at the end of the interval - standard length or mass at the beginning of the interval) × interval length in days⁻¹. Most fish were recaptured only once during the whole 10-month period, which precluded the use of LMMs to analyze growth. Rather, we simply excluded any earlier recaptures for fish recaptured more than once, and kept a single growth value per fish (corresponding to growth between the day of tagging and the last recapture day; mean interval duration = 107 days, range = 33 - 307 days). We then used ANCOVA to test for effects of stream watershed, land use, and their interaction on length or mass growth. Growth values were log transformed prior to the analysis (adding +1 to compensate for slightly negative growth values) to normalize the variance. Body size was included as a covariate (wet mass for mass growth and standard length for length

growth). We used type III sum of squares to compute F ratios because the number of recaptured fish varied considerably among streams, in part due to abundance differences among sites (see Results). To compare field growth rates with growth in the acclimation experiment, we also calculated mass-adjusted growth rate of recaptured fish using the same equation and scaling exponent as for the laboratory growth rates.

Finally, we also calculated the condition of fish at the time of initial capture, to obtain another measure of individual performance in the field. Condition (relative mass) was measured as $100 \times (\text{mass} \times \text{length}^{-2.884})$. The mass-length exponent (2.884) was calculated using all marked fish from the four populations pooled together. We analyzed the effects of watershed, stream land use, and their interaction on fish condition using a two-way ANOVA.

4.3.5 Fish-invertebrate interaction

We used a bioenergetics approach to evaluate top-down trophic interaction strength, by quantifying the percentage of prey production required to sustain *B. neumayeri* RMR and growth in each stream, during one day, at the time of fish marking for the mark-recapture study. Table D1 in Appendix D provides all equations and variables used to measure interaction strength. Fish growth, fish RMR, and prey production had to be expressed in a common unit, namely J day⁻¹. The growth of all marked fish for one day was estimated by applying a growth model based on body size, the only variable that we measured that had an influence on growth (see Results). We pooled all recaptured fish from all populations and used non-linear least squares to fit a power function predicting mass growth from body mass at the time of capture (Table D1). We used the same mass-scaling exponent for growth than what was observed in the temperature acclimation experiment (-0.7464). The growth model based solely on body size fitted the field recapture data

well (Pearson's r between predicted and observed growth value = 0.49). To convert predicted daily growth from mass units (g day⁻¹) into energy units (J day⁻¹), we used the mean of seven published energy densities of similar-sized cyprinids (values and references provided in Table D1). Daily energy expenditure for RMR for all marked fish was predicted using the following equation adapted from Brown et al. (2004): $i_0 M^{0.7958} e^{-E/kT}$, where i_0 is a normalization constant, M is fish individual body mass, 0.7958 is the mass-scaling exponent for RMR that we calculated in the temperature acclimation experiment, E is the activation energy (temperature-dependence) for RMR, k is the Boltzmann's constant, and T is site temperature in Kelvins. i_0 and E were estimated with our laboratory RMR data, after conversion of RMR from mg O_2 h⁻¹ to watts (J s⁻¹) assuming an energy value of 13.57 J per mg of O₂ consumed (Elliott and Davison 1975). We fitted a linear regression model between $\ln(\text{mass-adjusted RMR})$ and $\ln(1 \times \text{temperature during})$ RMR measurement⁻¹ × k^{-1}); the slope and intercept of this regression give E and ln(i_0). respectively (Brown et al. 2004). Site temperature (T) was calculated at 15-min intervals during a 'an average' day/24-hrs period, by averaging all 12 temperature measurements taken at a given time and site after converting values from C to K. Energy need for RMR was calculated for each 15-min interval and then summed to get total daily energy need. Finally, we summed the energy need for growth and RMR (now both in J day⁻¹) for all marked fish to get their total daily energy requirement for these two components of the energy budget.

To measure prey production, 10 benthic invertebrate samples were collected in each stream at 10-m intervals using a quantitative Surber sampler with a quadrat area of 929 cm² and a mesh size of 500 μ m (Rickly Hydrological Company: Colombus, OH). Samples were preserved in formalin and then sorted under a dissecting microscope in the laboratory (see Chapter 3 for more details). All animals were identified to family level, with the exception of

chironomids (identified to major subfamilies or tribes) and oligochaetes (a class). Each individual was measured for body length using an optical micrometer. We used published lengthmass relationships (Leeper and Taylor 1998, Benke et al. 1999) to convert length to individual dry mass (Table D2 in Appendix D provides all coefficients). Invertebrates were classified as potential previtems based on a previous study of stomach contents in *B. neumaveri* from Kibale (Schaack and Chapman 2004), on FishBase (Froese and Pauly 2015), and on our own qualitative inspection of stomach contents from some recaptured fish in all populations. All taxa occurring in at least one stomach in any of these three sources were considered as potential prey items (Table D2). Excluded taxa contributed <5% of total invertebrate biomass sampled. We calculated the total biomass and mean individual body mass of each prey taxon at each site. We then calculated the instantaneous growth rate of each taxon at each site using taxon-specific empirical models predicting growth rate from mean individual body mass and mean site temperature (Morin and Dumont 1994). Area-specific instantaneous production (mg dry mass \times m⁻² \times dav⁻¹) of each prey taxon at each site was obtained by multiplying area-specific biomass with instantaneous growth rate. Production in units of dry mass was converted to wet mass using proportional dry mass (pDM; dry mass \times wet mass⁻¹) values provided by James et al. (2012). For taxa expected *a priori* to contribute a large fraction of total prey availability, we calculated pDM ourselves by weighing samples of individuals of different size classes before and after 48 h of drying at 60 °C. We converted production of each taxon at each site from $g m^{-2} day^{-1}$ to energy values based on pDM (James et al. 2012). Finally, we summed production of all taxa within a site to obtain total area-specific prey production in J m⁻² day⁻¹ (Table D1).

We calculated the proportion of prey production required to sustain costs of RMR and growth (henceforth 'interaction strength') both *per capita* (RMR + growth of individual fish \times

prey production⁻¹) and at the population-level for all marked fish, after controlling for variation in reach area among sites (RMR + growth of all fish \times reach area⁻¹ \times prev production⁻¹). The latter metric was meant to reveal the impact of among-site variation in fish density on interaction strength. We tested for site differences in *per capita* interaction strength with a two-way ANOVA with watershed, land use, and their interaction as independent variables. No statistical test was used to compare population-level interaction strength as fish abundance was only measured once per site. We examined the relative influence of various impacts of land use on interaction strength by calculating the difference in interaction strength between the farm and forest site within each watershed, and then decomposing that intra-watershed difference into several effects. Decomposition of effect was achieved by modifying the value of the variable of interest to match farm sites to the corresponding forest site from the same watershed, and then recording the resulting decrease or increase in farm-forest difference in interaction strength. For example, to examine effects of warming-induced increases in fish metabolism on interaction strength, we matched the water temperature of farm sites to the temperature of forest sites when measuring energy costs of RMR, and then measured interaction strength again; the **decrease** in farm-forest difference in interaction strength corresponds to the **positive** effect of warminginduced increases in metabolic costs on interaction strength. For *per capita* interaction strength, we manipulated (i.e., examined the relative contribution of) fish mean body mass (affecting growth and RMR), site temperature (affecting RMR and prey production), and 'other' effects of land use on prey production (i.e., the combined effect of changes in prey biomass, composition, and mean body mass). For population-level interaction strength, we also manipulated fish density.

4.4 Results

4.4.1 Stream temperature

Land use strongly influenced diel water temperature variation, with farm streams reaching much higher temperature than forested sites in the afternoon (Figure 4.1a). Around 3PM, mean temperature differed by 5 °C between land use categories (mean temperature of two forest and two farm streams = 19.4 °C and 24.4 °C, respectively). Minimum daily temperature did not differ between farm and forest streams (planned contrast, effect of land use: $F_{1,3} = 3.33$, p= 0.076; Figure 4.1b). Maximum daily temperature was consistently higher at farm than forest streams throughout the sampling period (planned contrast, effect of land use: $F_{1,3} = 57.0$, p <0.001; Figure 4.1c).

4.4.2 Temperature acclimation experiment and respirometry

Both temperature treatment and body mass had a strong positive effect on the resting metabolic rate (RMR) of *B. neumayeri* (Table 4.1; Figure 4.2a). The mass-scaling exponent of RMR was 0.7958. Mean mass-adjusted RMR was 0.095 mg O_2 h⁻¹ at 18 °C and 0.117 mg O_2 h⁻¹ at 23 °C, representing a 23% increase in metabolic rate. Watershed or land use around population of origin did not have an effect on RMR (Table 4.1; Figure 4.2a). Growth rate was also strongly influenced by temperature treatment and body mass, with warm acclimation and greater mass both reducing growth (Table 4.1; Figure 4.2b). Mean mass-adjusted growth was 11.9 mg wet mass day⁻¹ at 18 °C and 6.1 mg wet mass day⁻¹ at 23 °C, a 49% decrease in growth. Growth was not significantly related to watershed or land use around population of origin (Table 4.1; Figure 4.2b). When considering fish from all populations together, mass-adjusted growth rate was negatively related to mass-adjusted RMR after controlling for the effect of temperature treatment

on growth (Table 4.1; Figure 4.2c). Maximum mass-adjusted growth was also negatively related to mass-adjusted RMR (Table 4.1; Figure 4.2c). In summary, warmer temperature led to a higher metabolic rate and a lower growth rate in all populations, and individual variation in metabolic rate correlated negatively with growth rate within each temperature treatment.

4.4.3 Mark-recapture study

A total of 475 *B. neumayeri* were captured and marked at the four sites. In total, 137 fish were recaptured at least once during the 10 months of recapture effort, resulting in a recapture rate of 28.8%. All fish were recaptured at the stream where they were marked. Watershed and stream land use had no effect on fish length growth (Table 4.1; Figure D3a in Appendix D) nor mass growth (Table 4.1; Figure D3b). Body size (length or mass) had a significant negative effect on growth (Table 4.1; Figure D3a,b). The mean mass-adjusted growth rate for all recaptured fish was 10.6 mg wet mass day⁻¹, a value within the range of growth rates observed in the acclimation experiment. There was a significant interaction between land use and watershed for the condition of marked fish (Table 4.1). In watershed 1, fish from the forest stream were in better condition than fish from the farm stream, while the converse was true for watershed 2 (Figure D3c).

4.4.4 Fish-invertebrate interaction

In addition to water temperature, sites differed in other model parameters influencing interaction strength, namely fish mean wet mass (range = 2.5 - 4 g), fish density (range = 0.4 - 4.8 fish m⁻²), prey community composition, prey mean individual body mass (range = 0.24 - 0.64 mg), and total prey biomass (range = 0.11 - 0.47 g m⁻²; Table D3 in Appendix D). These

differences led to clear site divergence in estimated prey production and energy needs for fish growth and RMR (Table D3). Two strong patterns emerged: 1) prey production was much lower at farm sites than forest sites, and 2) population-level energy needs for fish growth and RMR were much larger at one of the two farm sites than at all other sites due to very high fish density (Table D3).

Per capita fish-invertebrate interaction strength (% of prey production needed to sustain the growth and RMR of an individual fish) was much higher at farm sites than forest sites (ANOVA, main effect of land use: $F_{(1,471)} = 205.82$, p < 0.001; Figure 4.3a). There was a significant interaction between land use and watershed, indicating a stronger effect of land use in one of the two watersheds ($F_{(1,471)} = 35.16$, p < 0.001). The main effect of watershed on *per capita* interaction strength was not significant ($F_{(1,471)} = 0.41$, p = 0.522). Decomposing the difference in interaction strength within each forest-farm stream pair revealed that the increased interaction strength at farm sites was primarily related to a reduction in prey production (Figure 4.3b). This reduction was caused by changes in prey community composition, biomass, and mean body size. In both watersheds, elevated temperature at farm sites increased prey production more than it increased fish metabolic costs, and therefore had a net weakening effect on interaction strength (Figure 4.3b).

The area-specific, population-level interaction strength was similar at the two forest sites and at one of the farm sites (watershed 2), but much higher at the farm site from watershed 1 (Figure 4.3c). At this farm site, the percentage of prey production needed to sustain fish growth and RMR exceeded 300%, compared to only 39% at the corresponding forest site. The much higher fish density at the farm site (4.78 fish m⁻²) than the forest site (1.32 fish m⁻²) in watershed 1 was largely responsible for the substantial difference in interaction strength within this stream pair (Figure 4.3d; Table D3 in Appendix D). Temperature effects on fish metabolic rate and prey production had little impact on interaction strength relative to effects of fish density and temperature-unrelated influences on prey production (Figure 4.3d).

4.5 Discussion

We measured the effect of deforestation-associated warming on the resting metabolic rate (RMR), growth rate, and top-down trophic interactions of an afrotropical cyprinid fish inhabiting both forested and deforested streams. We combined evolutionary, physiological, and ecological approaches, an integrative perspective that is seldom adopted in studies of global change. We found that fish from all populations showed a similar increase in RMR with elevated water temperature, suggesting that no adaptive divergence in thermal physiology has occurred between forest and farm populations. Increased RMR with higher water temperature translated into lower growth in the laboratory, where food availability was limited. In the field, where it is likely that fish could simply consume more prey to compensate for increased metabolic costs, growth rates were similar for forest and farm populations. Despite leading to presumably higher consumption, elevated temperature at farm streams did not result in stronger fish-prey interactions because it increased invertebrate production more than fish metabolism. Warming thus had a net weakening effect on fish-invertebrate interaction strength. Most importantly, the combined effects of warming on fish metabolism and prey production were relatively unimportant in determining interaction strength compared to site differences in fish density, prey biomass, and prey community composition. We now discuss in turn each of our main findings.

There is currently much discussion about the possibility that organisms can adapt to warmer climates (e.g., Merilä and Hendry 2014). Acclimation or acclimatization (i.e., phenotypic

plasticity) and adaption to local thermal conditions (i.e., adaptive evolution) can reduce temperature influences on both metabolism and growth (Conover and Present 1990, Angilletta 2009, Donelson et al. 2011, Eliason et al. 2011, Sandblom et al. 2014). In our acclimation experiment, we observed no population divergence in the thermal reaction norm of either metabolic or growth rate. We used wild-caught mature fish, and also included a long acclimation period to a common water temperature before respiration measurements were taken (4 to 6 months); this suggests that neither adaptation nor phenotypic plasticity could lower the RMR of fish from farm streams at high temperature (or, alternatively, that acclimation allowed forestadapted fish to perform equally-well than farm-adapted fish). Gene flow could prevent adaptive divergence between farm and forest populations, yet our mark recapture study indicated no apparent dispersal between farm and forest sites or across watersheds (see also Harniman et al. 2013). Another possible explanation for the lack of adaptive divergence is that the deforestation event was too recent, thus not providing enough time for adaptation to proceed. This hypothesis is also unlikely given that adaptive change in RMR and other physiological traits can occur over only a few generations in some freshwater fishes (Barrett et al. 2011, Handelsman et al. 2013), and that our farm streams were deforested around 50 years ago. If not caused by gene flow or insufficient time for adaptation, the absence of population differences in RMR could be due to: 1) no selection on RMR because metabolic costs of warming do not influence fitness, as our results for natural growth rates suggest; 2) low heritability of RMR (but see Burton et al. 2011); 3) insufficient trait variation for selection to act upon, although we did observe much variation in both RMR and the temperature-dependence of RMR across fish in the laboratory; 4) 'cryptic adaptive evolution' caused by opposing effects of adaptation and phenotypic plasticity (Conover and Schultz 1995, Grether 2005), whereby exposure to warm temperatures could lead to both

negative selection on RMR and a plastic increase in RMR and thus no net change in phenotype. Regardless of the process at play, the outcome is similar: the RMR of fish from farm and forest streams responded similarly to temperature, which should ultimately determine fitness and trophic consequences of metabolic rate variation.

When thermal adaptation does not compensate for the metabolic costs of warming, maintaining equal investment in growth and reproduction (and thus fitness) could be achieved via increased consumption if sufficient resources are available. Some field studies have, like our acclimation experiment, revealed negative relationships between metabolic rate and growth, suggesting that resource limitations can also limit compensatory increases in consumption in nature (Álvarez and Nicieza 2005, Robertsen et al. 2014). Other studies show no effect or positive effects of metabolic rate on growth depending on food availability, which indicates that relationships between RMR and growth are context-dependent (Burton et al. 2011, Auer et al. 2015). Metabolic costs of warming might therefore have greater fitness consequences on predators in top-heavy food webs with strong competition and/or resource limitation. Interestingly, the fraction of benthic prey production needed to sustain fish RMR and growth at one of the two farm sites reached 300%. Fish at that site presumably need to compensate for the insufficient energy availability in the form of benthic invertebrate prey by consuming alternative, lower-quality food sources such as periphyton or detritus, which also form part of *B. neumayeri*'s diet (Schaack and Chapman 2004, see Skelton et al. 2012 for a general discussion of the feeding ecology of small African barbs). Quantitative diet analysis incorporating seasonal variation will be needed to test this prediction. Importantly, even at this farm site where intraspecific competition for benthic prey items should be strong, metabolic costs of warming did not result in lower growth rates.

When interaction strength is defined as the fraction of biomass produced by one species that is consumed by another species (Gilbert et al. 2014), effects of warming on predator-prey interactions depend on the temperature-dependence of both predator consumption and prey production. We found that the higher temperature at farm streams increased prey production more than fish metabolism, leading to a net weakening effect of warming on interaction strength. This finding could be incorrect if we overestimated temperature effects on prey production or underestimated temperature effects on fish consumption. We measured prey production using an empirical model based on 579 field production estimates from various taxa experiencing stream temperature ranging from 0.1 to 25 °C; this model could explain 96% of the variation in production values reported in an independent set of studies not used for model development (Morin and Dumont 1994). It seems extremely unlikely that different parameters would be the main drivers of production in our study streams, or that production of Kibale invertebrates follow a completely distinct temperature scaling. Our estimates of production should thus have captured much of the existing variation among sites. We could have underestimated the effects of temperature on fish energetic needs (and consumption) if other components of the energy budget besides RMR and growth also increase with temperature. However, energy allocation for RMR and growth combined was shown to account for up to 65% of the energy budget of small cyprinid fishes growing at a similar rate than what we report here (Hofer et al. 1985), and even RMR on its own can account for 50% of an ectotherm's energy budget (Burton et al. 2011). Moreover, active (swimming) metabolic rate, the other key component of the energy budget, is often less temperature-dependent than RMR in fish (e.g., Sandblom et al. 2014), such that including it in our analysis would lead to stronger interactions but no increase in the relative effect of temperature on interaction strength. Variation in RMR and growth should therefore be

the main drivers of variation in prey biomass consumed by *B. neumayeri*, and measuring additional components of the energy budget would likely not change the qualitative pattern that we report, i.e. that prey production increased more with warming than predator metabolism and consumption. Natural stream warming experiments in Iceland have shown that warming increases invertebrate biomass even in the presence of invertivorous fish, and even if fish feeding rates increase, which suggests that increases in prey production exceeded increases in predator consumption in this system as well (O'Gorman et al. 2012, Hannesdóttir et al. 2013). Warming might generally have a net weakening effect on fish-invertebrate interactions in lotic systems, but this question remains open.

Regardless of weakening effects of temperature, the *per capita* fish-invertebrate interaction was much stronger at the two farm sites. This effect was due to large reductions in prey production associated with shifts in biomass and composition of the prey community. These effects were almost certainly due to habitat degradation associated with deforestation, for example silt deposition on the stream bed (Wantzen 2006; Chapters 2 and 3). Land use effects on stream invertebrate abundance and community composition are strong and well documented (Allan 2004, Ramirez et al. 2008), hence the use of invertebrate community metrics for biomonitoring of stream water quality (Barbour et al. 1999, Jacobsen et al. 2008). Our two farm streams had invertebrate communities typical of degraded stream habitats, namely a low abundance of sensitive insects (e.g., mayflies and caddisflies) and a high abundance of tolerant dipterans (e.g., chironomids) and non-insect taxa (e.g. oligochaetes). In addition to habitat degradation, the lower biomass of invertebrates at farm sites could have been due in part to increased fish consumption. We obviously sampled the biomass of prey that was not consumed by fish, which should be influenced by fish feeding rates. However, the fact that invertebrate

biomass was similar at the two farm sites despite one site having a fish density roughly 12 times higher than the other site (4.8 vs. 0.4 fish m⁻²) suggests a habitat effect independent of fish consumption (Chapter 3). Warmer temperatures at farm sites could also have lowered invertebrate biomass by excluding some taxa requiring cooler water, but this too would be a habitat-quality effect unrelated to predator consumption. When no taxa are lost from the community, warming in itself does not reduce benthic invertebrate biomass, as shown by a pioneer stream warming experiment (Hogg and Williams 1996). Therefore, we suggest that habitat degradation caused by temperature-unrelated effects of land use led to the local extirpation of many taxa from farm streams, leading to lower invertebrate biomass and production, and consequently stronger fish-invertebrate top-down interactions.

Population-level fish top-down interactions were especially strong at the farm site with unexpectedly high fish density. Even though deforestation can lower fish density via a loss of woody debris (Wright and Flecker 2004), it is possible that agricultural land use instead improved fish habitat quality (or quantity) at that site. A large section of this stream was covered with emergent macrophytes, perhaps because of fertilizer runoff from an upslope field. Significant macrophyte cover should provide structure used by *B. neumayeri* for reproduction, which could have beneficial effects on fish abundance (Skelton et al. 2012). The other farm site with a low density of *B. neumayeri* had a lower macrophyte cover. This hypothesis is highly speculative and would require further testing, as the results reported here do not allow us to precisely understand all impacts of land use on fish density and trophic interactions. The important conclusion that can be derived from the current data is that site-specific effects on fish density had a much greater potential to influence population-level interaction strength than
increases in water temperature. Consequently, even if both farm streams were warmer than their forest counterpart, only one farm stream had stronger population-level top-down interactions.

In conclusion, our study demonstrates that small increases in predator metabolic rate caused by a few degrees of warming can have little impact on either predator performance or predator-prey interactions in nature. Many ectotherms are likely to be found in thermal environments with maximum temperature well below the temperature at which respiratory function is impaired, as is presumably the case for *B. neumayeri*, such that the metabolic costs of warming can be offset with small increases in prey consumption that hardly influence overall energy flow within the food web. Other consequences of anthropogenic disturbances such as nutrient enrichment (e.g., Shurin et al. 2012) or changes in abundance (e.g., this study) are likely to have a much stronger influence on food web interactions. We recommend that laboratory studies on the metabolic effects of warming should be corroborated with field performance data before concluding that warming will be detrimental to a given species in nature. Finally, we also suggest that future research on the temperature-dependence of trophic interactions not only test for significant effects of temperature, but also assess the magnitude of these effects and compare them with other influences on interaction strength.

4.6 Tables

Table 4.1. Results of statistical models testing effects on laboratory RMR and growth, or field growth and condition. Significance of fixed effects in mixed models was assessed using likelihood ratio tests. Maximum mass-adjusted growth was modeled using a linear quantile mixed effect model. All interactions that did not significantly influence model fit were removed from models. Fish mass corresponds to wet mass. RMR: resting metabolic rate.

Response variable	Fixed effect	Test statistic (χ^2 or <i>F</i>)	р					
Laboratory results (linear or quantile mixed effects models with fish as a random effect)								
RMR (mg O ₂ h ⁻¹)	mass (g) 59.96		< 0.0001					
	temperature	21.02	< 0.0001					
	land use	1.16	0.2823					
	watershed	0.27	0.6020					
mass growth (g day ⁻¹)	mass (g)	5.97	0.0146					
	temperature	20.14	< 0.0001					
	land use	0.19	0.6645					
	watershed	0.48	0.4905					
mass-adjusted growth	temperature	6.88	0.0087					
	mass-adjusted RMR	4.74	0.0294					
mass-adjusted growth (max)	mass-adjusted RMR	9.32	0.0023					
Field results (ANCOVA or ANOVA)								
log (1+length growth)	log standard length	25.52	< 0.0001					
	land use	0.02	0.8856					
	watershed	0.02	0.9026					
log (1+mass growth)	log mass	13.32	0.0003					
	land use	0.01	0.9764					
	watershed	0.77	0.3817					
condition	land use	6.61	0.0114					
	watershed	6.45	0.0104					
	land use : watershed	9.99	0.0016					

4.7 Figure captions

Figure 4.1. Water temperature of study streams. (a) Diel temperature variation at the four sites. Thick lines represent mean temperature at every 15 min time interval, calculated from twelve 24 h time series. Shaded polygons around thick lines indicate 95% confidence interval of the mean. (b,c) Minimum (b) and maximum (c) daily temperature recorded at each site during 12 weeks of temperature measurements. Vertical dotted lines indicate the beginning of the rainy season.

Figure 4.2. Laboratory results showing temperature effects on *B. neumayeri* growth and RMR. (a) Mass-adjusted RMR of fish from all populations when acclimated to the two experimental temperatures. Thick lines indicate population means. Thin lines represent individual fish. (b) Mass-adjusted growth rate of fish from all populations when acclimated to the two experimental temperatures. Symbols as in (a). (c) Relationship between mass-adjusted growth rate and mass-adjusted RMR at both experimental temperatures. Red and blue symbols indicate measurements after warm and cold acclimation, respectively. Thin grey lines connect data points from the same fish. Thick lines depict results of a LMM testing for an effect of RMR on growth at both temperatures. The dotted line gives the results of a linear quantile mixed model estimating maximum growth from RMR.

Figure 4.3. B. neumayeri trophic interaction strength in the four study streams. (a) % of daily invertebrate production (J m⁻² day⁻¹) required to sustain the growth and RMR of individual fish in each population (J day⁻¹). Symbols indicate mean values; error bars represent 95% confidence intervals calculated from variance among fish. (b) Decomposition of several effects contributing to intra-watershed differences illustrated in (a). Positive and negative values are effects that

respectively increased or decreased %prey production needed at farm sites, compared to forest sites. 'Other' effects on prey production include changes in invertebrate community composition, mean body mass, or total biomass. (c) % of daily invertebrate production (J m⁻² day⁻¹) required to sustain the area-specific growth and RMR of each *B. neumayeri* population (J m⁻² day⁻¹). (d) Decomposition of several effects contributing to intra-watershed differences illustrated in (c). RMR: resting metabolic rate. T: temperature.





Figure 4.2







Summary and general conclusion

In this thesis, I demonstrated using a meta-analytical approach the important research bias against tropical Africa in the limnological literature on effects of deforestation on inland waters. I then combined several approaches (field surveys of environmental parameters and invertebrate communities, ecosystem functioning assays, laboratory acclimation experiments, respirometry, mark-recapture methods, bioenergetics modelling, and a diversity of statistical procedures) to document strong impacts of land use on streams ecosystems in and around Kibale National Park, Uganda. Deforestation and agricultural expansion in this region affected streams at different levels of biological organization, from organismal physiology to community interactions, biodiversity, and ecosystem functioning. In this general conclusion I summarize the major empirical findings and inferences from this body of work and highlight key areas for future study.

In Chapter 1, I aimed to identify critical areas for future research on deforestation impacts on inland waters based on a consideration of both relative research need and past research effort. I analyzed country-specific data on recent deforestation rates, freshwater fish diversity, water scarcity, importance of inland fisheries for local food security and economic production, and research effort, which was quantified with a systematic literature review. I found that tropical countries exhibited the strongest overlap among deforestation intensity, biodiversity, and reliance of local human populations on ecosystem services provided by inland waters. Furthermore, this analysis revealed that economic development (GDP), not research need, is the best predictor of research effort. Finally, I identified tropical Africa as the only region of the world with a high

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research need and a low research effort, and suggested that future research on impacts of deforestation on aquatic systems should focus on this region.

In Chapter 2, I compared environmental parameters and invertebrate communities of 34 forest and farm stream sites inside and around Kibale National Park, Uganda. I found that land use strongly modified the habitat, community composition, and biodiversity of Kibale streams. Relative to forest streams, farm streams had higher water temperature, a finer benthic substrate, and lower dissolved oxygen, as well as a strikingly different invertebrate community composition. Farm streams were characterized by lower alpha diversity than forest streams; however, among-stream beta diversity was greater in the agricultural landscape than inside Kibale, which led to similar gamma diversity in both landscapes. Recent methods of beta diversity decomposition (Podani and Schmera 2011, Podani et al. 2013, Legendre 2014) confirmed that taxa replacement contributed a similar fraction to total beta diversity in both landscapes.

The primary objective of Chapter 3 was to document land use impacts on afrotropical stream functioning. Here, I first focused in on two forest-farm stream pairs from two watersheds of the Kibale region and measured multiple ecosystem stocks and functions, many of which were significantly affected by land use. Farm streams exhibited higher stocks of benthic algae but lower stocks of all invertebrate functional feeding groups except predators. Relative to forest streams, farm streams were also characterized by higher whole-stream GPP and P/R ratio (although they were still strongly heterotrophic), much slower detritus decomposition rates, and lower overall secondary production of invertebrates. I then re-analysed the invertebrate abundance dataset presented in Chapter 2 (including 34 sites), applying the functional feeding group classification developed for invertebrate samples from the four focal streams. This

functional feeding group analysis confirmed the almost complete absence of shredders at all 23 farm sites, suggesting that at least some our results are generalizable at a larger spatial scale encompassing the whole region around Kibale.

In Chapter 4, I measured the effect of deforestation-associated warming on the resting metabolic rate (RMR), growth rate, and top-down trophic interactions of the cyprinid fish Barbus *neumayeri*, a species that occurs in both forested and deforested streams around Kibale. Using a long-term acclimation experiment exposing fish from four different populations (two farm and two forest populations) to two ecologically relevant temperatures (with each fish being exposed to each temperature for six months). I found that fish from all populations showed a similar increase in RMR with elevated water temperature, suggesting that farm populations did not adapt (thermally) to deforested conditions. Elevated water temperature reduced growth in the acclimation experiment but not in the field, as shown with a mark-recapture study conducted over several months in all four populations. I then used data on invertebrate production (Chapter 3) to show that elevated temperature at farm sites increased prey production more than fish metabolism, and thus that warming in this system is unlikely to result in stronger top-down trophic interactions, as predicted by theory and mesocosm experiments (Hoekman 2010, Shurin et al. 2012, Gilbert et al. 2014). By comparing various influences on the fraction of prey production required at each site to sustain the energy requirements of *B. neumayeri* for growth and RMR, I then found that temperature effects on both prey production and fish metabolism were relatively unimportant compared to temperature-unrelated impacts of land use on prey and fish biomass. I concluded that deforestation in this region is more likely to affect stream food web interactions via habitat modification than via warming.

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The results obtained in this thesis narrow some of the knowledge gaps described in the introduction. Chapter 1 confirmed quantitatively that land use impacts on African inland waters remain poorly studied, as was previously suggested in the tropical limnology literature (e.g., Chapman and Chapman 2003, Thieme et al. 2005, Jacobsen et al. 2008, Masese et al. 2014a). In an attempt to partly remediate to this situation, Chapters 2 and 3 provide the first studies of land use impacts on stream beta diversity and stream ecosystem multi-functionality conducted in tropical Africa. These two studies complement and expand on previous studies documenting effects of deforestation on stream community composition and alpha diversity (Benstead et al. 2003, Benstead and Pringle 2004, Kasangaki et al. 2008, Masese et al. 2014b), or on single ecosystem function (Masese et al. 2014a). Chapter 2 also contributes one of the few (and the first tropical) case studies of land use impacts on stream beta diversity, a topic for which there is currently much interest in stream community ecology (Johnson and Angeler 2014, Hawkins et al. 2015). Measurements of stream ecosystem function in Chapter 3 provide the first values of whole-stream metabolism and invertebrate secondary production ever measured in the afrotropics. Chapter 4 is, to my knowledge, one of two existing studies testing for contemporary adaptation to deforested conditions in a stream fish (the other being Schwartz and Hendry 2010). Chapter 4 is also unusually integrative among ecophysiological studies documenting responses of ectotherms to global change, not only examining impacts of warming on metabolic rate and performance, but also on prey production and trophic interactions. This last chapter also outlines the need to further study land use-associated warming in freshwater ecosystems, as the magnitude of such warming can be comparable or sometimes greater than what is expected to result from global climate change (e.g., Kaushal et al. 2010, Macedo et al. 2013).

Although this thesis contributes significantly to the advancement of knowledge on terrestrial-aquatic linkages in stream ecosystems, especially in the afrotropics, many questions emerged from this study, and addressing those questions would lead to a more comprehensive understanding of deforestation effects on stream organisms, biodiversity, and functioning. For example, we do not know which metacommunity process is responsible for the greater amongstream beta diversity of agricultural sites (Chapter 2; see also Hawkins et al. 2015). It has been argued that only experimental approaches can unambiguously reveal mechanisms of community assembly underlying biodiversity patterns uncovered with survey data (Anderson et al. 2011). However, manipulating key factors influencing beta diversity (e.g., invertebrate dispersal, wholestream productivity, or among-stream habitat heterogeneity) over relevant time scales and with sufficient replication would be logistically impractical in this system, such that a mesocosm approach could be more appropriate (e.g., Chase 2010). Streamside mesocosms have recently been employed to establish causal relationships between multiple anthropogenic stressors and stream community composition or alpha diversity (Piggott et al. 2015a, Piggott et al. 2015b), but this approach has yet to be used to study beta diversity (to my knowledge). For Chapter 3, two important questions that emerge from the results are whether the relatively modest increase in stream primary production observed at agricultural sites is caused by nutrient limitation, and if so whether it underlies declines in stream secondary production. Nutrient enrichment experiments have been conducted in similar-sized streams elsewhere (Nelson et al. 2012, Rosemond et al. 2015), and this could be a promising approach to answer these two questions. Determining the cause of the decline in invertebrate production at farm sites would also be useful to better understand how land use influenced fish-invertebrate trophic interactions (Chapter 4), as these effects were largely based on site variation in invertebrate production. Another important

question left unanswered by Chapter 4 is how fish in forest streams achieve similar growth rates despite higher metabolic costs. I discounted thermal refugia and decreased investment in reproduction as potential explanations based on the shallow depth of the streams and on the high population size at one the two farm sites, respectively. I concluded that fish in farm streams most likely increased their prey consumption to equilibrate their energy budget; it would be interesting to quantify consumption directly to test this hypothesis. Measuring the functional responses of *B. neumayeri* at different temperatures would also allow for more precise modeling of fish-invertebrate interaction strength (see Gilbert et al. 2014). Yet another possible extension for this chapter would be to confirm empirically that top-down trophic interactions at farm sites are indeed stronger (even if not because of temperature increases), using enclosure/exclosure experiments (e.g., Power 1990, Flecker 1996).

Finally, as suggested throughout the thesis, future research should explore management options to alleviate land use impacts on Ugandan streams. For instance, maintaining riparian buffer zones along agricultural streams was shown to be an effective strategy to mitigate effects of land use on the community composition, biodiversity, and functioning of neotropical streams (Lorion and Kennedy 2009b, Lorion and Kennedy 2009a, Iñiguez–Armijos et al. 2014, Silva-Junior et al. 2014). In the afrotropics, forested buffer strips can provide important habitat for terrestrial herpetofauna (Maritz and Alexander 2007) or influence soil nutrient budgets (Enanga et al. 2011), but their impact on streams remain largely unexplored. Given the likely expansion and intensification of agricultural land use in the afrotropics in coming years (Laurance et al. 2014), testing and implementing riparian buffer zones in this region should be considered important from both a research and a conservation perspective.

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Appendix A: Supplementary material for Chapter 1

Table A1. Pearson correlation coefficient between all deforestation, biodiversity, and vulnerability variables. Variables were standardized before the analysis. Asterisks indicate statistically-significant coefficients (*p < 0.05; **p < 0.01; ***p < 0.001).

	Forest loss	Forest loss	Fish	Fish	Water	Fish
	(FAO)	(Hansen)	richness	endemics	scarcity	in diet
Forest loss (Hansen)	0.35**					
Fish richness	0.17*	0.49**				
Fish endemics	0.08	0.36**	0.79***			
Water scarcity	-0.09	-0.43**	-0.52**	-0.35**		
Fish in diet	0.21*	0.25*	0.52**	0.30**	-0.13	
Fish exports	-0.17*	0.08	0.06	-0.07	-0.19*	0.01

Figure A1. Correlation biplot from principal components analysis. Arrows indicate relationships among the first two principal components (PC; dotted lines) and all deforestation (green arrows), fish diversity (blue arrows), and vulnerability (black arrows) variables. Variance explained (%) by each PC is reported in parenthesis. Data points represent individual countries, with the filling color indicating the region to which the country belongs following FAO classification. CAM: Central America; CAR: Caribbean; EAS: East Asia; ESA: East and South Africa; EUR: Europe; NAF: North Africa; NAM: North America; OCE: Oceania; SAM: South America; SSA: South and Southeast Asia; WAS: West and Central Asia; WCA: West and Central Africa.



Appendix B: Supplementary material for Chapter 2

Figure B1. Invertebrate community composition of forest and farm streams. On the heat map, each column represents a site; the same site codes were used as in Figure 2.2. The color saturation of each square within a site column represents the proportion of a given taxon out of the total site abundance, with more saturated square indicating greater relative abundance. Rare taxa (< 20 individuals collected at all 34 sites) were excluded from the heat map (but not from analyses) to reduce figure size. A dendrogram of site community dissimilarity (a rotated version of Figure 2.2a, right panel) is provided above the heat map to facilitate interpretation.


Figure B2. Principal coordinates biplot showing Raup-Crick distance between assemblages within each land use type. Large red circles indicate group centroids, while dotted lines represent the minimum convex hulls around each group.



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Moor (2002a); ⁷Day and de Moor (2002b); ⁸Day et al. (2002); ⁹de Moor et al. (2003a); ¹⁰de Moor et al. (2003b); ¹¹Masese et al. al. (1999); ²Edwards et al. (2009); ³Ganihar (1997); ⁴Leeper and Taylor (1998). FFG references: ⁵Day et al. (2001a); ⁶Day and de biomass was calculated. cg: collector-gatherer; cf: collector-filterer; pr: predator; sc: scraper; sh: shredder. L-M references: 'Benke et M coefficients from another taxon with a similar body shape were used; when this is the case the substitute taxon is indicated after the L-M reference. Taxa without L-M coefficients occurred in the abundance dataset but not in the four study streams for which FFG invertebrate taxa present at our sites. L-M coefficients are used in the following equation: dry mass = a length^b. For some families, L-(2014b); ¹²Merritt et al. (2008); ¹³Stals and de Moor (2007). Table C1. Length-mass (L-M) coefficients, functional feeding group (FFG) classification, and corresponding references (ref) for all

Class	Order	Family	L-M a	L-M b	L-M ref (substitute)	FFG	FFG2	FFG ref
Arachnida			0.1004	3.0526	4	pr	I	11
Bivalvia	Veneroida	Sphaeriidae	I	I	1	cf	I	11
Collembola			0.1533	2.3002	3	cg	I	11
Crustacea	Decapoda	Atyidae	I	I	1	cg		11
Crustacea	Decapoda	Potamonautidae	ı	I	1	sh	ı	11
Crustacea	Ostracoda		0.0299	2.257	4	cg	ı	5
Gastropoda	Caenogastropoda	Hydrobiidae	ı	I	1	SC	I	7
Gastropoda	Heterobranchia	Bithyniidae	ı	I	1	SC	ı	11
Gastropoda	Heterobranchia	Lymnaeidae	ı	I	1	SC	ı	11
Gastropoda	Heterobranchia	Planorbidae	ı	I	1	SC	cg	11

cg	SC	1	2.875	0.0053	Baetidae	Ephemeroptera	Insecta
ı	sh	1	2.681	0.0029	Tipulidae	Diptera	Insecta
ı	pr	1	2.591	0.005	Tabanidae	Diptera	Insecta
	cg	1			Syrphidae	Diptera	Insecta
ı	cf	, <u> </u>	3.011	0.002	Simuliidae	Diptera	Insecta
	pr	1 (Diptera)	2.692	0.0025	Psychodidae	Diptera	Insecta
	cg	1 (Empididae)	2.546	0.0054	Muscidae	Diptera	Insecta
ı	pr	1 (Tipulidae)	2.681	0.0029	Limoniidae	Diptera	Insecta
1	pr	1 (Empididae)	2.546	0.0054	Ephydridae	Diptera	Insecta
ı	pr		2.546	0.0054	Empididae	Diptera	Insecta
	cg	1 (Tanypodinae)	2.503	0.0026	Dixidae	Diptera	Insecta
cg	cf	1			Culicidae	Diptera	Insecta
cg	cf	,	2.728	0.0008	Chironomidae	Diptera	Insecta
	pr		2.503	0.0026	Chironomidae	Diptera	Insecta
sc	cg		2.254	0.002	Chironomidae	Diptera	Insecta
	cg		2.952	0.0007	Chironomidae	Diptera	Insecta
pr	cg	1	ı	ı	Chironomidae	Diptera	Insecta
1	pr		2.469	0.0025	Ceratopogonidae	Diptera	Insecta
	pr	<u> </u>	2.586	0.004	Athericidae	Diptera	Insecta
	sc	1 (Coleoptera)	2.91	0.0077	Scirtidae	Coleoptera	Insecta
1	sh		3.1	0.0011	Ptilodactylidae	Coleoptera	Insecta
	sc		2.906	0.0123	Psephenidae	Coleoptera	Insecta
	pr	4	2.9214	0.0385	Noteridae	Coleoptera	Insecta
	pr	1 (Coleoptera)	2.91	0.0077	Hydrophylidae	Coleoptera	Insecta
sc	cg	4	2.9214	0.0385	Hydraenidae	Coleoptera	Insecta
	pr	1 (Coleoptera)	2.91	0.0077	Gyrinidae	Coleoptera	Insecta
	sc		2.879	0.0074	Elmidae (larvae)	Coleoptera	Insecta
	sc	4	2.9214	0.0385	Elmidae (adult)	Coleoptera	Insecta
	pr	4	2.9214	0.0385	Dytiscidae	Coleoptera	Insecta
ı	pr	2	2.22	0.0408	Hirudinidae	Hirudiformes	Hirudinea

Insecta	Insecta	Insecta	Insecta	Insecta	Insecta	Insecta	Insecta	Insecta	Insecta	Insecta	Insecta	Insecta	Insecta	Insecta	Insecta	Insecta	Insecta	Insecta	Insecta	Insecta	Insecta	Insecta	Insecta	Insecta	Insecta	Insecta	Insecta	Insecta	Insecta
Trichoptera	Trichoptera	Trichoptera	Trichoptera	Trichoptera	Plecoptera	Odonata	Odonata	Odonata	Odonata	Odonata	Odonata	Odonata	Odonata	Lepidoptera	Hemiptera	Hemiptera	Hemiptera	Hemiptera	Hemiptera	Hemiptera	Hemiptera	Hemiptera	Hemiptera	Ephemeroptera	Ephemeroptera	Ephemeroptera	Ephemeroptera	Ephemeroptera	Ephemeroptera
Lepidostomatidae	Hydroptilidae	Hydropsychidae	Glossosomatidae	Calamoceratidae	Perlidae	Protoneuridae	Libellulidae	Lestidae	Gomphidae	Coenagrionidae	Chlorocyphidae	Calopterygidae	Aeshnidae	Pyralidae	Veliidae	Pleidae	Notonectidae	Nepidae	Naucoridae	Hebridae	Gerridae	Corixidae	Belostomatidae	Tricorythidae	Prosopistomatidae	Oligoneuriidae	Leptophlebiidae	Heptageniidae	Caenidae
0.0079	0.0046	0.0046	·	0.004	0.0099	0.0051	0.0076	1	0.0088	0.0051	ı	0.005	0.0082	0.0033	0.0126	0.0099	ı		0.0108	0.0108	0.015	0.0031	0.0108	ı			0.0047	0.0108	0.0054
2.649	2.926	2.926	ı	2.933	2.879	2.785	2.809	ı	2.787	2.785	ı	2.742	2.813	2.918	2.719	3.2164	ı	ı	2.734	2.734	2.596	2.904	2.734	ı	ı	ı	2.686	2.754	2.772
1	1 (Hydropsychidae)	1		1 (Limnephilidae)	1	1 (Coenagrionidae)	<u> </u>		1	1		1	1	1	1	4 (Notonectidae)			1 (Hemiptera)	1 (Hemiptera)	1	1	1 (Hemiptera)			•	1		1
sh	sc	cf	sc	sh	pr	pr	pr	pr	pr	pr	pr	pr	pr	sh	pr	pr	pr	pr	pr	pr	pr	cg	pr	sc	sc	cf	cg	sc	cg
ı	ı	ı	ı		1		ı	ı	ı	ı	ı	ı	ı	sc	ı	ī	ı	1	ı	ı	ı	pr	ı	ı	ı		sc	ı	sc
11	11	11	11	11	11	9	11	11	11	11	9	9	11	11	11	11	11	11	11	10	11	10, 11	10	11	11	12	11	11	11

Turbellaria	Oligochaeta	Insecta	Insecta	Insecta	Insecta	Insecta	Insecta
	Haplotaxida	Trichoptera	Trichoptera	Trichoptera	Trichoptera	Trichoptera	Trichoptera
	Tubificidae	Xiphocentronidae	Psychomyiidae	Polycentropodidae	Pisuliidae	Philopotamidae	Leptoceridae
0.0082	0.0025	0.0056	I	0.0047	0.004	0.005	0.0034
2.168	1.7167	2.839	I	2.705	2.933	2.511	3.212
1	4	1 (Trichoptera)	1	1	1 (Limnephilidae)	1	1
pr	cg	cg	SC	pr	sh	cf	pr
I	ı	I	ı	ı	ı	ı	ı
11	6, 11	12	11	11	11	11	11

Appendix D: Supplementary material for Chapter 4

Figure D1. Maps of field site. (a) Outline of Kibale National Park (KNP) showing the location of Makerere University Biological Field Station (MUBFS) and the main tributaries of the two watersheds draining the park (Mpanga and Dura). (b) Map of area surrounding MUBFS indicating land use, the divide between the Mpanga and Dura watersheds, and the location of the four study streams. Each farm-forest stream pair is separated by a hypoxic papyrus swamp preventing gene flow between stream-adapted populations of *B. neumayeri*.







Figure D3. Field growth rates and condition of fish from the four study populations. (a) Relationship between length growth and standard length at time of marking for fish from all populations. Symbols indicate individual fish; thick lines represent results of ANCOVA model. (b) Relationship between mass growth and mass at time of marking for fish from all populations. Symbols as in (a). Blue and red polygons indicate 95% confidence for growth at a given body mass at 18 or 23 °C, respectively, as predicted from laboratory results. (c) Condition of all marked fish from the four populations. Small symbols represent individual fish; large symbols indicate population means. Symbol nomenclature as in (a).



Variable	Abb.	Equation	Notes
Fish individual growth	GRi	0.0116 M ^{-0.7464}	M: fish wet mass. The same coefficients were used for all fish
rate (g day ⁻¹)			given the lack of population effect on growth rate.
Energy needed for	$\mathrm{GR}_{\mathrm{nrg}}$	4669.82 GR _i	Energy density based on energy density of 4 other cyprinid
growth (J day ⁻¹)			species with a mean body size similar to B. neumayeri
			(mean=4669.82 J g ⁻¹ ; range=3908-5159) ^{1,2,3} .
Individual RMR (J s ⁻¹)	RMR _i	$459.62 \text{ M}^{0.7958} e^{-0.3537/kT}$	Equation from ⁴ . M: body mass; k: Boltzmann's constant; T:
			absolute temperature in K. Normalization constant (459.62),
			mass-scaling exponent (0.7958), and activation energy (0.3537)
			of individual RMR were estimated using laboratory RMR data.
Energy needed for RMR	RMR _{nrg}	86400 RMR _i	Unit conversion of rate denominator from seconds to days.
(J day ⁻¹)			
Individual minimum	EN_{i}	$GR_{nrg} + RMR_{nrg}$	Minimum energy needed (J) by individual fish to sustain RMR
energy need (J day ⁻¹)			and growth for one day.
Energy need of	$\mathrm{EN}_{\mathrm{pop}}$	$(\Sigma EN_i) RA^{-1}$	RA: reach area (m ²). Minimum energy needed (J) by whole fish
population (J m ⁻² day ⁻¹)			population to sustain RMR and growth for one day, expressed
			in unit area.

Table D1. Variables and equations used to model per capita and population-level B. neumayeri trophic interaction strength. Abb.:

abbreviation. RMR: resting metabolic rate.

Prey instantaneous	IG _{tax}	$10^{(a+b \log IM+c TC)}$	IM: mean individual dry mass (mg) of prey taxon at site. TC:
growth rate, taxon-			mean site temperature in °C. Equation and taxon-specific
specific (day ⁻¹)			coefficients (a,b,c,) from ⁵ .
Prey instantaneous	PP _{tax}	IG _{tax} BM PDM ⁻¹	BM: taxon biomass in g of dry mass m ⁻² . PDM: taxon-specific
production, taxon-			% dry mass values to convert production in g of dry mass to g
specific (g m ⁻² day ⁻¹)			of wet mass (see Table D2 for values).
Prey instantaneous	$\mathrm{PP}_{\mathrm{nrg}}$	PP _{tax} (22960 PDM-174.2)	PDM: taxon-specific % dry mass values. Energy density
production, taxon-			equation from ⁶ .
specific (J m ⁻² day ⁻¹)			
Total prey production (J	\mathbf{PP}_{tot}	ΣPP_{mg}	
m^{-2} day ⁻¹)			
Prey production needed		EN _i PP _{tot} ⁻¹	Per capita trophic interaction strength. Figure 4.3a.
per fish (%)			
Prey production needed		ENpop PPtot ⁻¹	Population-level trophic interaction strength. Figure 4.3c.
by population (%)			
¹ Bryan et al. (1996)			
² Duffy (1998)			
³ Ruetz III et al. (2009)			
⁴ Brown et al. (2004)			
⁵ Morin and Dumont (1994	Ċ		

⁶James et al. (2012)

9.84	measured	17	Benke	2.503	0.0026	Tanypodinae	Diptera
12.18	measured	14	Benke	2.926	0.0046	Hydropsychidae	Trichoptera
% of total energy	pDM method	pDM	L-M reference	L-M b	L-M a	Family or <i>subfamily/tribe</i>	Order or <i>class</i>
						y across all sites.	energy availabilit
ite to total prey	t they contribu	ng to the fraction tha	are sorted accordi	rein. Taxa	references the	s et al. (2012) and other	values from Jame
ted using	ctly or estima	either measured dire	ntheses. pDM was	ted in pare	axon is indica	the case the substitute t	used; when this is
her taxon were	ents from anot	milies, L-M coefficie	1998). For some f <i>ä</i>	d Taylor (99); Leeper an	ences: Benke et al. (199	length ^b . L-M refe
mass = a	equation: dry	ants in the following	taxa-specific const	cients are	es. L-M coeffi	jor subfamilies and tribe	were split into ma
iironomids	production. Ch	used to model prey p	nass (pDM) values	onal dry m	s and proporti	-mass (L-M) coefficient	Table D2. Length

1.42	measured	9	Benke	2.591	0.005	Tabanidae	Diptera
1.58	estimated	30	Benke	2.879	0.0074	Elmidae	Coleoptera
2.39	measured	17	Benke (Coenagrionidae)	2.785	0.0051	Protoneuridae	Odonata
2.91	measured	15	Benke	2.875	0.0053	Baetidae	Ephemeroptera
3.48	measured	17	Benke	2.728	0.0008	Tanytarsini	Diptera
5.12	measured	14	Benke	2.809	0.0076	Libellulidae	Odonata
5.74	measured	16	Benke	2.649	0.0079	Lepidostomatidae	Trichoptera
5.93	measured	17	Benke	2.952	0.0007	Chironomini	Diptera
5.95	measured	10	Leeper & Taylor	1.7167	0.0025		Oligochaeta
7.95	measured	17	Benke	2.772	0.0054	Caenidae	Ephemeroptera
7.98	measured	14	Benke (Limnephilidae)	2.933	0.004	Calamoceratidae	Trichoptera
8.05	measured	20	Benke	3.011	0.002	Simuliidae	Diptera
9.43	measured	16	Benke	2.686	0.0047	Leptophlebiidae	Ephemeroptera
9.84	measured	17	Benke	2.503	0.0026	Tanypodinae	Diptera
12.18	measured	14	Benke	2.926	0.0046	Hydropsychidae	Trichoptera
% of total energy	pDM method	pDM	L-M reference	L-M b	L-M a	Family or <i>subfamily/tribe</i>	Order or <i>class</i>

Trichoptera	Diptera	Coleoptera	Coleoptera	Lepidoptera	Trichoptera	Diptera	Coleoptera	Diptera	Diptera	Odonata	Odonata	Plecoptera	Diptera	Trichoptera	Coleoptera	Diptera	Odonata	Coleoptera	Odonata	Ephemeroptera	Trichoptera	Coleoptera	Diptera	Diptera	Diptera	Trichoptera
Hydroptilidae	Limoniidae	Gyrinidae	Chrysomelidae	Pyralidae	Polycentropodidae	Muscidae	Hydrophylidae	Psychodidae	Empididae	Coenagrionidae	Calopterygidae	Perlidae	Dixidae	Philopotamidae	Psephenidae	Ephydridae	Gomphidae	Scirtidae	Aeshnidae	Heptageniidae	Leptoceridae	Ptilodactylidae	Orthocladiinae	Athericidae	Ceratopogonidae	Xiphocentronidae
0.0046	0.0029	0.0077	0.0392	0.0033	0.0047	0.0054	0.0077	0.0025	0.0054	0.0051	0.005	0.0099	0.0026	0.005	0.0123	0.0054	0.0088	0.0077	0.0082	0.0108	0.0034	0.0011	0.002	0.004	0.0025	0.0056
2.926	2.681	2.91	3.111	2.918	2.705	2.546	2.91	2.692	2.546	2.785	2.742	2.879	2.503	2.511	2.906	2.546	2.787	2.91	2.813	2.754	3.212	3.1	2.254	2.586	2.469	2.839
Benke (Hydropsychidae)	Benke (Tipulidae)	Benke (Coleoptera)	Benke	Benke	Benke	Benke (Empididae)	Benke (Coleoptera)	Benke (Diptera)	Benke	Benke	Benke	Benke	Benke (Tanypodinae)	Benke	Benke	Benke (Empididae)	Benke	Benke (Coleoptera)	Benke	Benke	Benke	Benke	Benke	Benke	Benke	Benke (Trichoptera)
14	7	30	30	25	14	15	30	17	23	14	10	18	17	14	30	23	14	30	15	17	40	30	17	15	17	14
estimated	estimated	estimated	estimated	estimated	estimated	estimated	estimated	estimated	measured	estimated	measured	estimated	estimated	estimated	estimated	estimated	measured	estimated	estimated	estimated	measured	measured	estimated	estimated	estimated	estimated
0.01	0.02	0.02	0.03	0.03	0.04	0.05	0.09	0.12	0.15	0.18	0.18	0.19	0.23	0.23	0.27	0.30	0.36	0.42	0.69	0.71	0.77	0.92	0.92	0.94	1.09	1.09

<i>Table D3</i> . Important site parameters and model outputs	influencing B. net	<i>umayeri</i> trophic int	eraction strength in	each study stream.
WM: wet mass. DM: dry mass. RMR: resting metaboli	c rate. sd: standarc	l deviation.		
	Forest 1	Farm 1	Forest 2	Farm 2
Site parameters influencing interaction strength				
Mean water temperature (°C)	17.86	20.28	18.09	19.63
Mean diel water temperature range (°C)	16.4 - 19.2	17.2 - 24.9	16.7 - 19.7	17.3 - 23.9
Fish body mass (g WM), mean \pm sd	2.73 ± 1.02	2.51 ± 1.21	3.18 ± 1.97	3.99 ± 2.21
Fish density (fish m ⁻²)	1.32	4.78	0.49	0.38
Prey community composition (% of total biomass):				
Diptera	7.14	14.56	6.92	21.74
Ephemeroptera	10.95	28.43	18.52	1.67
Trichoptera	68.88	1.82	63.68	12.14
Other taxa	13.08	55.20	10.88	74.93
Mean prey body mass (mg DM)	0.5938	0.2426	0.6383	0.3912
Total prey biomass (g DM m ⁻²)	0.4665	0.1071	0.3554	0.1496
Model results				
Energy need for growth (J fish ⁻¹ day ⁻¹), mean \pm sd	26.60 ± 8.47	30.53 ± 11.1	29.50 ± 17.17	24.17 ± 16.85
Population-level energy need for growth (J $m^{-2} day^{-1}$)	35.04	145.89	14.36	9.16
Energy need for RMR (J fish ⁻¹ day ⁻¹), mean \pm sd	65.65 ± 18.91	68.45 ± 25.15	72.95 ± 36.04	94.94 ± 43.36
Population-level energy need for RMR (J m ⁻² day ⁻¹)	86.46	327.04	35.5	35.98
Prey production (J m ⁻² day ⁻¹)	312.92	144.75	252.74	168.04