Macroecology of temperate riverine ecosystems

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Taylor Woods
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ABSTRACT

Macroecology seeks to understand processes underlying biodiversity patterns at large spatiotemporal scales. Aided by increases in publicly available datasets, macroecologists have made substantial progress towards these aims in recent decades. However, much of this knowledge comes from terrestrial habitats, with comparably fewer macroecological studies in freshwaters. Freshwater environments are interesting contexts for macroecological research owed to high biodiversity, particularly in ectothermic taxa that may be disproportionately threatened by global change. Therefore, large scale approaches will be necessary to adequately assess risks posed to these systems by regional to global anthropogenic stressors. This dissertation leverages recently available datasets to advance the field of freshwater macroecology. I use data-intensive analyses and syntheses to test and evaluate hypothesized mechanisms underlying patterns in freshwater biodiversity, biomass, and phenology. I synthesize freshwater phenology literature to identify prevalent abiotic and intrinsic drivers of phenology regimes and use this information to provide recommendations for more robust assessments of phenological change in freshwaters. I assess mechanisms underlying the biodiversity-ecosystem functioning relationship in riverine stream fish assemblages and assess how non-native species introductions can affect this relationship. I conduct a survey and synthesis of contemporary freshwater community science sampling efforts to inform where freshwater macroecologists can leverage these emerging data sources and identify sampling and participation gaps which could be prioritized by novel sampling efforts. I unify processes underlying patterns in stream fish body size across biological scales to overcome discrepancies created by prior data limited research. This dissertation fills knowledge gaps in freshwater macroecology and provides novel lines of inquiry to be explored by future research efforts.

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INTRODUCTION

Macroecology is a relatively young discipline among the ecological sciences. Since seminal papers that defined the field in the 1980s (Brown 1981, Rabinowitz 1984, Brown and Maurer 1989, Brown and Nicoletto 1991, Gaston 1998), macroecological research has narrowed knowledge gaps in processes underlying biodiversity patterns at large (regional to global) spatial scales. Macroecology has also made substantial contributions to biological conservation. For example, large-scale approaches can elucidate spatial patterns in threatened biodiversity and inform placement of protected areas, globally (Brooks et al. 2006, Venter et al. 2014).

Despite these advances, macroecological research has not been evenly distributed among ecological systems. While large-scale studies of terrestrial bird, mammal, and plant biodiversity are common, less is known about processes underlying regional to global biodiversity patterns in freshwaters. One freshwater context that is particularly interesting is riverine systems. These habitats present exciting opportunities for macroecology research. For example, riverine fish biodiversity is the most biodiverse, per unit area among habitats on Earth (Dudgeon et al. 2006). Further, these systems are characterized by ectothermic organisms which may be disproportionately affected by global change relative to endothermic taxa (Thackeray et al. 2016).

Recent increases in publicly available freshwater datasets present prime opportunities to apply macroecological concepts established in other systems to freshwaters. This dissertation uses these novel datasets to advance macroecology with a focus on temperate riverine systems. The chapters address common macroecological themes including patterns in biodiversity, body size, and phenology in flowing waters. I explore these patterns and seek to understand they may be altered by multiple global change stressors. I synthesize current literature on freshwater phenology to identify knowledge gaps and pathways for future research to incorporate novel data sources to fill gaps. I test the biodiversity-ecosystem functioning relationship in riverine fish assemblages. I detail survey efforts in underutilized freshwater community science datasets to identify where freshwater macroecologists can leverage these novel data sources and inform priority areas for community science programs to recruit future participants. I unify riverine fish body size patterns across biological scales with the aid of a comprehensive, individual body mass dataset. These chapters indicate how robust analyses of macroecological concepts previously unexplored in freshwater contexts warrant urgent attention considering the rise of novel publicly available datasets.

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CHAPTER 1
PHENOLOGY IN FRESHWATERS: A REVIEW AND RECOMMENDATIONS

A version of this chapter was originally published by Taylor Woods, Anna Kaz, and Xingli Giam:

Taylor Woods, Anna Kaz, Xingli Giam. “Phenology in Freshwaters: A Review and Recommendations.” *Ecography* (2021).

Taylor Woods, Anna Kaz, and Xingli Giam conceptualized the project. Taylor Woods and Anna Kaz performed the literature review. Taylor Woods led the writing and created figures. All authors contributed to manuscript revisions and editing.

Abstract

Phenology changes are increasingly recognized as a common response of species to ongoing global change. Phenology can be influenced by environmental cues that impact the initiation or duration of life history events as well as intrinsic organismal traits that may affect how different species respond to such environmental cues. Despite the importance of phenology for biodiversity conservation as demonstrated by terrestrial and marine research, freshwater phenology is understudied. Therefore, we conducted a literature review on freshwater phenology research to summarize the spatial, taxonomic, and temporal biases of studies; as well as relationships between phenology metrics, environmental cues, and intrinsic species traits studied in these systems. We find that phenology research in freshwaters may be limited by a lack of long-term time-series data, especially in lotic habitats. Phenology metrics studied differed between lotic and lentic habitats, with limnological research focused on planktonic population growth whereas macroinvertebrate emergence and fish spawning seasons are the most frequently studied aspects of phenology in streams and rivers. Across habitats, temperature is the most investigated environmental cue, with additional research attention to resources and hydrology in influencing phenology events in lentic and lotic environments, respectively. Knowledge gaps in contemporary freshwater phenology research include relationships between phenology and environmental cues in tropical systems, understanding of non-salmonid fish phenology, and testing hypotheses related to intrinsic traits. We recommend that future research broaden the biological, spatial, and temporal scales of phenology studies in these systems, and make use of novel data sources, methods, and technologies to address contemporary research gaps.

Introduction

Changes in the timing of seasonal life history events (i.e., phenology) are recognized as a common response of organisms to ongoing global change (Stenseth et al. 2002, Parmesan and Yohe 2003, Root et al. 2003, Visser and Both 2005, Menzel et al. 2006, Parmesan 2006). Quantifying shifts in organisms’ phenology is important because these responses can scale up to impact population dynamics and demography (Miller-Rushing et al. 2010) and community structure and function (Diez et al. 2012). For example, phenology responses to changing environmental contexts may skew community size distributions towards smaller-bodied individuals (Lurgi et al. 2012), disrupt synchrony between species and trophic resources (e.g., trophic mismatch) (Stenseth et al. 2002, Visser

and Both 2005, Kharouba et al. 2018, Renner and Zohner 2018), alter the relative strengths of competitive interactions between coexisting species (Yang and Rudolf 2010, Carter et al. 2018, Rudolf 2019), and determine range shifts via physiological limits to species redistribution (Chuine 2010, Walther 2010, Macgregor et al. 2019).

Studies of species phenology can be informed by knowledge of external abiotic and biotic cues that indicate optimal environmental conditions for fitness, reproduction, and survival (Visser and Both 2005, Mcnamara et al. 2011) and intrinsic traits that may affect organismal responses to such external cues (Altermatt 2010a, Walther 2010, Chmura et al. 2019). For example, phenology changes in response to increasing temperature are documented in terrestrial ectotherms (Scranton and Amarasekare 2017, Davies 2019), endotherms (Gordo and Sanz 2006, Moyes et al. 2011), and plants (Menzel et al. 2006, Vitasse et al. 2018, Heberling et al. 2019, Piao et al. 2019). Additionally, phenological regimes may vary among species in relation to the trophic characteristics (Visser and Both 2005, Altermatt 2010a, Thackeray et al. 2010, 2016), reproductive timing (e.g., early or late season species) (Menzel et al. 2006, Sherry et al. 2007), or generation time (Macgregor et al. 2019) of the species considered. While some of these traits may indeed affect phenology and phenological shifts directly (e.g., generation time), other traits such as reproductive timing and trophic characteristics might be linked to phenology at least in part because they are correlated with differential exposure to environmental cues and/or other unmeasured traits (e.g., physiological sensitivity to environmental cues) that may affect organismal responses to these cues (Chmura et al. 2019). Therefore, to advance our understanding on how phenology might respond to global change, we will need to account for both the environmental cues and the intrinsic traits that can jointly inform our knowledge of the timing of seasonal life history events.

Quantifying how extrinsic environmental conditions and intrinsic traits may inform species phenology can also contribute to biodiversity conservation. For example, drivers of life history events can be used to understand and predict the introduction, success, and expansion of invasive species in novel habitats (Chapman et al. 2014, Capellini et al. 2015), and extinction risk may be informed, in part, by reproductive and life history characteristics that affect population growth rates and ability to recover from perturbations (Purvis et al. 2000, Hutchings et al. 2013). Differential shifts in the phenology across interacting species or between species and the abiotic conditions they require may alter species demography and population dynamics, potentially affecting species persistence (Miller-Rushing et al. 2010). Therefore, knowledge of species' phenology related to extrinsic cues and intrinsic traits will play an important role in mitigating contemporary and future biodiversity loss from multiple stressors.

Despite the demonstrated importance of phenology for the maintenance and conservation of biodiversity, species phenology in freshwater systems remains relatively understudied (Thackeray et al. 2010) compared to terrestrial (Tang et al. 2016, Renner and Zohner 2018, Piao et al. 2019) and marine (Staudinger et al. 2019, Ardyna and Arrigo 2020) systems. This is surprising because freshwater systems represent an interesting context for phenology research. Freshwaters are dominated by ectothermic organisms which are more sensitive to changes in environmental temperature and, therefore, likely to experience stronger impacts to phenology from global change, compared to endotherms

(Thackeray et al. 2010, Chmura et al. 2019). Organisms in freshwater food webs are generalizable into three main trophic levels (predators, herbivorous consumers, and primary producers) each of which undergo seasonal life history events, which may indicate potential for trophic mismatches. Freshwater phenology may depend on environmental cues from allochthonous inputs, hydrology, riparian shading, and temperature. Differences between species can be informed by intrinsic traits such as generation time, reproductive timing, thermal sensitivity, or trophic level. However, we lack a consensus on prevalent cues and traits across studies and taxa. Finally, freshwaters harbor greater biodiversity per unit area, of which disproportionately more taxa are threatened, than terrestrial and marine systems (Dudgeon et al. 2006, Harrison et al. 2018) and a synthesis of phenology research is urgently needed to better understand risks posed to these organisms. These characteristics suggest that the environmental cues important for species phenology and the magnitude of global change impacts on phenology regimes in freshwaters may differ from patterns observed in other, well-studied systems and have potential to provide novel insights into our understanding of ongoing phenology shifts.

Given the importance of conserving freshwater systems and their potential to provide unique insights into impacts of shifts in species phenology on biodiversity, we contend that there is an urgent need to synthesize and summarize existing freshwater phenology research as a first step toward identifying current research biases and potential knowledge gaps. Synthesizing freshwater phenology may also help identify whether phenology responses to global change observed in terrestrial and marine communities are generalizable across other systems and may therefore be informative to make robust assessments about threats to biodiversity, globally. Here, we conducted a systematic literature review to summarize the: (1) spatial, taxonomic, and temporal scopes, (2) phenological metrics, (3) environmental cues; and (4) intrinsic species traits investigated in freshwater phenological research. Our synthesis aims to provide a research agenda to advance the understanding of species phenology in freshwater ecosystems and the implications of global change on biodiversity persistence via its effects on phenology.

Literature review

We conducted a systematic review of species phenology research in freshwater systems by conducting Web of Science and Google Scholar searches for published papers using the query: ((stream* OR river* OR lake* OR freshwater* OR lotic OR lentic OR aquatic OR creek*) AND (phenology)). These search terms were decided after exploring alternative keyword combinations because we found them to identify a large number of potentially relevant studies, while minimizing the number of studies beyond the scope of our review. We exported all returned articles from Web of Science and the first 150 articles from the Google Scholar search (sorted by relevance; titles of articles ranked above 150 indicated that they were of no or minimal relevance), which resulted in 2,409 candidate articles for our literature review.

We initially inspected the title and abstract of each of these studies, and papers identified as potentially relevant to our review were read in full. Specifically, we included primary literature that analyzed temporal variation in seasonal life history or life cycle events (i.e., phenology) of freshwater organisms using field, laboratory, or model-based

methods. We omitted studies that quantified seasonal changes in community composition without associated life history events, those which measured solely abiotic ecosystem phenology (e.g., lake stratification, hydrologic events), or those from estuaries because environmental cues in brackish systems may differ from freshwaters. We included anadromous and amphidromous fish taxa in our review as these species provide resources for freshwater environments (Samways et al. 2018). After filtering the original list of 2,409 articles, we identified 419 studies that met the above criteria for inclusion in our literature review (Appendix, List A1).

For each study included in our review, we recorded information on the spatial, taxonomic, and temporal scope, as well as the phenological metrics, environmental cues, intrinsic species traits, and biotic interactions investigated by the study (Tables 1–3). For spatial variables, we recorded the country, geographic coordinates, and habitat (lotic [flowing water; streams, rivers, creeks] or lentic [non-flowing water; lakes, ponds]) of the study. For wetland studies, we classified habitats according to descriptions of individual study sites sampled within the system. In cases where coordinates were not provided, we approximated locations when possible based on named features (e.g., National Park, research station, or named waterbody) to visualize the distribution of phenological studies. For temporal variables, we recorded the start year, end year, length of study (number of years from first sample to the last sample in the dataset), and the temporal grain of the analysis on an annual scale as: daily, weekly, monthly, or seasonal (sampling occurred during certain months of the year).

To characterize the organisms investigated, we recorded the identities of taxa as well as the total number of taxa examined in each study. For groups of organisms where species-level identifications were less frequently reported (e.g., phytoplankton and zooplankton), the number of taxa often reflected broader taxonomic resolution (e.g., genera, diatoms, or copepods) rather than the number of species. We recorded the group(s) of taxa studied as: amphibians/aquatic reptiles, crustaceans/mollusks (excluding zooplankton), fish, macroinvertebrates, primary producers (majority phytoplankton and diatoms, with fewer observations from macrophytes), vertebrates other than fish (e.g., waterfowl, beavers), or zooplankton. For studies of fish phenology, we also recorded whether the study focused on salmonids (family Salmonidae) or non-salmonids. Additionally, we recorded whether a biotic interaction was hypothesized or tested, and if so, classified this interaction as trophic (e.g., predation, parasitism), competition, mutualism, commensalism, ammensalism, or an interaction between aquatic and terrestrial organisms (e.g., trophic interactions between aquatic and terrestrial organisms).

Next, we characterized the phenological metrics measured into functional categories based on a priori knowledge of freshwater seasonal life history events across freshwater taxa: egg/hatching characteristics (e.g., time to hatch, date of hatching), emergence, juvenile recruitment, metamorphosis, migrations, primary production/growing season, or reproductive season (Table 1). Although these metrics may have submetrics (e.g., date of start, date of peak, duration of event), we focused on these broader functional categories to investigate general links between phenological metrics, and their potential environmental drivers (see below) investigated in the literature.

Table 1 Description of freshwater phenology metrics. For each functional class of phenology metric, the taxa for which it may apply are provided, as well as taxon-specific metrics (variables measured in studies).

Phenology metric	Taxa	Taxon metric
Egg/hatching	All	Hatching
Emergence	Macroinvertebrate	Emergence
	Macroinvertebrate	Flight period
Population growth or production season	Macrophytes	Biomass, Cover
	Phytoplankton	Abundance
	Zooplankton	Abundance
Juvenile recruitment	Fish	Young-of-year arrival
	All	First juvenile appearance
Metamorphosis	Amphibian	Metamorphosis
Migration	Amphibian, Reptiles, Waterfowl	Breeding
	Fish	Spawning, smolting
Reproductive season	Amphibian	Breeding, calling
	Amphibian, macroinvertebrate	Oviposition
	Crustaceans and mollusks	Brooding, spawning
	Crustaceans and mollusks, fish	Gonadosomatic Index (GSI)
	Fish	Spawning
	Reptiles, Waterfowl	Breeding, nesting

Table 2. Environmental cues recorded in our review. For each cue, we provide a description, as well as examples of variables measured in studies which would be classified as the respective environmental cues.

Environmental cue	Description	Variables
Biotic	Factors related to the presence of or interactions with other conspecific or heterospecific organisms influence phenology events	Density dependence, predation pressure, competition
Degree days	Phenology events require an accumulated number of days above a thermal threshold	Growing degree days, degree days, accumulated thermal units
Elevation	Phenology events differ in timing due to the elevation at which they occur	Elevation
Hydrology	Phenology events require a stimulus related to an aspect of the hydrologic regime	Discharge, streamflow, drought, flooding, water levels
Latitude	Phenology events differ in timing due to the latitude at which they occur	Latitude
Photoperiod	Phenology events require a stimulus related to day length	Day length, lunar phases
Precipitation	Rainfall triggers phenology event (without reference to hydrology)	Precipitation
Resources	The presence or abundance of abiotic or biotic resources can stimulate phenology events	Allochthonous input, autochthonous production, nutrients, prey
Temperature	Factors related to environmental temperature can stimulate phenology	Water temperature, air temperature, temperature variation, ice-off

Table 3. Intrinsic traits investigated by our review. For each trait, we provide a description, and variables that may be reported by studies and classified to a specific trait class.

Trait	Description	Variables
Ecological specialization	Species' responses to cues differ based on their degree of specialization	Generalist vs. specialist species;
Generation time	Species may differ in responses to cues based on generation time	Voltinism; generation time; duration of life cycle
Habitat use	Species differ in phenology responses based on the habitat occupied	Habitat type (lotic vs. lentic); use of specific habitat (e.g., floodplain) for spawning
Migratory status	Migratory characteristics associated with life history or life cycle events	Migrant or non-migrant; migratory class (anadromous, potadromous, catadromous)
Reproductive timing	Species may differ in responses to environmental cues based on the relative seasonal timing of events	Early (spawners, migrants) vs. late (spawners, migrants); Spring vs. summer
Thermal sensitivity	Thermal traits or limits cause species to differ in responses to environmental cues	Thermal guilds (cool, cold, or warm-water), critical thermal maxima or minima
Trophic level	Dietary or trophic characteristics can drive differential responses of species to environmental cues	Functional feeding guilds, trophic level, diet

We recorded environmental cues, defined as extrinsic variables that can drive life history or life cycle events (Chmura et al. 2019), that were found to be associated with a given phenological metric investigated by each study. We classified environmental cues into the following groups: biotic, temperature, hydrology, elevation, latitude, photoperiod, resources (food, nutrients), precipitation, or none (Table 2).

For each study, we recorded intrinsic traits reported to describe differences in species phenology via differential exposure to environmental cues or correlation with underlying mechanisms that affect sensitivity to environmental cues (Chmura et al. 2019). We classified intrinsic characteristics as: generation time (including voltinism), trophic level (functional feeding guilds), migratory status, thermal sensitivity, ecological specialization, habitat use, other, or none (Table 3). Contrary to environmental cues, we found that few studies examined hypothesized relationships between intrinsic traits and species phenology. For example, studies might provide information on the thermal sensitivities of taxa without using statistical tests to test the hypothesis that species with higher thermal maxima have different seasonal timing of life history events than those with low thermal maxima. Therefore, we recorded traits used to describe differences in species phenology, even when they were not assessed using statistical tests. This allowed us to identify intrinsic traits that may be associated with mechanisms by which species differ in phenology that should be investigated by future studies.

In the following section, we summarize the findings of our literature review, with particular attention to identifying general patterns in: (1) spatial and taxonomic gaps in research efforts, (2) relationships between phenology events and environmental cues, (3) intrinsic traits that may can describe differences in phenology across species; and (4) biotic interactions that may be affected by asynchronous phenology between co-occurring species.

Summary of contemporary phenology research

Spatial, taxonomic, and temporal distribution of studies

Studies included in our review encompassed 57 countries across six continents and exhibited a geographic bias towards Europe and North America (Fig. 1). European research showed a greater emphasis on limnological studies, whereas North American studies skewed more towards lotic habitats (Fig. 1). By comparison, there were fewer studies on freshwater phenology in Africa, Central and Southeastern Asia, Oceania, and South America.

Research efforts showed a bias towards temperate habitats for all taxa (Fig. 2). Fish phenology research extended to higher latitudes than other taxonomic groups (Fig. 2a), which may reflect a focus on cold-water salmonids in contemporary fisheries research (Myers et al. 2017). Long-term trends in annual salmonid spawning and smolting migrations were particularly well-studied in high latitude European countries and Alaska (Mundy and Evenson 2011, Kovach et al. 2015, Haraldstad et al. 2017, Campbell et al. 2019, Sparks et al. 2019). Research efforts on primary producers and zooplankton showed clusters in Europe, indicating a preponderance of long-term plankton monitoring programs in European lakes (Blenckner et al. 2007).

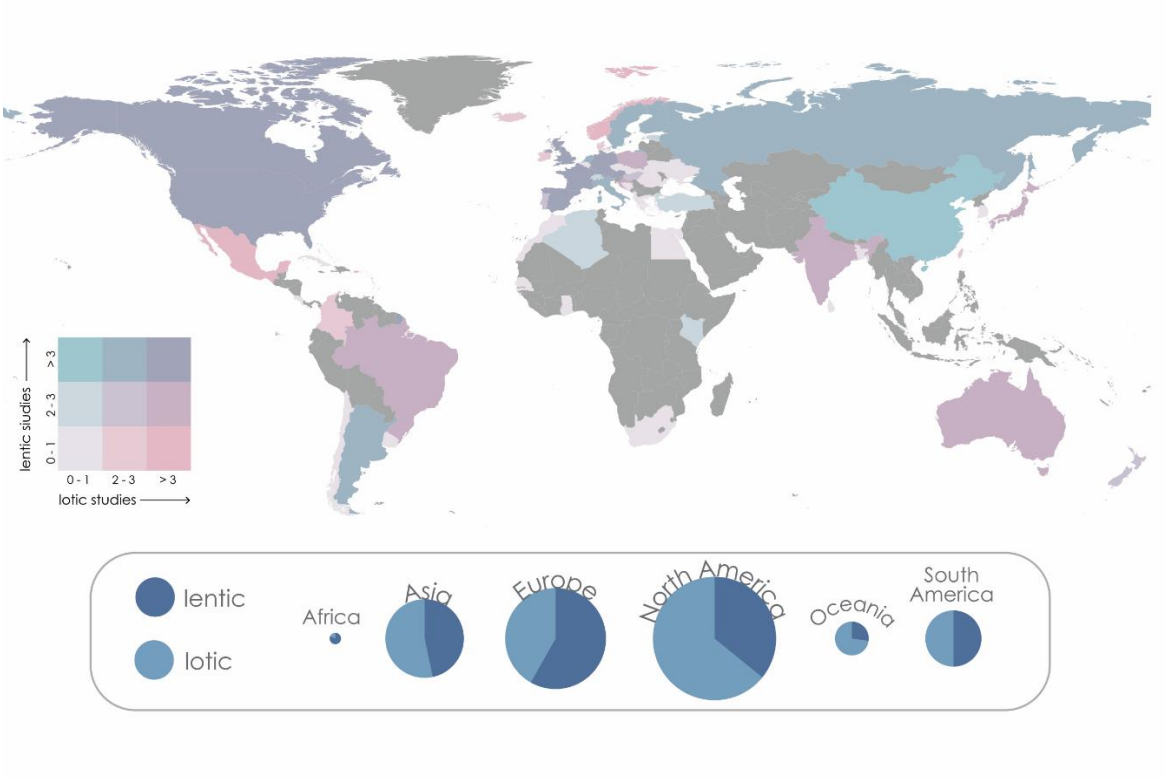

Figure 1. Map of the distribution of contemporary freshwater phenology research. The bivariate color scale illustrates the number of lotic and lentic studies in each county (countries lacking a study are colored grey). The pie charts below the map show the number of lotic and lentic studies, pooled by continents. The size of the pie charts indicates the absolute ranking (1–6) of total studies by continent.

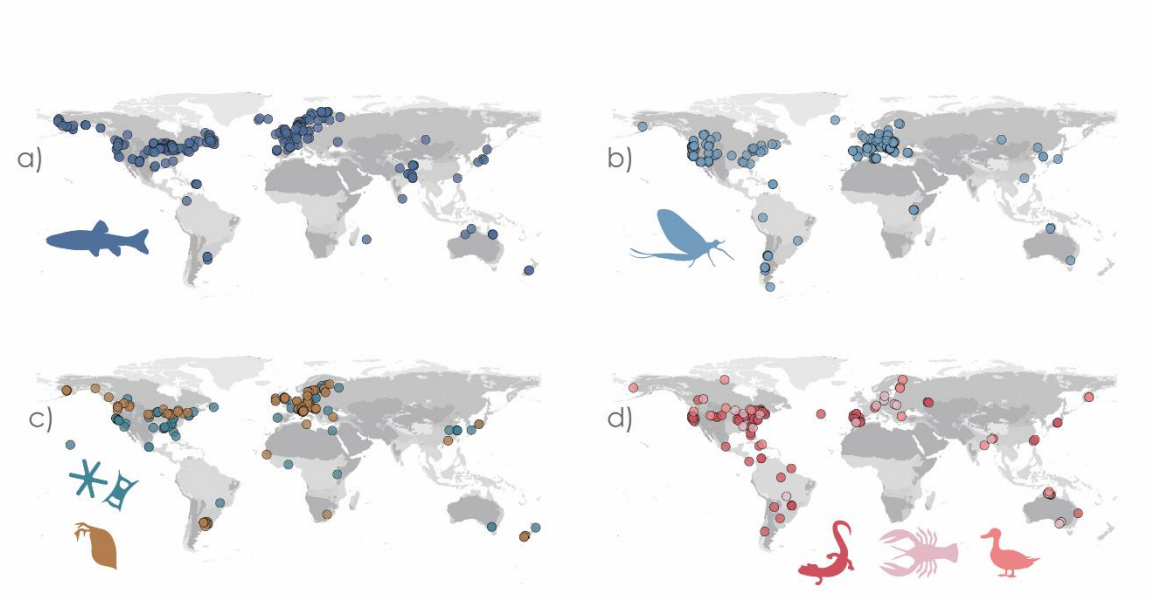

Figure 2. Locations of studies with known geographic coordinates. The panels are separated and colored by taxa class studied as: a) fish, b) macroinvertebrates, c) primary producers (green) and zooplankton (brown), and d) (colors indicated by icons from left - right) amphibians, crustaceans and mollusks, and vertebrates other than fishes. Shaded grey polygons are Köppen-Geiger climate regions from Beck et al. (2018).

Different taxonomic groups dominated research efforts between habitats. Phenology research in lentic systems focused on primary producers and zooplankton, whereas fishes and macroinvertebrates were the research foci in lotic habitats (Fig. 3). Among fish studies in both lentic and lotic habitats, roughly half (47.0%) examined salmonid phenology. The disproportionate research towards this family likely reflects the economic importance of salmonid fisheries (Criddle and Shimizu 2014).

Lotic studies characterized the phenology of more taxa per study (median = 2, interquartile range [IQR] = 1–14 taxa per study), compared to lentic studies (median = 2, IQR = 1–8) (Fig. 4). However, we note that the taxonomic resolution presented in lentic studies is often coarser than species level; therefore, our estimates likely underestimate the number of species measured in lentic systems. Regardless, the relatively high biodiversity considered per study in both lotic and lentic systems indicates that the potential for future analyses to use data in the existing literature to study community-level patterns in phenology, i.e., the timing of events across many, possibly interacting, species.

Studies in lentic habitats characterized phenology over longer time periods (median = 3, IQR = 1–18 years) than studies in lotic habitats (median = 2, IQR = 1–8.6) (Fig. 4). Regarding the temporal grain of analysis, seasonal or monthly sampling regimes were the most frequently reported sampling regimes for all taxa (97.9% [amphibians], 93.8% [crustaceans/mollusks], 96.6% [fishes], 88.9% [macroinvertebrates], 100.0% [other vertebrates], 82.8% [primary producers], 84.1% [zooplankton] of studies) (Fig. 5). The incidence of daily or weekly sampling regimes was highest in studies focusing on primary producers (mostly comprising lentic phytoplankton and diatoms; 17.3% of studies), macroinvertebrates (11.1%), and zooplankton (15.8%) although it was always less frequently employed than seasonal or monthly sampling. These results suggest some, albeit limited, correspondence between fine temporal grain sampling approaches and phenology research on taxa with faster life histories.

Phenology metrics

In lentic habitats, the population growth and production season for planktonic organisms and primary producers was the most-studied phenology metric (Fig. 6a), which may reflect the tendency for lentic research in lake habitats to emphasize bottom-up effects as the processes at lower trophic levels are recognized as important structuring force in these food webs. Contrary to the majority of lotic systems, autochthonous production provides the resource base for lentic food webs (Galloway et al. 2014, Lau et al. 2014). Phytoplankton and diatoms are trophic resources for zooplanktonic grazers, which are, in turn, prey for insects and larval fish (Ohlberger et al. 2014). Therefore, shifts in production regimes in these systems may impact trophic interactions at higher trophic levels. Additionally, understanding the drivers of seasonal dynamics of cyanobacteria blooms in lentic systems is also important due to the risks posed to public health and economies by these events (Coffer et al. 2020).

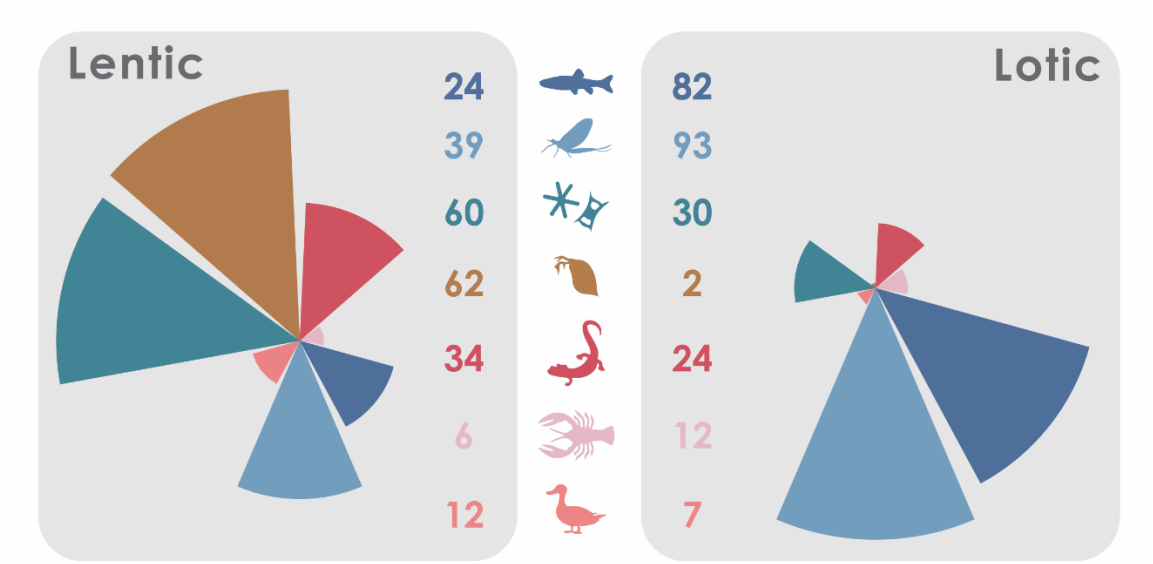

Figure 3. The number of studies with reported measures of phenology for each group of taxa in lentic and lotic habitats. Bar chart colors indicate taxa as (from top to bottom in icon legend): fish, macroinvertebrates, primary producers, zooplankton, amphibians, crustaceans and mollusks, and vertebrates other than fishes. The number of studies within each habitat that studied taxa groups is provided next to the legend icon.

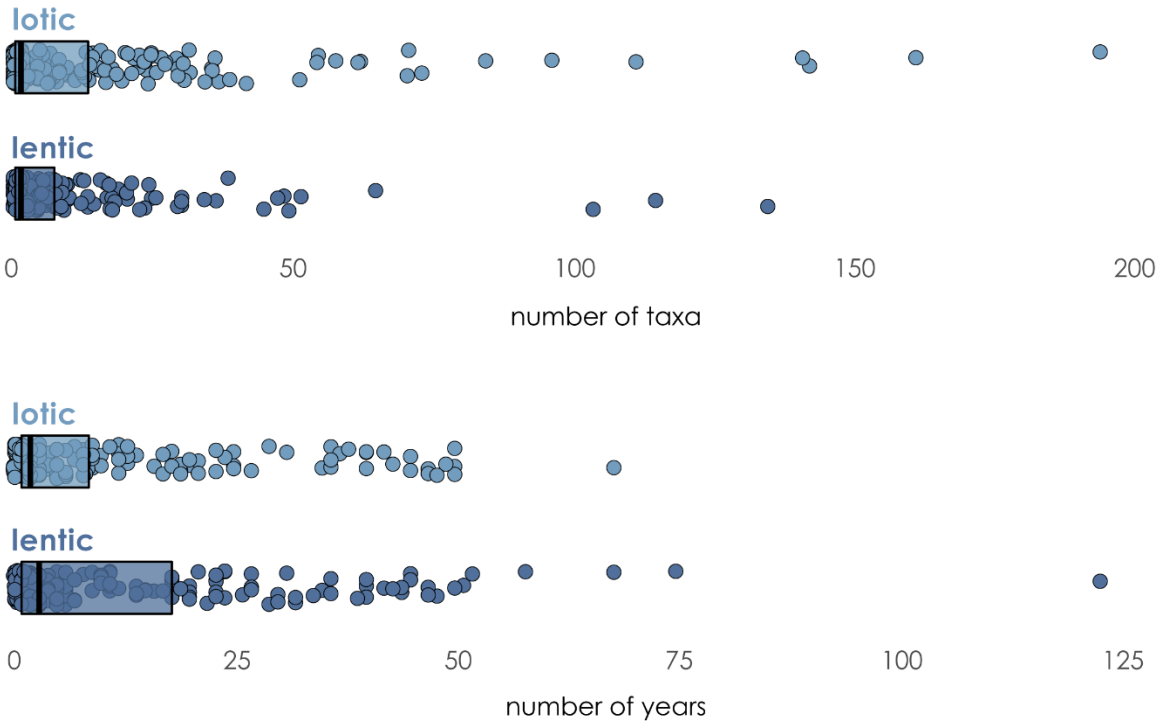

Figure 4. The number of taxa (top) and study length (bottom) reported in studies of lotic (light blue) and lentic (dark blue) phenology. Points show values for individual studies and cross bars show median and interquartile ranges for each habitat.

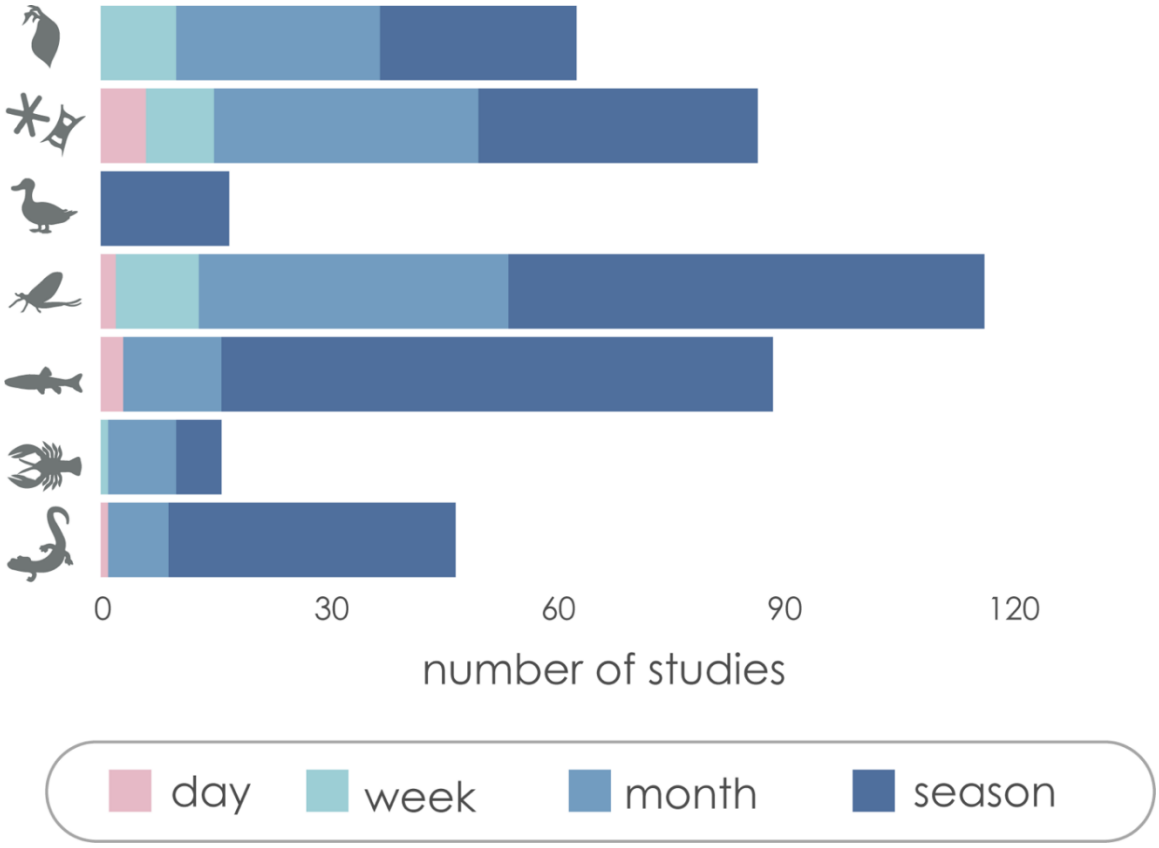

Figure 5. Temporal grain of analysis across studies identified in the review. For each group of taxa, the number of studies reporting each temporal grain classification is shown. Taxa groups shown are (from top to bottom): zooplankton, primary producers, other vertebrates, macroinvertebrates, fishes, crustaceans/mollusks, and amphibians/aquatic reptiles.

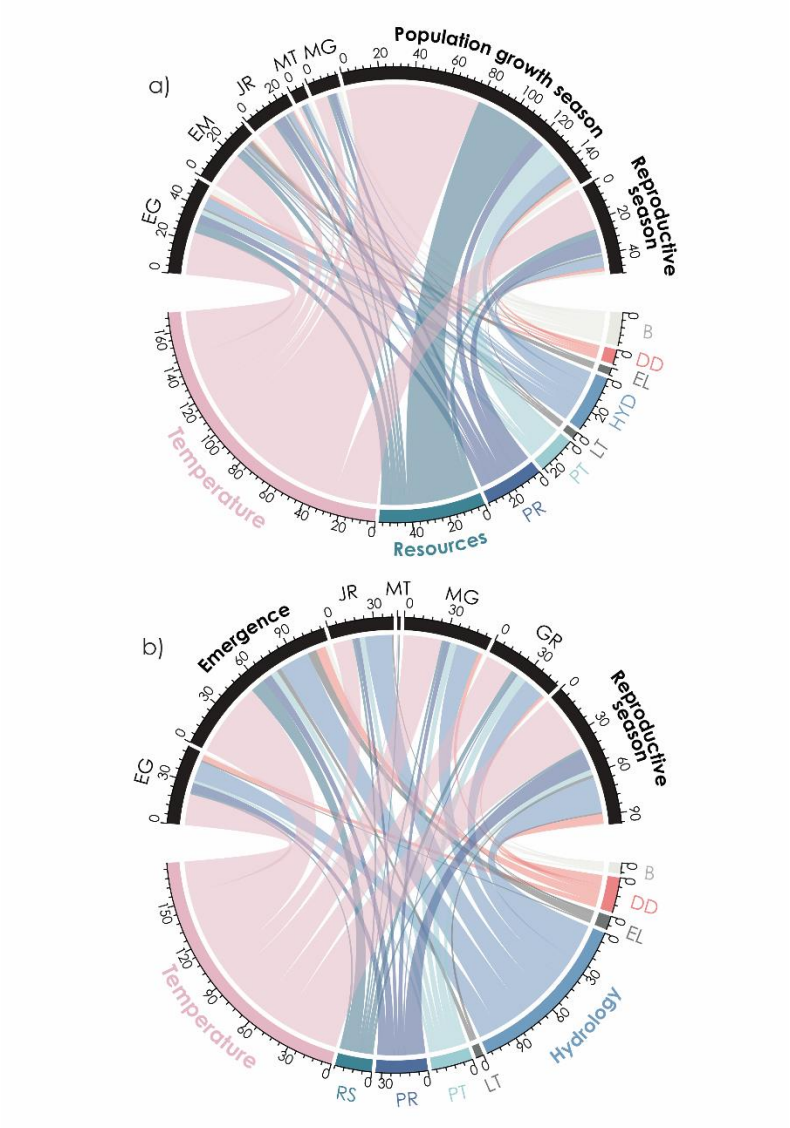

Figure 6. Diagrams showing relationships between environmental cues and phenology metrics in lentic (a) and lotic (b) habitats. Numbers on the edges indicate the number of studies examining phenology metrics (upper half circle) and environmental cues (lower half circle, coded by color). The thickness of lines connecting cues and phenology metrics indicates the number of studies reporting a relationship between the variable pairs, with thicker lines showing greater research attention towards the relationship. Abbreviations for phenology metrics are egg/hatching (EG), emergence (EM), juvenile recruitment (JR), metamorphosis (MT), migration (MG), and population growth/production season (GR). Abbreviations for environmental cues are resources (RS), precipitation (PR), photoperiod (PT), latitude (LT), hydrology (HYD), elevation (EL), degree days (DD), and biotic factors (B). Studies that did not investigate an environmental cue–phenology metric relationship are omitted from the figure.

In lotic systems, the phenology metrics that received the most research attention were emergence and reproductive seasons (Fig. 6b). Macroinvertebrate emergence is important because the flux of adult insects provides trophic resources for terrestrial consumers, and changes in emergence phenology may impact the strength of aquatic-terrestrial linkages (Larsen et al. 2016). Emergence phenology is also important for resource fluxes in instream environments where allochthonous leaf litter input composes the base of food webs and macroinvertebrate detritivores control seasonal breakdown rates of organic matter (Benstead and Huryn 2011). The timing of migratory and reproductive events of fish and other vertebrates is important to the functioning of lotic systems because the structuring role that adults and juveniles play as predators (Giam and Olden 2016), and the carcasses of semelparous salmonid species can shape the activity and phenology of terrestrial scavengers which depend on these anadromous trophic resources (Lisi and Schindler 2011, Deacy et al. 2019, Rubenstein et al. 2019).

Environmental cues

Across all metrics and habitats considered, the most studied environmental cue for phenology was temperature (Fig. 6). A research foci on temperature-based cues for freshwater phenology likely reflects the temperature-dependence of growth, performance, and metabolism in ectotherms (Gillooly et al. 2001, 2002, Huey and Berrigan 2001). In addition, temperature determines the birth rate, mortality rate, and development time in ectotherm populations, affecting the timing and duration of phenological events (Scranton and Amarasekare 2017). These results indicate that ongoing and future climate warming may have strong impacts on timing of phenology events in freshwater systems. Increasing temperatures have advanced or delayed emergence dates in macroinvertebrates (Hassall et al. 2007, Anderson et al. 2019, Baranov et al. 2020), migration and spawning events in fishes (Kovach et al. 2016, Lynch et al. 2016, Austin et al. 2019), production blooms in phytoplankton (Elliott 2012a, Winder and Sommer 2012, Walters et al. 2013), and population growth peaks in zooplankton (Wojtal-Frankiewicz 2012). However, fewer studies have investigated the potential implications of these phenology shifts for community size structure, biomass production, or ecosystem functioning.

In lentic habitats, secondary to temperature, resources were important environmental cues for phenology events and particularly the timing of the production and growing seasons for planktonic organisms (Fig. 6a). Phytoplankton peaks may occur earlier and have a higher magnitude with increasing nutrients compared to scenarios of nutrient limitation (Elliott et al. 2006, Thackeray et al. 2008, Elliott 2012b). The phenology of zooplankton may respond to shifts in phytoplankton trophic resources by matching trends in producer peaks, or they may become decoupled from their prey (de Senerpont Domis et al. 2007, Winder et al. 2009, Nicolle et al. 2012). Therefore, changes in the trophic state of lentic habitats are likely to interact with temperature to influence planktonic phenology, as well as the phenology of abiotic lake processes, such as the timing and duration of the clear water phase (de Senerpont Domis et al. 2007, Elliott 2012b, McMeans et al. 2019).

In lotic habitats, in addition to temperature, hydrology cued phenology events (Fig. 6b). The role of hydroclimatic cues for fish phenology has been recognized by Flitcroft et al. (2016) who proposed a framework that accounts for discharge and temperature to

characterize seasonal migratory and spawning events, and Heim et al. (2019) who suggested streamflow impacts on phenology be examined based on the seasonal availability of temporary habitats that are important for growth, spawning, and refuge. For many fish species, spawning peaks may occur during or shortly following high flows (Smith 1991, Gorman and Stone 1999, Krabbenhoft et al. 2014a, Catalano and Bozek 2015, Valdez et al. 2019) which make available habitat and resources critical for survival and rearing of eggs and juveniles (e.g., inundation of floodplain habitats) (Peterson and VanderKooy 1995, Turner et al. 2010). However, some opportunistic species may spawn during low flows due to increased water temperature, stable environment, and protection from piscivores (King et al. 2020).

For macroinvertebrates, low flow events can cue emergence to terrestrial stages by indicating declining optimal habitat for aquatic larvae (Giberson and Garnett 1996, Harper and Peckarsky 2006, Castro-Rebolledo and Donato-Rondon 2015) or increasing availability of suitable sites for oviposition (Peckarsky et al. 2000). Alterations to the natural flow regime from anthropogenic modifications can decrease habitat availability for fishes that require specific substrates for spawning or juvenile rearing (Peterson and VanderKooy 1995, Meneks et al. 2003), and create ecological traps for aquatic larvae of rheophilic macroinvertebrate species when adults oviposit near modified habitats (Hardersen 2008). Climate change-induced alterations to the duration, magnitude, and timing of streamflow events may cause macroinvertebrates to emerge earlier, at smaller sizes, and less fecund (Harper and Peckarsky 2006), or reduce temporal partitioning between spawning fish species (Krabbenhoft et al. 2014a).

Intrinsic traits

Most studies failed to provide intrinsic traits that may be associated with mechanisms that explain patterns of phenology across species (Fig. 7). Of those that did, reproductive timing was the most investigated trait. With respect to hydrologic cues, summer spawning fishes advanced phenology with earlier flows whereas spring spawning species did not (Krabbenhoft et al. 2014a). However, with respect to temperature cues, spring spawners advanced timing with warming while summer spawners did not shift (Lyons et al. 2015). In macroinvertebrates, species with spring emergence periods showed greater phenology advances in response to increasing temperature compared to summer-emerging species (Hassall et al. 2007). In phytoplankton, community advances in annual blooming events can be attributed to disproportionate gains in abundance of early season taxa, relative to late season taxa (Elliott et al. 2006, Walters et al. 2013).

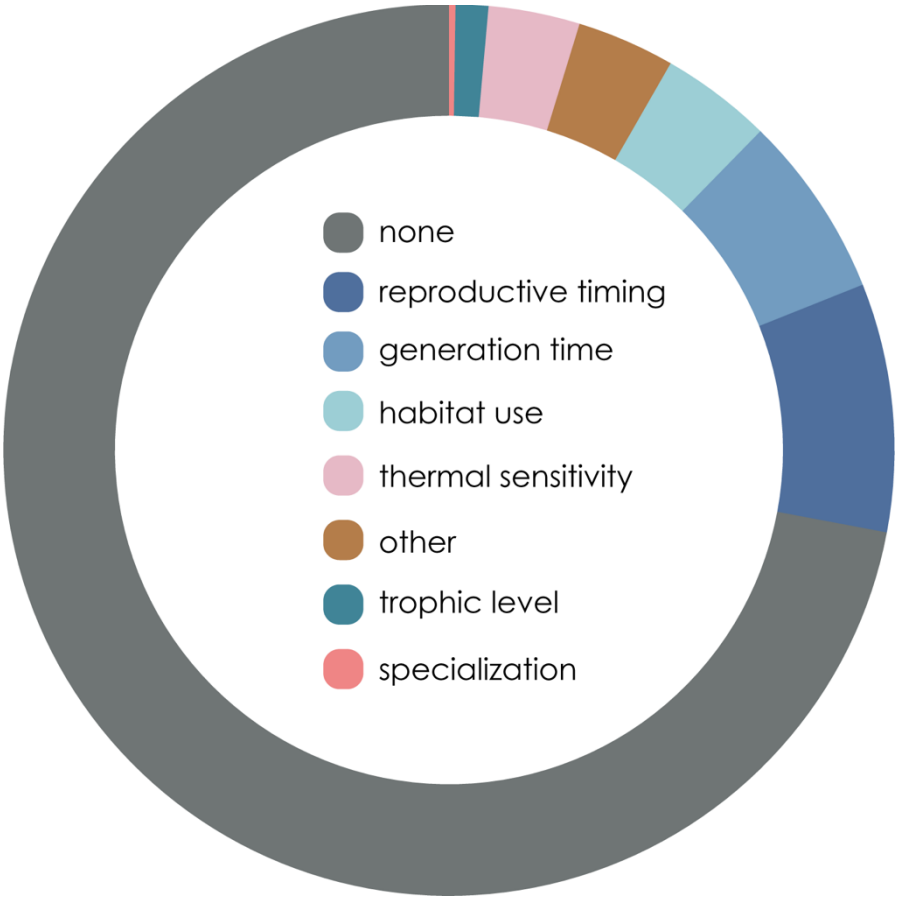

Figure 7. Intrinsic traits investigated by studies in our review. For each trait, the number of studies reporting the trait is shown by the length of the bar.

Generation time may also describe variation in phenology regimes across species. Planktonic organisms with shorter life cycles synchronously advanced production peaks, whereas those with longer life cycles become asynchronous (Adrian et al. 2006). Voltinism (i.e., number of generations per year) is a trait that is often reported for invertebrates but the potential effect of this trait on species-specific phenology is rarely tested in aquatic invertebrates, in contrast to terrestrial invertebrates (Macgregor et al. 2019). Exemplar questions on patterns of species phenology as related to voltinism include: (1) are taxa with longer (uni- or semivoltine) or shorter generation time (multivoltine) more likely to shift the timing of emergence or production peaks in response to environmental cues; and (2) which taxa can shift their life cycles (e.g., facultative voltinism) in response to changes in various environmental cues (Jönsson et al. 2009, Altermatt 2010b)?

Another intrinsic trait that may warrant further investigation in describing phenology across species, and specifically patterns related to temperature cues, is thermal sensitivity. With increasing temperatures, cold-water spawning fishes may delay spawning events, while cool and warm water species advance spawning seasons (Shuter et al. 2012). Zooplankton taxa with broader thermal ranges may be less responsive to increasing temperatures, whereas thermophilic species can increase the magnitude of their annual population growth peaks (Gerten and Adrian 2002).

Biotic interactions

Relatively few studies investigated phenology with regard to biotic interactions associated with these events (67 of 419 studies; Fig. 8). Of these 67 studies, the most frequently examined interactions were trophic interactions (50 studies). In lentic habitats, ongoing global change may cause temporal mismatches between phytoplankton and zooplankton phenology and this asynchrony could alter bottom-up resource flow to higher trophic levels (de Senerpont Domis et al. 2007, Seebens et al. 2009, Donnelly et al. 2011, Winder and Sommer 2012). Trophic mismatches may also occur in top-down predation effects of lentic fishes and predaceous invertebrates on zooplankton (Schindler et al. 2005, Wagner and Benndorf 2007, Brodersen et al. 2011, Wagner et al. 2013), but some limnological studies found fish phenology was able to track shifts in prey resources (Jolley et al. 2010, Hovel et al. 2019). In lotic systems, changes in the timing of anadromous salmon carcasses and emerged aquatic insect pulses can cause trophic mismatches with terrestrial consumers (Lisi and Schindler 2011, Larsen et al. 2016, Deacy et al. 2019, Rubenstein et al. 2019), whereas fishes were found to track emerged insect resource pulses (Bell et al. 2017, Hansen et al. 2020). These contrasting results indicate that more research is needed to understand the ecological contexts under which trophic mismatches will occur in freshwater systems.

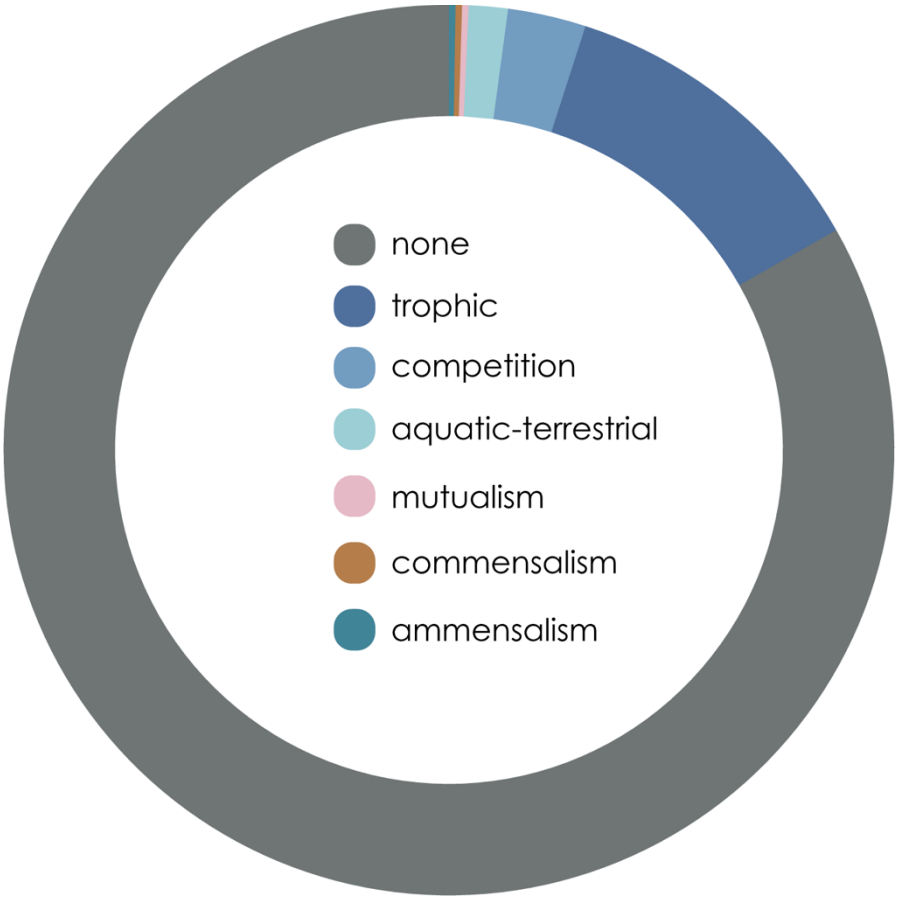

Figure 8. Biotic interactions investigated by studies in our review. For each trait, the number of studies reporting the interaction is shown by the length of the bar.

Following trophic interactions, competition and terrestrial-aquatic linkages were the most investigated biotic interactions (12 and 6 studies, respectively; Fig. 8). Competitive interactions associated with phenology are likely to be particularly important when phenology events are timed to lessen competition for food resources. For example, shifts in the timing of lotic larval fish appearance and lentic zooplankton peaks may increase temporal overlap between species and competition for limited resources (Adrian et al. 1999, Duffy 2010, Turner et al. 2010). Research on the phenology of terrestrial-aquatic interactions has focused on the timing of marine subsidies of salmonid carcasses on terrestrial consumers (Lisi and Schindler 2011, Deacy et al. 2016, 2019, Rubenstein et al. 2019), whereas timing in subsidies of emergent aquatic insects on riparian consumers are relatively unstudied (Larsen et al. 2016). Another biotic interaction that may warrant investigation is the interaction between nest building and nest associate fish species as shifts in the phenology of either species could alter synchronous spawning with its mutualistic partner (Kim and Kanno 2020). Our review indicates that the implications of potential shifts in these positive interactions is largely unknown.

Knowledge gaps and future directions

Spatial, taxonomic, and temporal biases

Our review identified several spatial, taxonomic, and temporal knowledge gaps in contemporary freshwater phenology research. Phenology studies skew towards Northern hemisphere temperate ecosystems and the lack of tropical studies can bias our knowledge of environmental cues. For example, the prevalence of temperature-dependent phenological regimes may be biased by the disproportionate representation of temperate systems where seasonal variation in temperature plays a structuring role in biological communities. It remains to be seen whether lower seasonal temperature variation in tropical environments means that other environmental cues are better indicators of organisms' phenology (Chambers et al. 2013). For example, Castro-Rebolledo and Donato-Rondon (2015) suggest that hydrology may be the primary cue for macroinvertebrate emergence in tropical environments, and future research should continue to clarify the environmental drivers of freshwater phenology in tropical systems.

Although salmonid species are of economic and ecological importance, we suggest that future freshwater fish phenology research efforts should emphasize phenology of non-salmonid species and could incorporate an existing life history strategy framework into fish phenology research (Mims et al. 2010, Mims and Olden 2012, 2013). For example, understanding whether periodic strategists (long-lived, large bodied, high fecundity) respond to different environmental cues than opportunistic (short-lived, small bodied, low fecundity) strategists (Chevalier et al. 2014) could be useful to generalize which species may be more sensitive to shifts in phenology.

A limitation of contemporary phenology research in lotic habitats is a lack of long-term datasets. Research shows that shorter time series may be insufficient to detect trends in phenology, therefore limit the potential to monitor ongoing phenology shifts in these environments (Olsen et al. 2020). To address this research gap, studies could conduct contemporary surveys at sites with records of past phenology measurements or employ space-for-time substitution approaches (Blois et al. 2013). In addition, long-term stream

monitoring programs such as the National Rivers and Streams Assessment (NRSA; https://www.epa.gov/national-aquatic-resource-surveys/nrsa) and National Ecological Observatory Network (NEON; https://www.neonscience.org/) in the US, and Office français de la biodiversité (OFB) freshwater fish monitoring program (http://www.naiades.eaufrance.fr/) in France, should consider characterizing species phenology in a small subset of their monitoring sites, for example, in locations expected to experience the greatest changes in climate and other environmental cues such as flow.

Environmental cues and intrinsic traits

Temperature was the most frequently examined environmental cue, but future research should also investigate how climate change may interact with multiple global change stressors to influence phenology. The effects of nutrient loading and increasing temperatures may synergistically affect the timing of lentic phytoplankton production (Elliott et al. 2006, Elliott 2012b), land use and cover change may exacerbate temperature-driven phenology shifts in macroinvertebrate emergence (Villalobos-Jiménez and Hassall 2017, Anderson et al. 2019), and hydroclimatic stressors may synergistically impact fish migration, recruitment, and spawning (Ayllón et al. 2019). Future research should continue to quantify how temperature and other environmental cues influence phenology of different species and how additional stressors can amplify or mitigate these effects.

Alterations to the streamflow regime from climate change or fragmentation may also impact species phenology in lotic systems (Krabbenhoft et al. 2014b, Flitcroft et al. 2016). Changes in the duration, magnitude, or timing of high and low flow events can reduce reproductive success owed to mortality of eggs or juveniles via scouring or desiccation. Although flow requirements for emergence and spawning are less well-studied than thermal requirements, the recent availability of hydrologic time-series data (Ruhi et al. 2018a, Global Runoff Data Centre 2020) and advances in time-series analytic methods such as Multivariate Autoregressive State-Space (MARSS) models (Holmes et al. 2012) and wavelet mean field (Sheppard et al. 2016) present opportunities to investigate relationships between flow and species phenology. For example, Ruhi et al. (2018b) used MARSS models to show associations between dam hydropeaking intensity and the abundance of macroinvertebrate taxa with particular trait states at downstream reaches, and similar techniques could be applied to examine temporal emergence patterns. Of particular interest for future research could be investigating potential impacts of streamflow alterations on larval fish and juvenile recruitment phenology. The timing of these events is often associated with access to temporary habitats and resources created by flow events that benefit the growth and survival of juveniles (Peterson and VanderKooy 1995, Rodger et al. 2016). Therefore, flow regime changes and associated impacts on larval abundances or biomass may alter freshwater fish community structure and function, as has been shown for coastal and marine systems (Asch 2015, Auth et al. 2018).

Another opportunity for future research is to clarify the role of intrinsic traits in describing differential patterns of phenology across species. Publicly available trait datasets exist for amphibians (Trochet et al. 2014, Oliveira et al. 2017, Mendoza-Henao et al. 2019), crayfish (Bland 2017), fishes (Frimpong and Angermeier 2009, Schmidt-Kloiber et al. 2015, Froese and Pauly 2018), macroinvertebrates (Charvet et al. 2000, Usseglio-

Polatera et al. 2000, Poff et al. 2006, Vieira et al. 2006), as well as thermal tolerances (Bennett et al. 2018) and phylogenetic relationships across taxa (Chang et al. 2019). Use of these large-scale datasets could investigate intrinsic traits that may describe differential timing or sensitivity of species phenology and whether environmental or organismal mechanisms underlie these patterns (Chmura et al. 2019).

Phenology beyond the species-level

Species' phenology shifts do not happen in isolation but within ecological networks of interacting species (Miller-Rushing et al. 2010, Walther 2010, Hua et al. 2016). However, our literature review indicates that the potential implications of asynchronous phenology for freshwater community structure and function remain relatively unexplored. We suggest that future research efforts address how asynchronous phenology can modify freshwater food webs, including trophic mismatches and interaction strengths (Thackeray 2016). For example, predictions of shifts in the phenologies of multiple interacting species based on abiotic time-series data can be used to test hypotheses regarding seasonal variation in food web metrics such as connectance, linkage diversity, or chain lengths (Compson et al. 2019, Takimoto and Sato 2020). Such food web model approaches will be important to understand potential implications of changes in biodiversity for freshwater ecosystem functioning (Thompson et al. 2012).

Freshwater phenology research could also investigate patterns and distributions among multiple communities across broad spatial scales. For example, patterns indicating later phenology events with increasing altitude and latitude are known in terrestrial systems (Hopkins 1919, 1920, Vitasse et al. 2018), but spatial gradients in community phenology have received comparatively less attention in freshwaters. Frameworks that incorporate thermal mechanisms to development and physiology may be one way to examine phenological seasonality in temperate freshwaters at large spatial scales (Newbold et al. 1994). Body size mediates many ecological processes in freshwater environments (Hildrew et al. 2007) and organisms in these systems may exhibit greater sensitivity to effects of warming on body size, compared to terrestrial taxa (Forster et al. 2012). Therefore, future research could investigate whether potential warming-induced changes in timing of phenology events are associated with impacts on body size distributions or the strength of size-structured trophic interactions.

Conservation implications of phenology

Knowledge of species' life history can inform biodiversity conservation and our literature review identified a number of applications in which phenology can benefit freshwater conservation. Phenology events can inform invasive species management to identify potential areas susceptible for expansion and methods to control the spread of established introduced species populations (Liang et al. 2005, Dexter et al. 2015, Gooding et al. 2018, Bondarev et al. 2019, O'Brien et al. 2019, Suresh et al. 2019, Giménez et al. 2020). Detailed studies on the phenology of imperiled and declining species may also assist in species recovery plans (Gorman and Stone 1999, Joshi et al. 2018, Watanabe et al. 2020). For lotic fish and invertebrates, flow requirements for emergence, spawning, and larval recruitment should be used to inform management of water resources, including planning

of dams which may fragment migratory patterns or timed dam releases (Gorman and Stone 1999, Valdez et al. 2019). Finally, phenology events can be used to inform species distribution models and improve assessments of potential species range shifts in response to ongoing global change (Chuine 2010, Macgregor et al. 2019).

Novel data sources and technologies

Our review identified novel data sources and technologies that can be applied to future freshwater phenology research. For example, citizen science datasets will be invaluable in filling data gaps, particularly in under sampled regions, and show particular promise for monitoring macroinvertebrate emergence at relatively large spatial scales (Hassall et al. 2007). Natural history collections and museum specimens may also provide access to data on phenology events spanning several decades and have identified phenology shifts in plants and invertebrates (Brooks et al. 2014, Meineke and Davies 2019, DeLeo et al. 2020, Olsen et al. 2020). One potential utility of these data not yet explored is whether they can be used to quantify phenology of non-salmonid freshwater fishes, for example to identify dates of presence of spawning condition individuals or arrival dates of juveniles and migrants.

Novel technologies can also help elucidate trends in phenology events. For example, meteorology radar data can be used to monitor macroinvertebrate emergence (Hansen et al. 2020), video cameras and environmental DNA can provide dates of fish spawning migration events (Kuczynski et al. 2017, Thalinger et al. 2019), and web images can be digitized to estimate phenology dates based on morphological features (e.g., presence of nuptial coloration) (Atsumi and Koizumi 2017).

Conclusion

Consistent in the above knowledge gaps is the need to adopt a more macroscale approach towards freshwater phenology research. Thus far, the body of research has been conducted at relatively small biological, spatial, and temporal scales, but quantifying phenology shifts in response to global change and their implications for biodiversity and ecosystem functioning will demand broader perspectives in each of these dimensions (Thackeray 2016). Additionally, future research should investigate phenology by testing mechanistic hypotheses to assess environmental cues and intrinsic traits (Chmura et al. 2019). Analyses of phenology events across broad latitudinal and elevational gradients can be helpful to elucidate environmental and organismal mechanisms underlying variation at large spatial scales but have seldom been applied in freshwater habitats. Creative combinations and applications of emerging and existing data sources with novel methods and technologies will be necessary to expand the scope of freshwater phenology research.

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Appendix

List A1. List of studies included in our literature review.

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CHAPTER 2
TESTING THE DIVERSITY-BIOMASS RELATIONSHIP IN RIVERINE FISH COMMUNITIES

A version of this chapter was originally published by Taylor Woods, Lise Comte, Pablo Tedesco, and Xingli Giam:

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Taylor Woods, Lise Comte, Pablo Tedesco, and Xingli Giam conceptualized the project. Taylor Woods led the analysis and created figures with input from all authors. Taylor Woods led writing of the first draft and all authors contributed to manuscript revisions and editing.

Abstract

We analyzed the relationship between biodiversity (species richness and functional diversity) and fish community biomass at 1357 stream sites distributed throughout France. We used piecewise path analysis to quantify effects of abiotic and biodiversity variables on biomass and assess relative contributions of native and non-native species on the diversity-biomass relationship. Biodiversity showed a direct positive relationship with biomass after controlling for sampling effort, and direct effects of biodiversity variables on community biomass exceeded those of climate and physical habitat variables. Our analysis indicates that positive effects of species richness on biomass exceeded those of functional diversity. Indirect effects of abiotic variables mediated by biodiversity metrics indicated biomass increased in warmer, lowland habitats. Human impact had no effect on native biodiversity, but positively affected non-native biodiversity. We provide evidence that direct effects of biodiversity on community biomass outweigh those of abiotic variables in riverine fish communities, but resource partitioning alone is unlikely to drive biodiversity effects on biomass in this system. Quantifying the relative roles of anthropogenic impacts, biodiversity, and environmental context in regulating ecosystem functioning will be necessary to understand potential consequences of ongoing global change.

Introduction

The biodiversity-ecosystem functioning relationship (BEF) has received considerable research attention in ecological studies over the past several decades (Tilman et al., 2014; Isbell et al., 2015; Lefcheck & Duffy, 2015; Duffy et al., 2016; Ammer, 2019; Le Bagousse-Pinguet et al., 2019) as researchers seek to better understand the effects of ongoing biodiversity loss (Alroy, 2017; Giam, 2017) on ecosystem functioning (Naeem et al., 1994; Chapin III et al., 2000; Duffy, 2009; Hooper et al., 2012; Macdougall et al., 2013). The BEF describes how ecosystem functioning varies as a direct consequence of the level of biodiversity in a given system (Tilman et al., 1997). Extensive literature on this topic generally supports a positive BEF (Loreau et al., 2001; Hooper et al., 2005; Cardinale et al., 2007) that may arise through a variety of mechanisms. For example, positive effects of local biodiversity on ecosystem functioning may arise via niche partitioning that enhances resource use efficiency in biodiverse systems (i.e., niche complementarity;

Tilman et al., 1997). Alternatively, biodiverse communities may be more likely to contain species that are highly productive under local environmental conditions; and therefore, increased biodiversity may promote ecosystem functioning via 'selection effects' (Tilman et al., 1997; Loreau, 2000; Loreau et al., 2001, García et al. 2018, Isbell et al. 2018).

Functional traits have become a key component of studies investigating BEF because they characterize how organisms interact with their abiotic and biotic environment (Petchey & Gaston, 2006), and are therefore useful to test the existence of niche-based mechanisms for postive BEF (Cardinale et al., 2012; Cadotte, 2017). Direct comparisons of functional and taxonomic diversity metrics on ecosystem functioning often indicate that functional effects can outweigh those of their taxonomic counterparts, supporting predictions of the niche complementarity hypothesis (Mokany et al., 2008; Gagic et al., 2015; Lefcheck & Duffy, 2015). However, taxonomic diversity is also important to consider because it can reveal effects of biodiversity on ecosystem functioning that may arise independently of functional diversity properties. For example, species richness effects on ecosystem functioning may exceed those of functional metrics if niche differences among cooccurring species rely upon variables unrelated to functional traits or are not related to traits used to quantify functional diversity metrics (Craven et al., 2018). Therefore, adequate assessment of BEF may benefit from incorporating both functional and taxonomic diversity metrics to account for multiple pathways through which biodiversity may enhance ecosystem functioning (Cadotte et al., 2011; Roscher et al., 2012).

Abiotic factors that affect the magnitude of biodiversity in a system are also important to include in BEF analyses (Cardinale et al., 2000; Hooper et al., 2005; Fornara & Tilman, 2009). For example, gradients in climate (Lavers & Field, 2006; Ma et al., 2010) and topography (Homeier et al., 2009; Belote et al., 2011) are well-established drivers of diversity; and anthropogenic impacts may cause deviations from BEF observed in undisturbed communities (Flynn et al., 2009; Mayfield et al., 2010; Allan et al., 2015). Considering the many factors that may influence BEF in natural systems, documenting these interrelationships is crucial to understand potential impacts of global change and biodiversity loss on ecosystem functioning (Loreau et al., 2001; Srivastava & Vellend, 2005; Allan et al., 2015).

Despite the extensive literature supporting a positive BEF, two main limitations of previous studies prevent broader understanding of the circumstances and contexts over which the relationship applies (Kaiser, 2000). First, the majority of BEF studies are based on experimental designs involving arbitrarily selected assemblages composed of limited numbers of species at relatively small spatial scales (Hodgson et al., 2002; Naeem, 2002). While experimental studies are valuable in isolating the biodiversity effect from other confounding factors, they may overlook important processes (e.g., community assembly) or anthropogenic influences (e.g., non-native species introductions) that operate in natural systems (Lepš, 2004; Jiang et al., 2009). Understanding the relative effects of biodiversity on BEF in natural systems may thus be more informative to quantify potential impacts of biodiversity loss on ecosystem functioning, compared to experimental designs (Duffy et al., 2017). Second, existing BEF research has focused on a limited set of taxonomic groups and systems: grassland (Lambers et al., 2004; Isbell et al., 2011), forest (Paquette &

Messier, 2011; Jucker et al., 2014; Forrester & Bauhus, 2016; Liang et al., 2016; Jactel et al., 2018), aquatic primary producer (Dodson et al., 2000; Cardinale, 2011; Santos et al., 2015), and marine fish (Mora et al., 2011; Duffy et al., 2016) communities have constituted the taxonomic basis for the majority of research on BEF. Expanding analyses to previously understudied systems across a range of natural environmental contexts could thus provide additional insights into the generality of these relationships and potential benefits of biodiversity conservation for preserving ecosystem functioning, globally (Srivastava & Vellend, 2005).

Focusing on an understudied group with regards to BEF, we test and explore this relationship in stream fish communities. As a model study system, we use the extensively sampled streams in France where the wide geographic coverage of surveys encompasses a variety of freshwater habitats and thus permits a robust analysis of BEF in natural, complex stream systems at a previously uninvestigated extent. We correlate community biomass with biodiversity drivers and assess whether biodiversity exerts a stronger influence on biomass than environmental variables. Specifically, we test the hypothesis that complementary resource use drives the magnitude of community biomass in more biodiverse stream communities [hereafter, the diversity-biomass relationship (DBR)]. To support this hypothesis, we predicted that: (1) biodiversity metrics will show a positive relationship with community biomass in natural stream systems, (2) functional diversity effects on biomass will exceed those of species richness, and (3) the influences of native biodiversity on biomass will be greater than those of non-native biodiversity.

Understanding the role of biodiversity in rivers and streams is important because these systems harbor more imperiled species per unit area, compared to terrestrial and marine environments (Balian et al., 2008; Harrison et al., 2018). Maintaining ecosystem functioning in these systems is important because of the many ecosystem services freshwaters provide to human populations (Dodds et al., 2013). For example, maintenance of water quality as well as recreational fishing, commercial fisheries, and aquaculture industries are services provided by freshwater fish that benefit the public health and economic well-being of human societies (Holmlund & Hammer, 1999; Wilson & Carpenter, 1999; Auerbach et al., 2014). Although it is largely unknown what role biodiversity plays in maintaining ecosystem functions in natural riverine environments, experimental evidence indicates that increasing aquatic biodiversity promotes better water quality (Cardinale et al., 2011). Therefore, adequate assessment of the threats posed to streams and rivers may require understanding the extent to which erosion of biodiversity may affect ecosystem functioning.

Methods

Data collection

We obtained fish community data from the Office français de la biodiversité (OFB) freshwater fish monitoring program (available at < http://www.naiades.eaufrance.fr/ >) which surveyed fish communities from 1977–2018 using a standardized electrofishing protocol based on stream width and depth. We referenced each site to its respective watershed following the French National Service for Water Data and Common Repositories Management watershed dataset (Sandre, 2018). We restricted our dataset to

sites sampled by backpack electrofishing using two passes to minimize potentially confounding effects of variable efficiency of different sampling gears. In addition to controlling for the number of passes at each site, we retained the surface area of the stream reach sampled (sampled area) for each survey to control for potential variation in sampling effort (Gotelli & Colwell, 2001; Table 4). We temporally restricted our dataset to 1992–2012, a period which occurred after major climatic shifts across Europe in the preceding decade (Reid et al., 2016), and therefore these occurrence records likely represented similar, contemporary climatic conditions. We selected only sampling events from low flow periods (April–September) to minimize potential effects of seasonal bias on biomass measures. We also removed surveys in which brown trout (*Salmo trutta*) was the only species recorded because these streams are likely stocked (Bohling et al., 2016), which may confound our analyses.

Next, we performed additional data screening procedures for statistical considerations. First, for any instance in the dataset where a site was surveyed during multiple years, we retained only the most recent survey to prevent pseudoreplication. Second, we constrained surveys to those with ≥ 100 individuals sampled and watersheds containing at least five surveys, to minimize potential biases from under sampling within surveys and watersheds, respectively (mean number of individuals per site = 697, SD = 859.2; mean site density per watershed = 0.004 sites/km^2, SD = 0.003). To examine the sensitivity of our results to potential spatial and temporal variation in sampling effort, we assessed effects of alternative survey selection criteria and found that results were qualitatively similar (i.e., the magnitude of predictor variable effects on biomass were comparable; Table 6); therefore we consider our results robust to potential sampling biases usual in observational studies that may affect inferences regarding biodiversity variables.

In total, the 1357 sites retained for our analysis spanned a wide variety of environments along longitudinal stream gradients (mean upstream catchment area = 346.3 km^2, SD = 3019.1) and across watersheds (75 watersheds out of 184 with a mean area = 2945 km^2, SD = 2310; Fig. 9). The substantial environmental variation encompassed by the dataset allowed us to achieve a more general understanding of BEF across a broad diversity of habitats and gradients in natural, complex lotic systems.

We selected total standing biomass as a measure of ecosystem functioning for each survey because biomass directly relates to metabolic constraints on energy use and has previously been used as an informative measure of ecosystem functioning for aquatic vertebrates (Mora et al., 2011; Duffy et al., 2016). The OFB dataset provided pooled biomass (weight in grams) measurements for all individuals of each species, therefore we summed biomass across all species for each sampling event to estimate total standing biomass in each site.

Table 4. Predictor variables included in all path models predicting fish biomass (weight), including descriptions, units, hypothesized direct effects on biomass [+ (positive) or – (negative)], and references for predicted effects: [a]Giam & Olden (2018), [b]Loreau et al. (2003), [c]Duffy et al. (2016), [d]Patrick et al. (2019). Transformations applied, if applicable, are listed after units and all variables were additionally standardized prior to analysis.

Variable	Definition	Effect	Reference
Catchment area	Total upstream drainage area (km^2; log_{10})	+	a
Free-flowing area	Unobstructed river area (km^2; ln_{x+1})	+	a, b
Functional diversity	Functional diversity (Rao's Q)	+	c
Human impact	Human footprint index	–	c
Native richness	Native species richness (ln_{x+1})	+	c
Non-native richness	Non-native species richness (ln_{x+1})	+	c
Precipitation	Mean Precipitation (mm; log_{10})	+	d
Slope	Slope along the stream reach (‰)	–	a
Species richness	Total community species richness (log_{10})	+	c
Sampled area	Surface area of sampled reach (m^2; log_{10})	+	
Temperature	Mean annual temperature (°C)	+	c

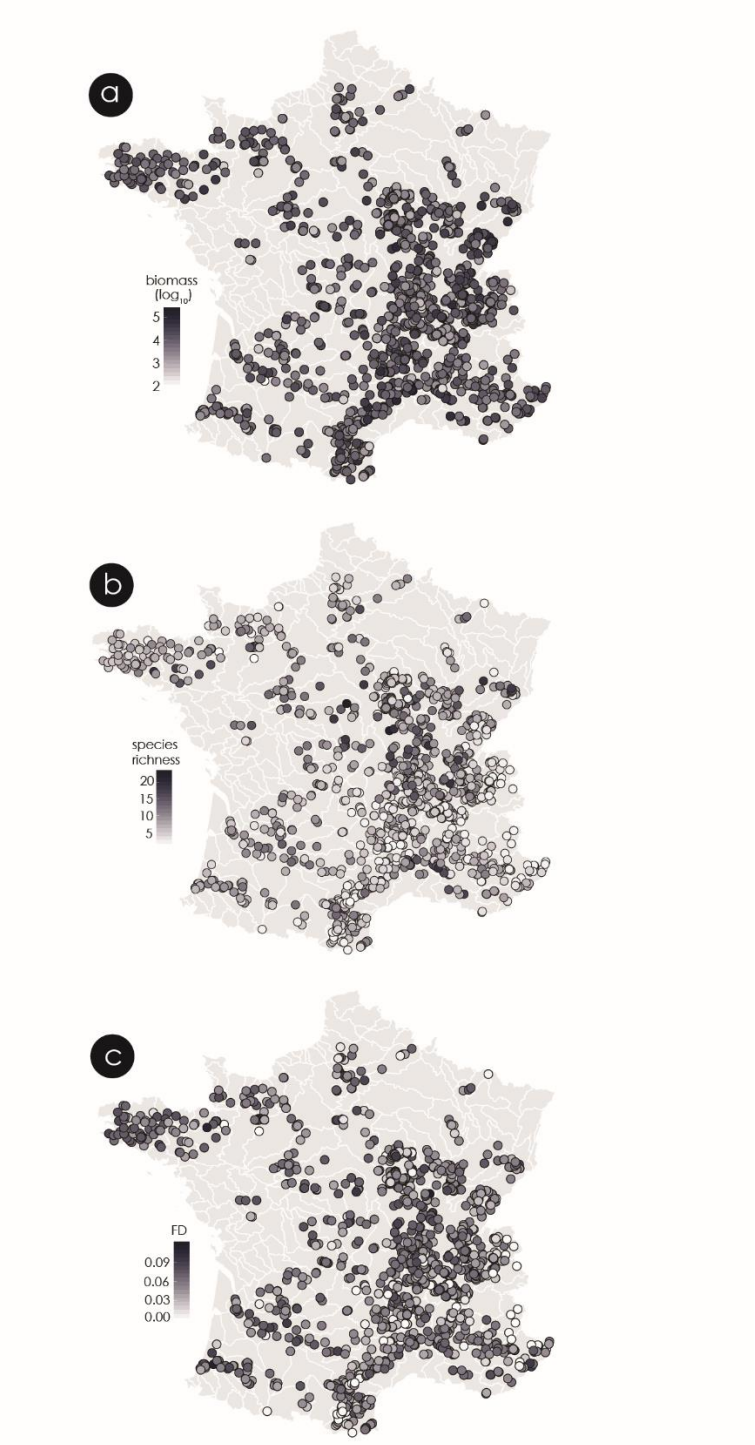

Figure 9. Map of fish sampling sites included in the analysis across French watersheds (grey polygons). Three maps are shown to illustrate the distribution of (a) community biomass, (b) species richness, and (c) functional diversity.

We estimated two biodiversity metrics for each sampling event: species richness and functional diversity (Table 4). We calculated functional diversity as abundance-weighted Rao's Quadratic Entropy (Rao's Q; Botta-Dukát, 2005) based on 10 functional traits obtained from FishBase (Froese & Pauly, 2018) and the Freshwater Information Platform (Schmidt-Kloiber & Hering, 2015; Table 5). We selected traits for inclusion based on a priori knowledge of fish functional diversity and potential functional axes along which niche partitioning may occur: habitat requirements, life history strategy, and trophic position (Duffy et al., 2016). Rao's Q measures functional diversity by estimating the dispersion of the community in functional trait space as the mean pairwise distance between species in multivariate trait space defined by principal coordinates analysis axes (Botta-Dukát, 2005; Laliberte & Legendre, 2010). It is therefore a useful metric to assess potential influences of niche partitioning in fish communities, while providing information independent of species diversity (Duffy et al., 2016). We used Gower's distance to construct the distance matrix used to calculate Rao's Q to accommodate mixed trait data types (Table 5; Gower, 1971). We used the package 'FD' (Laliberte et al., 2014) to compute Rao's Q in R (R Core Team, 2018).

In order to assess the relative effects of native versus non-native species on DBR, we classified each species in the dataset as native or non-native to each river basin using Tedesco et al. (2017). For a small number of species present in small coastal basins (104 occurrences out of 18,405 total occurrence records), native status was not available at the river basin scale. For these species occurrences, we used the United Nations Food and Agriculture Organization (FAO) Database on Introductions of Aquatic Species (FAO, 2005) to assign native status: species were assigned as native if they were not listed on the FAO dataset as being introduced to France. Following that, we calculated native and non-native species richness for each site.

To examine the direct and indirect effects of abiotic variables on diversity and biomass, we collected data on anthropogenic pressures, climate, and physical habitat (Table 4). We extracted local (i.e., site-level) mean annual temperature and precipitation from ClimateEU (Hamann et al., 2013) and averaged annual metrics over the period of analysis (1992–2012) to estimate climate conditions. We characterized variation in local instream habitat variables associated with the longitudinal position of the sampled site along the stream network (e.g., width, depth, and riparian shading; Vannote et al., 1980) using slope and upstream catchment area from the European River Catchments Network (European Environment Agency, 2012).

We assessed anthropogenic influences on DBR using the terrestrial Human Footprint Index (HFI; Venter et al., 2016) value extracted at each site (larger value = greater human impact) for the year 2009. HFI simultaneously accounts for cumulative impacts from multiple anthropogenic pressures (e.g., agriculture, urbanization, navigable waterways; Venter et al., 2016). We also assessed whether our results were more sensitive to HFI values corresponding to the beginning of our studied period by reevaluating our models using HFI values from 1993. We found that results using 1993 and 2009 HFI values were qualitatively similar (Table 7), therefore we only report results obtained using 2009 HFI in the main text.

Table 5. Functional traits used in the functional diversity analyses. The category indicates the facet of functional diversity represented by each trait (troph = trophic/diet, env = environmental/habitat requirements, rep = reproductive/life history). Multichoice nominal variables indicate categorical traits for which a species can be assigned to multiple categories.

Trait	Category	Type	Units or levels
Vertical feeding position	Troph	Multichoice nominal	Benthic, surface
Adult trophic guild	Troph	Nominal	Invertivore, invertivore–piscivore, piscivore, omnivore, herbivore–detritivore
Maximum total length	Rep	Continuous	Cm (log_{10})
Substrate affinity	Env	Multichoice nominal	Fine, coarse, rocky, vegetation
Habitat affinity	Env	Multichoice nominal	Creek, small river, large river, lake, spring
Altitudinal affinity	Env	Multichoice nominal	Lowland, montane, upland
Velocity preference	Env	Multichoice nominal	Fast, moderate, slow
Maximum total fecundity	Rep	Continuous	Number of eggs (log_{10})
Spawning season length	Rep	Continuous	Number of months
Reproductive guild	Rep	Nominal	Broadcast spawner (non–guarder), brood hider (non–guarder), substrate chooser (guarder), nest builder (guarder), substrate indifferent

In addition to external terrestrial stressors, freshwaters may experience unique stressors such as impoundment (damming) of waterways, which may restrict fish movement. To account for potential influences of river fragmentation on DBR (hereafter 'free-flowing area'), we obtained the area between artificial structures and impoundments of ≥ 1 m height from the French national obstacle inventory (ROE database, < http://carmen.carmencarto.fr/66/ka_roe_current_metropole.map >) complemented with modelled estimations from Januchowski-Hartley et al. (2019). A larger free-flowing area indicates a greater area of unobstructed river and therefore, larger habitat availability without fish dispersal constraints. We selected artificial structures of ≥ 1m height because obstructions of this height represent important dispersal barriers to many native French fish species and encompass a broad variety of stream habitat alterations imposed by barriers (Baudoin et al., 2014).

Data analysis

We used piecewise path analysis to examine direct and indirect drivers of the variation in local biomass across stream sites. Path analysis is an appropriate method to quantify DBR in observational analyses because it can discriminate between the relative importance of multiple covarying factors (Mokany et al., 2008) and account for complex interrelationships of predictor variables that affect biomass (Patrick et al., 2019). First, we constructed hypothesized causal models (Fig. 10) for two separate path models: a first one that did not discriminate between native and non-native species (hereafter 'total biodiversity model'; Fig. 10a), and a second where we assessed potential differences between native and non-native species richness in driving DBR (hereafter 'partitioned biodiversity model'; Fig. 10b). This approach did not require a prior specification of whether a given directional path was positive or negative.

To model endogenous piecewise components (biomass, functional diversity, and species richness), we used linear mixed-effects models with Gaussian error structures. We incorporated random intercepts based on watershed ID in all endogenous components because sites in the same watershed might have more similar responses owing to similarities in environmental conditions and/or species pools. We also included sampled area as a covariate in all endogenous piecewise components, which allowed us to quantify the influences of predictor variables, while controlling for variation in sampling effort. We also assessed whether sampling year may affect results and incorporated year as a covariate and these preliminary analyses indicated no effect (Table 8), therefore we selected the more parsimonious models without sampling year for analyses. Prior to fitting path models, we applied transformations where appropriate to predictor variables (see Table 4), log10 transformed biomass, and standardized (centered to mean = 0 and scaled to SD = 1) all variables to meet assumptions of normality of residuals imposed by Gaussian error structures.

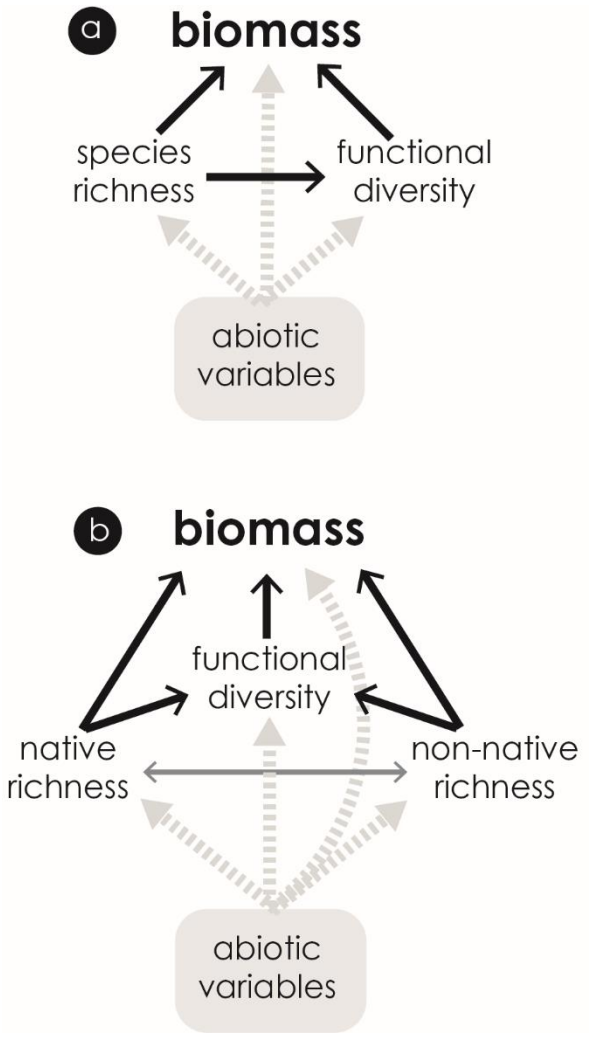

Figure 10. Hypothesized path models showing all potential direct and indirect relationships of predictor variables on biomass for the (a) *total biodiversity path model* and (b) *partitioned biodiversity path model*. Black lines show direct effects of endogenous variables, dashed grey lines illustrate combined effects of exogenous abiotic variables, and double-headed arrows illustrate bidirectional relationships. Paths between exogenous abiotic variables, all of which are treated as bidirectional correlations, are omitted.

We modelled biomass as a function of abiotic and biodiversity (species richness and functional diversity) variables plus sampled area. Sites within the same regional pool may also exhibit more similar responses of biomass to biodiversity effects. Therefore, we assessed the fit of the following candidate random effects structures applied to the global (all predictor variables included) biomass model: (1) random watershed intercepts, (2) random species richness slopes and watershed intercepts; and (3) random functional diversity slopes and watershed intercepts. We used small-sample Akaike Information Criterion (AICc) to select the most parsimonious random effect structure from the candidate models (i.e. model with the lowest AICc).

Next, we modelled species richness as a function of abiotic variables and sampled area; and modelled functional diversity as a function of species richness, abiotic variables, and sampled area (Fig. 10a). We specified a direct path from species richness to functional diversity to reflect the dependency of functional diversity on species richness (Flynn et al., 2011; Duffy et al., 2016; Craven et al., 2018). For each endogenous model (n = 3), we verified the absence of collinearity among the full suite of predictor variables using variance inflation factors (VIF < 4; Table 9).

For relationships between exogenous abiotic variables (catchment area, free-flowing area, human impact, precipitation, slope, and temperature), we specified all potential paths between variable pairs as bidirectional correlations because these variables covary with environmental context determined by geographic location and position within stream networks (Vannote et al., 1980; Harvey & Altermatt, 2019). Therefore, relationships between these variables are not based on causal mechanisms (Shipley, 2009, 2016). For example, annual temperature and human impact are likely positively related not through causal mechanisms, but because they both covary along longitudinal and geographical gradients. We treated sampled area the same as exogenous abiotic variables because sampled area is associated with variables (e.g., stream width and depth) that are likewise determined by regional and longitudinal position of the sampling site.

Next, for each endogenous variable, we identified important predictors via backward elimination of non-significant (p > 0.05) fixed effects starting from the full model (Kuznetsova et al., 2017). To assess the fit of each endogenous LMM, we inspected model residuals for the best-fit models and scatterplots of response and predictor variables and found no evidence of potential non-linearity with respect to relationships between biomass and biodiversity variables with environmental predictors. We examined Moran's correlograms from the residuals of the best-fit biomass model and found no evidence of residual spatial autocorrelation structure (Fig. 13), therefore we did not consider a spatial correlation structure as part of the random effects in the model.

Following identification of causal paths between piecewise components, we tested whether our final path model provided a good fit to the empirical data using the d-sep test, which quantifies whether unconnected variables are indeed independent after accounting for the influence of other variables in the model (Shipley, 2016). The d-sep test entails (1) decomposing the causal path model into a series of k conditional independence claims, (2) testing the validity of each claim using appropriate statistical methods, (3) combining p-values from each claim to obtain the Fisher's C statistic; and (4) testing C against a chi-squared distribution with 2k degrees of freedom (see Shipley, 2016). If the p-value from

the d-sep test is not significant ($p > 0.05$), this indicates effects in the path model are conditionally independent, therefore the path model provides an adequate fit to the data (Shipley, 2016).

We then examined more specifically how non-native species may affect pathways of community biomass within the partitioned biodiversity model. We maintained the same hypothesized causal model structure as in the total biodiversity model explained above but separated species richness into native and non-native species richness components. For the biomass model, we used AICc to select the optimal random effects structure from four candidate structures: (1) random watershed intercepts, (2) random slopes for native species richness and watershed intercepts, (3) random slopes for non-native species richness and watershed intercepts; and (4) random slopes for functional diversity and watershed intercepts. We specified direct paths from native and non-native species richness to functional diversity to assess the relative effects of native versus non-native species in driving functional diversity. We additionally incorporated a bidirectional correlation between native and non-native species richness because the relationship between these two variables is unresolved (Brown & Peet, 2003; Fridley et al., 2007). Model selection and d-sep test methods for the partitioned biodiversity model followed those used in the total biodiversity model.

We used the packages 'lme4' (Bates et al., 2015), 'lmertest' (Kuznetsova et al., 2017), 'MuMIn' (Barton, 2018), and 'piecewiseSEM' (Lefcheck, 2016) to fit and evaluate linear mixed-effects models and piecewise path models in R.

Results

The final total biodiversity model adequately fit the data ($C = 7.78$, 14 *df*, $p = 0.90$; Fig. 11a, Table 10). Results indicated regional variation in the response of biomass to species richness, as shown by an optimal random effect structure of random intercepts and random slopes for species richness across watersheds. After controlling for sampling effort, biodiversity variables (species richness and functional diversity) were direct, positive drivers of biomass (Fig. 11a). The cumulative direct effects of biodiversity on stream fish biomass exceeded those of abiotic variables (Fig. 12a). Biomass also increased as a direct consequence of precipitation and human impact and increased with decreasing temperature (Fig. 11a).

Species richness increased with increasing temperature, free-flowing area, and human impact, and decreased with increasing precipitation and slope. Functional diversity increased with increasing temperature and precipitation and decreased with increasing catchment area. Species richness showed a strong, positive relationship with functional diversity.

Precipitation had opposing indirect and direct effects; however, the overall effect of precipitation on biomass was positive (Fig. 12a). Temperature also had opposing indirect and direct effects; however, indirect positive effects of temperature on biomass exceeded the direct, negative effects (Fig. 12a). Overall, catchment area, free-flowing area, and temperature had indirect positive effects on biomass, whereas precipitation and slope had indirect negative effects on biomass, all of which were mediated through species richness and/or functional diversity (Fig. 11a, Fig. 12a).

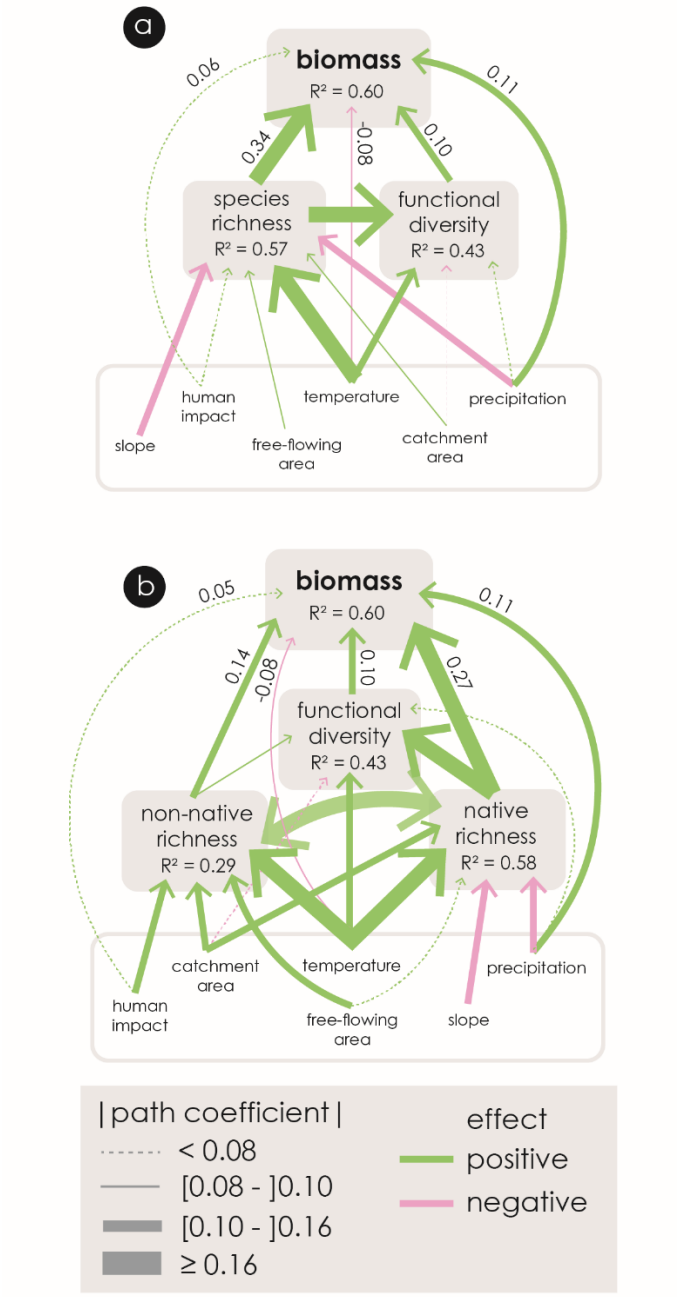

Figure 11. Final piecewise path models showing abiotic and biotic influences on fish biomass for the (a) *total biodiversity path model* and (b) *partitioned biodiversity path model*. All paths are significant at $p < 0.05$. Width of arrows represents the absolute value of the path coefficient (effect size) based on percentiles of the distribution of absolute path coefficients from the total biodiversity path model and color indicates the direction (positive or negative) of the effect. For clarity, bidirectional correlations are omitted, as well as sampled area because this variable served as a control.

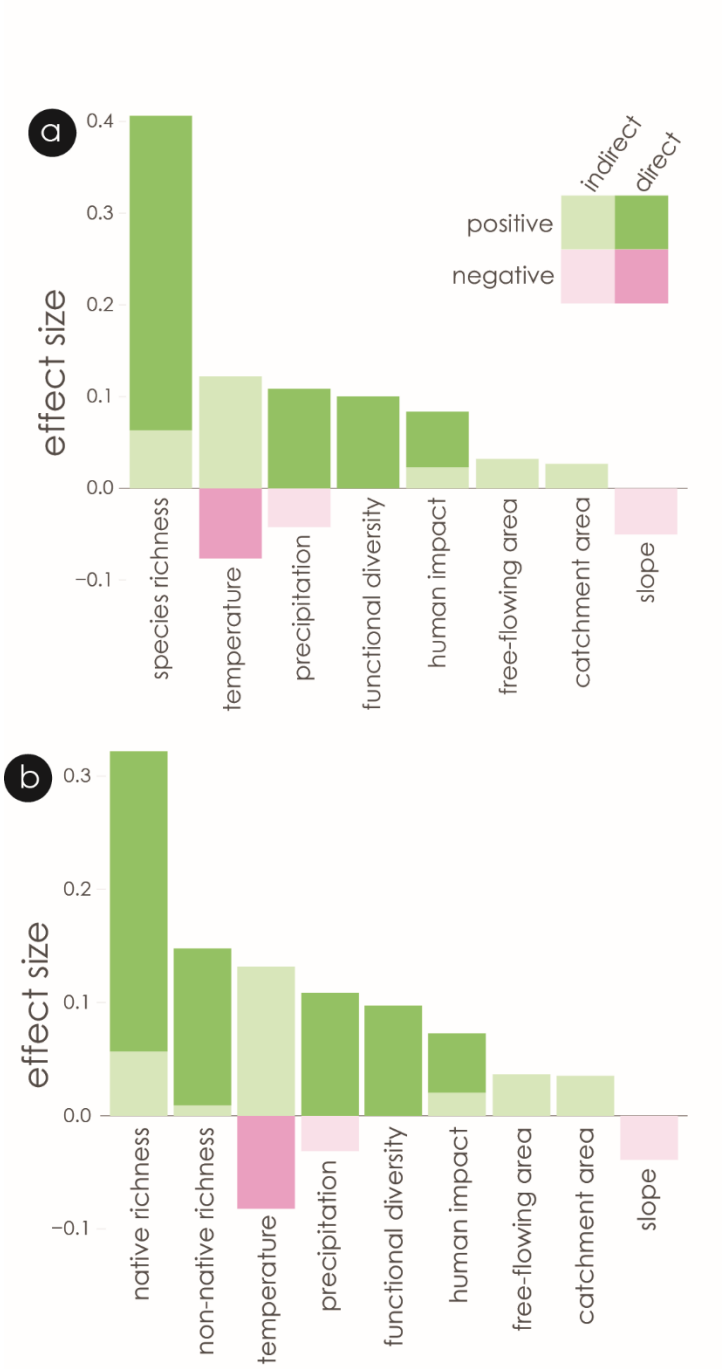

Figure 12. Direct and indirect effects of biodiversity and environmental factors on fish biomass from the path model for the (a) *total biodiversity path model* and (b) *partitioned biodiversity path model*.

The partitioned biodiversity model also provided an adequate fit to the data (C = 23.42, 20 df, p = 0.269; Table 12). Results indicated regional variation in the response of biomass to native species richness, as shown by an optimal random effects structure based on random watershed intercepts and random slopes for native species richness across watersheds. Native species richness showed the strongest effect on biomass, followed by non-native species richness, and functional diversity. Direct effects of abiotic variables on biomass were consistent with those in the total biodiversity model (Fig. 11b).

Native species richness showed a strong, positive correlation with non-native species richness. Native species richness was a stronger driver of functional diversity than non-native species richness. Functional diversity also increased with increasing temperature and decreasing upstream catchment area. Native and non-native species richness increased with increasing catchment area, free-flowing area, and temperature. Native species richness also increased with decreasing slope and precipitation (Fig. 11b). Human impact had no effect on native species richness, but showed a strong, positive effect on non-native species richness (Fig. 11b).

Discussion

Our analysis indicates that the DBR operates in a previously under-studied context (stream fish communities) and that multiple abiotic factors directly and indirectly contribute to the DBR in these systems. Biodiversity variables (species richness and functional diversity) had the strongest positive effects on biomass, and native species, compared to non-native species, contributed more to this relationship. Generally, indirect effects of abiotic variables on biomass reflected environmental conditions that vary along longitudinal stream gradients and suggested that fish biomass increased in warmer habitats (Myers et al., 2018). Although longitudinal stream gradients in fish productivity are less well-studied, analyses of aquatic primary production (McTammany et al., 2003) and macroinvertebrate secondary production (Grubaugh et al., 1996) suggest that productivity increases in lowland habitats. Although we did not assess community production in this study, standing biomass may in some cases provide a proxy for productivity (Mora et al., 2011). Therefore, our results complement these analyses by suggesting that productivity of aquatic primary producer, macroinvertebrate, and fish communities increase along longitudinal stream gradients.

After controlling for local environment and sampling effort, both functional diversity and species richness positively affected biomass, and the direct influences of biodiversity variables on biomass exceeded those (both direct and indirect) of abiotic variables. Our analyses indicate a positive role of biodiversity in promoting ecosystem functioning (Loreau et al., 2001; Cardinale et al., 2007) and do so across a large study extent encompassing complex ecological and environmental gradients that are difficult to incorporate in controlled experiments. These results add to the growing body of evidence that effects of biodiversity on ecosystem functioning often outweigh those of environmental variables in natural systems (Duffy et al., 2017). In the context of the multiple stressors that threaten freshwater biodiversity, a positive BEF suggest ongoing biodiversity loss will also impact the many ecosystem services provided by these systems (Dudgeon, 2010).

We found that species richness had a stronger effect on biomass than functional diversity, in contrast to predictions of the niche complementarity hypothesis. These results may support evidence that interspecific interactions play a limited role in structuring stream fish communities (Oberdorff et al., 1998; Peres-Neto, 2004; Giam & Olden, 2016). A stronger species richness effect on biomass relative to functional diversity may also suggest that more biodiverse systems are more productive due to mechanisms independent of functional diversity. In more speciose communities, the selection of dominant, productive species during community assembly may be increased, relative to communities with lower species richness (selection effects; Hector, 1998; Loreau & Hector, 2001). Stronger effects of taxonomic diversity indices on ecosystem functioning relative to functional diversity may also indicate factors driving niche partitioning are unrelated to the traits selected (Craven et al., 2018). Although the traits used in this analysis encompassed a broad spectrum of fish functional characteristics, resource partitioning in stream fish communities may be more adequately assessed using morphometric traits or stable isotope data (Comte et al., 2016). Regardless of the ultimate mechanisms underlying the relative effects of species richness compared to functional diversity, our results based on observational data provide evidence of strong, direct effects of biodiversity on biomass and therefore support a positive DBR.

We found that biodiversity effects on community biomass outweigh those of abiotic variables in natural, complex communities. However, environmental variables also directly and indirectly influence DBR. Our results indicate a direct, positive effect of precipitation on biomass, after controlling for biodiversity variables. A positive relationship between biomass and precipitation is well-established for terrestrial plant communities where droughts can limit community productivity (Ciais et al., 2005; Hogg et al., 2008; Ma et al., 2010; Zhao & Running, 2010). In streams, precipitation effects are mediated through the hydrologic regime, which may be a key regulator of aquatic macroinvertebrate secondary production (Grimm & Fisher, 2006; Chadwick & Huryn, 2007; Ledger et al., 2011; Patrick et al., 2019) and affects recruitment of stream fish via synchronization of life history events with streamflow (Bunn & Arthington, 2002; Lytle & Poff, 2004; Mims & Olden, 2012, 2013). Therefore, after accounting for indirect effects mediated by biodiversity variables, our results indicate a direct, positive effect of streamflow on fish community biomass, as indicated by analyses on other taxa. The effects of precipitation on biodiversity differed based on the biodiversity variable considered. We found a negative effect of precipitation on species richness, and a positive, but weaker, effects of precipitation on functional diversity. The moderate effect of precipitation on species richness may reflect biogeographical gradients in biodiversity from relatively less biodiverse but wetter temperate streams to more speciose but drier Mediterranean streams (Reyjol et al., 2006).

Temperature also showed contrasting direct and indirect effects on biomass. We found a weak negative direct effect of temperature on biomass, suggesting that cooler environments positively influence fish community biomass. However, indirect effects of temperature on biomass exceeded those of direct effects and suggested biomass increased with increasing temperature, as found for marine fish communities (Duffy et al., 2016). This suggests available energy limits fish species and functional diversity in stream systems, like many other taxonomic groups and ecological systems (Hawkins et al., 2003;

Clarke & Gaston, 2006; Field et al., 2009; Swenson et al., 2012; Chu et al., 2018). One potential mechanism that may explain the contrasting direct and indirect effects of temperature on biomass may be the observed inverse relationship between temperature and body size (Blanchet et al., 2010). In colder streams, although species richness and functional diversity may be lower, individuals may achieve larger body sizes, thus driving the inverse, direct relationship between biomass and temperature.

Human impact showed weak, but positive indirect effects on biomass, as was found for marine fish communities (Duffy et al., 2016). Streams in highly anthropogenic environments are often channelized and widened (Navratil et al., 2013), which may provide suitable habitat for larger-bodied species (Giam & Olden, 2018). Additionally, streams in catchments characterized by agricultural land use may show higher rates of primary production (Burrell et al., 2014), which may in turn drive increased fish community biomass in these areas. Our analyses also suggest that human-mediated habitat alterations contribute to the successful establishment of non-native species (Leprieur et al. 2008; Blanchet et al., 2009; Redding et al., 2019), which may drive the indirect, positive relationship between human impact and fish community biomass.

Upstream catchment area showed indirect effects on biomass, mediated through species richness and functional diversity. We found a strong positive relationship between catchment area and species richness. This indicates species richness increases along longitudinal stream gradients from the headwaters to lowland streams, consistent with established freshwater biodiversity patterns (Vannote et al., 1980). By contrast, we found a weak negative effect of catchment area on functional diversity, after controlling for species richness. One explanation for this is that lower-order (smaller) streams tend to have greater habitat heterogeneity (e.g., fast-flowing shallow riffles, slow-flowing deep pools, patches of woody debris and leaf litter) per unit area compared to higher-order (larger) streams (Forman, 1995). Although the directional effects of catchment area differed between biodiversity variables, positive effects of catchment area on biodiversity variables outweighed those of negative effects, resulting in an overall positive indirect effect of catchment area on fish community biomass, as found for other aquatic taxa (McTammany et al., 2003, Patrick et al., 2019).

We also found indirect positive effects of free-flowing area on biomass because larger free-flowing patches of river increased species richness. These results may indicate habitat connectivity can positively influence ecosystem functioning by facilitating dispersal in heterogeneous environments (i.e., spatial insurance effects; Loreau et al., 2003). It is somewhat notable that free-flowing area had a greater positive effect on non-native than native richness, but this result may reflect the larger habitat requirements of non-native species, many of which are large-bodied and migratory, and may disperse via large river habitats (Rahel et al. 2006; Guillerault et al. 2015; Rahel & McLaughlin, 2018). Prior investigations of BEF at small, experimental scales indicate biodiversity-mediated effects of dispersal can influence ecosystem functioning within metacommunities (France & Duffy, 2006). Results from our regional analysis complement these findings and suggest that habitat fragmentation in riverine ecosystems may negatively affect ecosystem functioning, via biodiversity loss. Clarifying the roles of spatial processes, such as

dispersal, in mediating BEF should be of particular importance to understand impacts of habitat fragmentation in natural systems (Gonzalez et al., 2009).

We found that effects of native species richness on community biomass and functional diversity far exceeded those of non-native species richness. The weaker effects of non-native species richness on functional diversity and biomass may reflect the increase in resource overlap following the introduction of omnivorous non-native species (Córdova-Tapia et al., 2014; Sagouis et al., 2015; Comte et al., 2016). Thereby the contributional increase in functional diversity and subsequent biomass provided by non-native species may be lower than that of native species due to higher functional redundancy in communities characterized by higher non-native species richness.

Increasing anthropogenic impact positively affected non-native species richness but not native species richness. Anthropogenic environments characterized by homogenized habitats may alter community assembly processes and select for limited subsets of traits capable of success in human-modified conditions (e.g., broad environmental tolerances), thus favoring non-native species establishment and success (MacDougall & Turkington, 2005). Although such anthropogenic impacts may generate short-term gains in ecosystem functioning via species richness, they may potentially alter or deteriorate BEF over longer temporal scales (Mori et al., 2018). With ongoing abiotic and biotic homogenization, it will be important to understand how changes in community structure from species introductions impact ecosystem functions (Olden et al., 2016, 2018), including potential alteration of BEF.

Our analyses are subject to a number of potential caveats. First, we likely omitted several variables that may affect stream DBR. For example, instream physiochemical conditions may better quantify anthropogenic pressures on stream fish than our terrestrial metric and hydrologic indices may better characterize streamflow regimes compared to precipitation. Second, the DBR and its underlying mechanisms may vary through time (van Ruijven & Berendse, 2005). Therefore, a temporal analysis of this relationship at sites with repeated sampling events could provide additional understanding of DBR in this system. Third, although we addressed DBR at local (i.e., stream reach) scales, niche partitioning effects in stream communities may be stronger at even finer scales (e.g., subreach microhabitats; Taylor, 1996; Holomuzki et al., 2010). Finally, studies suggest that phylogenetic diversity (Cadotte et al., 2009) or stable isotope data (Comte et al., 2016) may be informative predictors of niche complementarity or resource partitioning, therefore incorporating other biodiversity variables, in addition to functional and taxonomic diversity, could provide further insight on niche partitioning effects on biomass.

In summary, our study indicates biodiversity is the primary driver of community biomass in stream fish communities, compared to abiotic variables; and suggests that native species richness is the primary driver of the biodiversity effect. Direct and indirect effects of environmental variables on fish biomass highlight that ongoing and future environmental change may potentially alter ecosystem functioning. Our results advance the vast BEF literature by documenting a positive relationship between biodiversity and ecosystem functioning in stream fish communities, a group for which the BEF has not been investigated. Future work should continue to clarify the impacts of multiple stressors on

biodiversity and ecosystem functioning, especially in aquatic systems that provide many ecosystem services to humans.

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Appendix

Sensitivity analysis of the effects of alternative survey selection criteria.

Results presented in the main text are based upon a dataset with selection of the most recent fish survey event at each site between 1992–2012. To assess the sensitivity of our results to this criterion, we explored the effects of alternative scenarios for selection of survey events. For each alternative scenario (discussed below), we used the global model for biomass modeled with a linear mixed-effects model with random species richness slopes and watershed intercepts. We examined whether fixed effects of biodiversity, abiotic variables, and sampling effort on biomass production differed in magnitude of effect (beta coefficient) from the model presented in the main text.

First, we examined the sensitivity of our results to a regional drought that affected France in the year 2003 (Trigo et al., 2005), and we omitted surveys from 2003 in the global model (Table 6a). We also assessed whether results in the main text were robust to our decision to remove surveys where brown trout was the only species recorded. To do so, we reran the global model and included all surveys inclusive of brown trout singletons (Table 6b), as well as on a subset of surveys with at least two species recorded (Table 6c). We also examined the robustness of our results to the restriction of surveys to abundance ≥ 100 and sites per watershed ≥ 5 and reran global models using a selection of surveys where: abundance ≥ 150 and sites per watershed ≥ 5 (Table 6d), abundance ≥ 50 and sites per watershed ≥ 5 (Table 6e); and abundance ≥ 100 and sites per watershed ≥ 10 (Table 6f).

Results based on the alternate selection scenarios were qualitatively similar to the main text analysis (judged by magnitude and direction of beta); therefore, we retained the initial survey selection criteria.

Table 6. Results of the sensitivity analysis of beta coefficient estimates on alternative survey selection criteria. Values in the table are partial regression coefficients from the full biomass model described in the main text. Column labels indicate the subsets of surveys used for the global biomass model: (a) surveys from 2003 omitted, (b) brown trout singletons included in surveys, (c) all surveys where species richness ≥ 2, (d) surveys where abundance ≥ 150 and sites per watershed ≥ 5, (e) abundance ≥ 50 and sites per watershed ≥ 5; and (f) abundance ≥ 100 and sites per watershed ≥ 10.

Variable	a	b	c	d	e	f
Species richness	0.34	0.33	0.34	0.32	0.37	0.33
Sampled area	0.54	0.55	0.54	0.51	0.53	0.53
Temperature	-0.07	-0.06	-0.09	-0.07	-0.07	-0.08
Precipitation	0.12	0.11	0.11	0.10	0.10	0.13
Functional diversity	0.10	0.10	0.10	0.12	0.06	0.09
Human impact	0.05	0.06	0.06	0.07	0.05	0.05
Catchment area	-0.01	0.02	0.00	0.03	0.00	0.02
Slope	-0.02	-0.02	-0.02	-0.02	-0.01	-0.01
Free-flowing area	-0.03	-0.02	-0.02	-0.03	-0.02	-0.02

Table 7. Path coefficients from the full (all predictor variables) endogenous models predicting biomass, species richness, and functional diversity as a function of environmental predictor variables, using HFI values from 1993 not presented in the main text. Shown are piecewise path coefficients, *t*-values, and *p*-values. All coefficients (estimates) are fixed effects from linear mixed models as described in the main text.

Response	**Predictor**	**Coefficient**	**|*t*|**	***p*–value**
Biomass	Species richness	0.34	9.67	< 0.001
Biomass	Functional diversity	0.10	4.43	< 0.001
Biomass	Sampled area	0.53	23.57	< 0.001
Biomass	Temperature	-0.07	2.83	0.005
Biomass	Precipitation	0.11	4.10	< 0.001
Biomass	Human impact (1993)	0.06	2.88	0.004
Biomass	Catchment area	0.00	0.02	0.982
Biomass	Slope	-0.02	0.82	0.414
Biomass	Free-flowing area	-0.02	1.02	0.309
Species richness	Sampled area	0.28	11.08	< 0.001
Species richness	Temperature	0.32	8.83	< 0.001
Species richness	Precipitation	-0.14	3.69	< 0.001
Species richness	Human impact (1993)	0.07	3.14	0.002
Species richness	Catchment area	0.09	3.36	0.001
Species richness	Slope	-0.15	6.18	< 0.001
Species richness	Free-flowing area	0.09	4.59	< 0.001
Functional diversity	Species richness	0.64	23.43	< 0.001
Functional diversity	Sampled area	-0.02	0.79	0.431
Functional diversity	Temperature	0.11	3.86	< 0.001
Functional diversity	Precipitation	0.07	2.25	0.026
Functional diversity	Human impact (1993)	0.01	0.23	0.819
Functional diversity	Catchment area	-0.05	1.61	0.107
Functional diversity	Slope	0.00	0.08	0.936
Functional diversity	Free-flowing area	0.01	0.29	0.770

Table 8. **Path coefficients from the full (all predictor variables) model predicting biomass, species richness, and functional diversity as a function of environmental predictor variables, using sampling year as a covariate.** Shown are piecewise path coefficients, *t*-values, and *p*-values. All coefficients (estimates) are fixed effects from linear mixed models as described in the main text.

Predictor	**Coefficient**	**|*t*|**	***p*–value**
Species richness	0.35	9.84	< 0.001
Functional diversity	0.09	4.08	< 0.001
Sampled area	0.52	22.56	< 0.001
Temperature	-0.07	2.65	0.009
Precipitation	0.11	4.20	< 0.001
Human impact	0.06	3.23	0.001
Catchment area	0.01	0.24	0.813
Slope	-0.02	1.00	0.319
Free-flowing area	-0.02	0.94	0.346
year1993	0.01	0.08	0.939
year1994	0.09	0.56	0.576
year1995	-0.05	0.44	0.662
year1996	-0.09	0.73	0.464
year1997	-0.02	0.17	0.866
year1998	0.04	0.35	0.726
year1999	-0.13	1.15	0.249
year2000	-0.17	1.43	0.154
year2001	-0.16	1.32	0.187
year2002	-0.09	0.83	0.409
year2003	-0.18	1.53	0.127
year2004	-0.19	1.65	0.100
year2005	-0.20	1.77	0.077
year2006	-0.04	0.41	0.683
year2007	0.11	0.68	0.499
year2008	-0.05	0.36	0.717
year2009	-0.04	0.25	0.804
year2010	-0.29	1.15	0.250
year2011	-0.16	1.15	0.249
year2012	-0.10	0.79	0.429

Table 9. Results of VIF analysis for the full models described in the main text. We performed VIF analysis on the full (all predictors included) models for biomass, species richness, and functional diversity. We found that all VIF < 4 for all models, therefore collinearity among predictors was not an issue for our analysis.

Model	Variable	VIF
Biomass	Species richness	1.43
Biomass	Functional diversity	1.26
Biomass	Sampled area	1.41
Biomass	Temperature	1.34
Biomass	Precipitation	1.35
Biomass	Human impact	1.13
Biomass	Catchment area	1.62
Biomass	Slope	1.22
Biomass	Free-flowing area	1.02
Species richness	Sampled area	1.50
Species richness	Temperature	1.70
Species richness	Precipitation	1.73
Species richness	Human impact	1.20
Species richness	Catchment area	1.84
Species richness	Slope	1.32
Species richness	Free-flowing area	1.03
Functional diversity	Species richness	1.53
Functional diversity	Sampled area	1.54
Functional diversity	Temperature	1.45
Functional diversity	Precipitation	1.43
Functional diversity	Human impact	1.18
Functional diversity	Catchment area	1.81
Functional diversity	Slope	1.36
Functional diversity	Free-flowing area	1.03

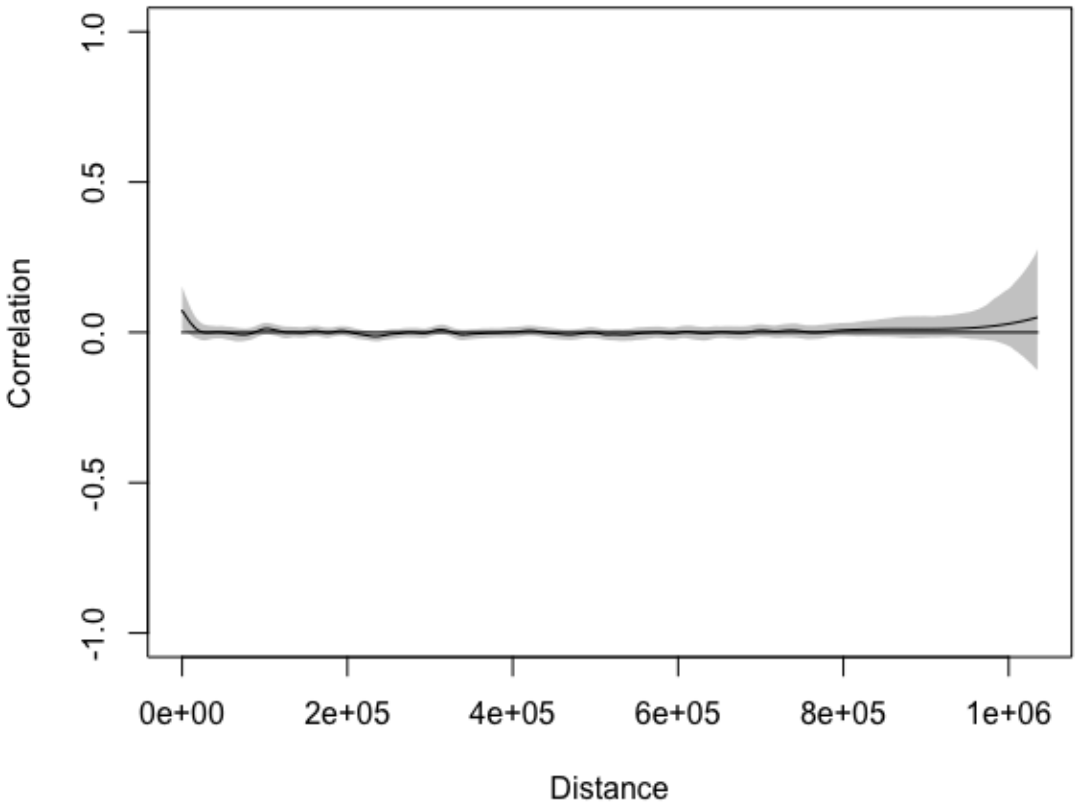

Figure 13. Spline correlogram showing potential spatial autocorrelation in residuals from the best-fit biomass model. Shown are Moran's I correlation for pairwise residuals as a function of pairwise site distance (in meters). Grey polygons indicate 95% confidence intervals obtained from bootstrapping.

Table 10. Evaluation of conditional independence claims in the *total biodiversity* path model shown in Fig. 11a. Abbreviations for predictors are: precipitation (PRCP), temperature (TMP), biomass (BIOM), functional diversity (FD), human impact (HFI), slope (SLP), species richness (SR), sampled area (SURF), upstream catchment area (UPCT), and free-flowing area (FFA).

Conditional independence claim	***p*–value**
1. (FD, SURF) | {TMP, PRCP, UPCT, SR}	0.405
2. (FD, HFI) | {TMP, PRCP, UPCT, SR}	0.795
3. (BIOM, UPCT) | {SURF, TMP, PRCP, HFI, SR, FD}	0.818
4. (BIOM, SLP) | {SURF, TMP, PRCP, HFI, SR, FD}	0.380
5. (FD, UPCT) | {TMP, PRCP, UPCT, SR}	0.947
6. (BIOM, FFA) | { SURF, TMP, PRCP, HFI, SR, FD}	0.308
7. (FD, FFA) | {TMP, PRCP, UPCT, SR}	0.700
$C = -2 \sum_{j=1}^{k} ln(p_j)$	7.781
Overall p–value ($\chi^2_{df=14}$)	0.900

Table 11. Evaluation of conditional independence claims in the *partitioned biodiversity* path model. Abbreviations for predictors are: precipitation (PRCP), temperature (TMP), biomass (BIOM), functional diversity (FD), native species richness (NAT), non-native species richness (INV), human impact (HFI), slope (SLP), sampled area (SURF), free-flowing area (FFA), and upstream catchment area (UPCT).

Conditional independence claim	***p*–value**
1. (FD, SURF) | {TMP, PRCP, UPCT, NAT, INV}	0.275
2. (INV, PRCP) | {SURF, TMP, HFI, UPCT, FFA}	0.075
3. (NAT, HFI) | {SURF, TMP, PRCP, UPCT, SLP, FFA}	0.072
4. (FD, HFI) | {TMP, PRCP, UPCT, NAT, INV}	0.667
5. (BIOM, UPCT) | {SURF, TMP, PRCP, HFI, NAT, INV, FD}	0.885
6. (INV, SLP) | {SURF, TMP, HFI, UPCT, FFA}	0.434
7. (FD, SLP) | {TMP, PRCP, UPCT, NAT, INV}	0.823
8. (BIOM, SLP) | {SURF, TMP, PRCP, HFI, NAT, INV, FD}	0.317
9. (FD, FFA) | {TMP, PRCP, UPCT, NAT, INV}	0.433
10. (BIOM, FFA) | {SURF, TMP, PRCP, HFI, NAT, INV, FD}	0.192
$C = -2 \sum_{j=1}^{k} ln(p_j)$	23.419
Overall *p*–value ($\chi^2_{df=20}$)	0.269

CHAPTER 3
TRENDS AND OPPORTUNITIES IN FRESHWATER COMMUNITY SCIENCE ACROSS SPATIAL SCALES

A version of this chapter is currently under review for publication by Taylor Woods, Luis Carrasco, Gengping Zhu, Guido A. Herrera-R, Anna Kaz, J. Cameron Niemeyer, Sarah Roth, Jeffery Stevens, and Xingli Giam:

Taylor Woods, Luis Carrasco, Gengping Zhu, Guido A. Herrera-R, Anna Kaz, J. Cameron Niemeyer, Sarah Roth, Jeffery Stevens, Xingli Giam. "Trends and opportunities in freshwater community science across spatial scales." *Freshwater Science*.

All authors conceptualized the project. Taylor Woods led the data collection, analysis, and created figures with input from all authors. All authors contributed to data collection of the community science database. Taylor Woods led writing of the first draft and all authors contributed to manuscript revisions and editing.

Abstract

Growing community science efforts over the past decades offer novel opportunities for data-intensive ecological research at broad spatial extents. In biologically important yet undersampled freshwater habitats, characterizing present community science efforts can identify sampling gaps to be targeted by emerging efforts. Here, we synthesize the scope of United States freshwater community science efforts and identify socioenvironmental drivers of survey effort across spatial scales. Across spatial scales, increasing population density and forest land-cover increase community science survey effort. At smaller spatial scales, survey effort also increases in areas of higher educational attainment, seasonal housing, and college densities. These results indicate that broad spatial gaps in present freshwater community science survey effort may relate to participation gaps where community science initiatives currently engage limited portions of the public. Freshwater community science programs could incorporate activities to recruit novel participants in sampling hotspots and develop partnerships to engage communities in undersampled areas.

Introduction

Community science (CS; also commonly referred to as citizen science) involves public participation in scientific research, often through data collection (Dickinson et al. 2012). Recent growth in CS arose, in part, because macroecological datasets may be more feasibly attained with sampling schemes involving public community members, rather than conventional scientific data collection methods (Hochachka et al. 2012; Poisson et al. 2019). Researchers now use CS data to model species distributions (Johnston et al. 2020), detect the establishment and expansion of aquatic invasive species (Larson et al. 2020b), and quantify physical habitat characteristics (Poisson et al. 2019). CS also plays an increasingly important role in environmental conservation and resource management (McKinley et al. 2017). For example, terrestrial CS data has documented butterfly (Forister et al. 2021) and bird (Rosenberg et al. 2019) population declines and informed livestock management practices to protect local watershed resources (McKinley et al. 2017). Therefore, community scientists can potentially play important roles in detecting, documenting, and mitigating global change impacts.

Despite the demonstrated value of CS data to ecology and conservation research, freshwater CS efforts lag those in terrestrial systems. Globally, approximately 30% of CS programs survey freshwater environments, compared to 82% that survey terrestrial habitats (Chandler et al. 2017). This sampling gap is noteworthy because freshwaters provide critical ecosystem services (e.g., water resources and recreation) which can engage local communities in participatory science through shared motivations in public health and environmental equity (Church et al. 2019). Thus, it is imminently important for freshwater research, conservation, and outreach to leverage the emerging contributions of community scientists and CS datasets.

Synthesizing the scope of existing CS programs can help identify opportunities to leverage CS datasets in freshwater research. This is important because CS data are often collected at spatiotemporal scales and resolutions uncommon in traditional datasets (Hochachka et al. 2012). For example, CS surveys in Ireland provided water quality at finer spatiotemporal grains, and better identified nutrient input sources along a gradient of urbanization, compared to government surveys (Hegarty et al. 2021). Such analyses can spur CS growth because impacting scientific research motivates participant recruitment and retention (Larson et al. 2020a). These motivations may be especially relevant for freshwater community scientists owed to public health concerns associated with water quality. A synthesis can also identify opportunities for partnerships among programs with complementary aims. This could expand freshwater CS from the local to continental/global scale, which is presently limited to programs involving terrestrial systems or taxa (e.g., birds) (La Sorte and Somveille 2020).

The spatial distribution of CS surveys often skews toward locations where programs can attract, recruit, and retain public participants (Isaac and Pocock 2015). Community members with time or monetary resources may also be more likely to participate in CS (Schuttler et al. 2018). These participation gaps may be especially prevalent in freshwaters where public sampling can be limited by hydrologic conditions that require specialized survey gear or safety equipment. Detailing socioenvironmental biases in the distribution of CS survey efforts can reveal these sampling and participation gaps which can be used to inform outreach. Filling sampling gaps can reduce biases in CS-enabled ecological research (Isaac and Pocock 2015) and narrowing participation gaps increases access to environmental awareness, engagement, and literacy benefits individuals derive from CS (MacLeod and Scott 2021). For example, participants in a riverine water quality CS program reported greater understanding and appreciation of watershed conservation following sampling activities (Church et al. 2019). While local (e.g., site level) gaps are commonly the foci of such analyses, macroecological analyses may also require assessment of sampling gaps at broader extents (e.g., regional to continental) (Zipkin et al. 2021). Understanding drivers of participation gaps at larger scales (e.g., counties to states) is important because individual-level gaps can scale up to impact which communities are incorporated into resource management decisions stemming from CS (Stepenuck and Green 2015).

Much prior freshwater CS research focused on water quality CS programs in the Great Lakes region (Lottig et al. 2014; Poisson et al. 2019). Although useful for detailed regional information on CS, a broader perspective spanning multiple habitats, taxa, and

metrics may provide a more complete overview of existing freshwater CS survey efforts. Therefore, we assembled a database to synthesize the scope of freshwater CS in the contiguous United States (CONUS). First, we summarized topical information on ecological foci (habitats and variables sampled) and organizational characteristics (organizing entity, geographic extent) among freshwater CS programs. Next, we analyzed drivers of freshwater CS survey effort at three scales representing common program spatial extents: state, county, and watershed. We used these results to identify where existing datasets can be leveraged in freshwater macroecology and inform outreach related to sampling and participation gaps.

Methods

Community science database

We assembled a database on freshwater CS using a systematic search of the literature, internet, and CS portals on 5 November 2019. For the literature review, we searched Web of Science for: TS = ((North America OR US) AND (aquatic OR freshwater OR pond OR lake OR stream OR creek OR river) AND (citizen OR volunteer OR participat*) AND (survey OR monitor* OR assess* OR research OR sampl* OR science)). For the internet search, we searched Google for: (Aquatic OR freshwater OR pond OR lake OR stream OR creek OR river) AND (citizen OR volunteer OR participat*) AND (survey OR monitor* OR assess* OR research OR sampl* OR science) and scraped URLs from the first 25 results pages with the Python module "googlesearch". For the CS portal search, we identified potentially relevant programs from citsci.org (<http://citsci.org>), iNaturalist (<http://iNaturalist.org>), and SciStarter (<http://scistarter.org>). We selected these portals because they contained ≥ 500 CS programs and therefore represent key databases that serve to organize interested participants into relevant US programs. We searched each portal using the habitat keywords: "aquatic", "freshwater", "pond", "lake", "stream", and "river" and extracted links to all potential programs returned.

Using the list of returned papers (n = 329), URLs (n = 230), and portal results (n = 1918) we determined whether the paper or URL contained freshwater CS programs for inclusion in the study. Papers were initially screened via titles and abstracts and then read in full. We included a program if it focused on freshwater ecosystems and provided observations for aquatic parameters of interest (see next paragraph) conducted by community scientists in the contiguous US. For included programs, we recorded program-level descriptive characteristics for: the aquatic habitat(s) as estuary/coast, lake/reservoir, pond/wetland, or stream/river; and variable(s) as amphibians/aquatic reptiles, fishes, other vertebrates (e.g., waterbirds, aquatic mammals), invasive species, invertebrates, primary producers (e.g., macrophytes), or water quality/associated characteristics (e.g., pH, temperature, hydrology) sampled. We also recorded the spatial extent of programs as national, state, county, watershed, or other (e.g., cross-boundary National Park), the start and end year (if no longer active) and classified the organizing entity of the program as government, non-governmental organization (NGO), university, or independent (in the case that community scientists themselves were the organizing entity).

We searched programs' websites for local (site-level) data and extracted geographic coordinates of survey sites when publicly available or requested this information from

programs when unavailable. We included all sites with CS surveys, regardless of data quality grading or sampling methodology because we aimed to analyze the distribution of CS survey efforts, rather than provide a quantitative analysis of abiotic or biodiversity data collected by CS programs.

We screened for and corrected likely errors in the spatial coordinates of sites in our dataset. Briefly, we identified cases in which latitude and longitude coordinates appeared to be swapped, corrected non-negative longitude values, and removed sites with missing latitude or longitude coordinates. Next, we removed duplicated site records (identical coordinate combinations within programs). We referenced sites to states and counties using shapefiles provided in the R package 'tidycensus' (Walker and Herman 2020) and to watersheds (8-digit Hydrologic Unit) using the Watershed Boundary Dataset (USGS 2012) and removed any sites falling outside the contiguous US (n = 11,156 sites) defined by state boundaries.

We referenced each site to a respective lentic or lotic waterbody using the National Hydrography Dataset (NHD) (McKay et al. 2012). First, we ascribed sites falling within a lentic waterbody as: lake, reservoir, or estuary. Next, for sites not falling within lentic waterbodies, we referenced sites to stream catchments using the NHD catchment dataset. We removed estuary sites (n = 8) and sites not associated with a stream catchment (e.g., sites on coastlines; n = 5490). This ensured that sites remaining within our dataset represented volunteer surveys of freshwater habitats.

Predictor variables

We used the 'tidycensus' (Walker and Herman 2020) R package and collected 2010 American Community Survey (ACS) data. For each CONUS state and the District of Columbia (DC; n = 49) and county (n = 3109), we collected population, median income, the proportion of residents of at least 25 years old with a bachelor's degree (hereafter, educational attainment), and the proportion of vacant housing classified as recreational or seasonal use (hereafter, seasonal housing). We selected the 2010 ACS because this was the median program start year in our CS database. For the watershed-scale analysis, we obtained 2010 ACS data within CONUS tracts (n = 72,271) from the Integrated Public Use Microdata Series National Historic GIS (Manson et al. 2020) and summarized variables within watersheds [Watershed Boundary Dataset 8-digit Hydrologic Units (HU8s), n = 2114] (USGS 2012). Among tracts within watersheds, we calculated population, educational attainment, seasonal housing, and median income. We calculated population density (residents/km^2) to use as a predictor variable and kept proportional and median values in their original units. At the county scale, one county did not have complete data in the 2010 ACS (Doña Ana County, New Mexico). This county was unlikely to influence our analysis because it showed low CS site density (0.0006 sites/km^2), therefore this county was omitted from the county-scale analysis (n = 3108 counties for analysis).

We used a US Geological Survey (USGS) Post-Secondary Education facilities dataset (Oak Ridge National Laboratory 2010) to calculate college density (number of colleges and universities/km^2) at each scale. We used the 2011 National Land Cover Dataset (NLCD) (Homer et al. 2015) and calculated the proportion of land-use/land-cover classes [open water, developed (open space, low, medium, and high intensity), forest

(deciduous, evergreen, and mixed), agricultural (pasture and cultivated crops), and wetland (woody and emergent herbaceous)] at each spatial scale. We used open water and wetland land-cover classes as control variables to account for potential effects of the amount of freshwater habitat available for CS sampling at each scale.

Data analysis

We calculated the number of CS sites within each state, county, and watershed (8-digit USGS hydrologic units) as response variables describing survey effort. We $\log_{10}(x)$ transformed population density, and applied natural $\log(x + 1)$ transformations to education facility density, open water, forest, and wetland land-cover, agricultural and developed land-use, and recreational housing density, and standardized (mean = 0, standard deviation = 1) all variables. Prior to analysis, we tested for multicollinearity ($|r|$ rounded to two decimal places ≥ 0.70; Dormann et al. 2013) and removed developed land-use from all models (correlated with population density and/or college density), and income (correlated with educational attainment) from the state model.

We used generalized linear models (GLMs) and generalized linear mixed-effects models (GLMMs) under a multimodel inference framework to identify drivers of CS survey effort across spatial scales using the R package 'glmmTMB' (Brooks et al. 2017). At each scale, we constructed global (all predictor variables included) GLMs (state) or GLMMs (county and watershed) with different model structures and used Akaike's Information Criterion with small-sample correction (AICc) to identify the optimal model structure. At the state scale, we compared GLMs built with Poisson, negative binomial with linear parameterization, and negative binomial with quadratic parametrization error distributions. At the county and watershed scales, we compared GLMMs with the same three distributions and the zero-inflated variations of each distribution (n = 6 candidate models) and incorporated random intercepts based on state and region (2-digit hydrologic unit), respectively. In all GLMs and GLMMs, we used the log link functions and incorporated the natural log–transformed area of each spatial unit as an offset term to model the density of survey sites.

Following identification of the optimal model structure, we used all-subsets model selection to identify the top AICc-ranked model for statistical inference (Burnham and Anderson 2002) with the 'MuMIn' package (Barton 2020). We used the R package 'DHARMa' (Hartig 2021) to perform model diagnostics of top models by (i) graphically inspecting a Q-Q plot of quantile residuals for substantial deviation from the expected uniform distribution, (ii) graphically inspecting a scatterplot of quantile residuals against predicted values to examine if the residuals are uniformly distributed across the range of predicted values, (iii) a simulation-based test for over/underdispersion via the function 'testDispersion()', and (iv) a simulation-based test for zero-inflation via the function 'testZeroInflation()'. Whereas quantile residuals of the state-scale model were consistent with the expected uniform distributions (Fig. 20a), quantile residuals of the county- and watershed-scale models deviated slightly from the expected normal distribution (slight deviation of points from red line in left panels of Fig. 20b,c) and there appears to be some variation in the distribution of residuals along the range of predicted variables (i.e., the quantile residuals become slightly higher than expected as predicted values increase; right

panels in Fig. 20b,c). In general, we contend that these deviations did not appear serious enough (e.g., S-shaped or highly curved Q-Q plot; large deviations from the theoretical 0.25, 0.5, 0.75 quantile lines; clustering of quantile residuals around 0 and 1 etc.) to affect our conclusions substantively. Further, all three top models did not suffer from over/underdispersion and zero-inflation (p = 0.136–1.0 for all tests). Overall, our model diagnostics indicate that our models fitted our data reasonably well.

We used standardized β-coefficients to quantify the effect sizes of predictors, $|z|$ statistics to quantify variable importance (Cade 2015), and R^2adjusted and R^2marginal to quantify the variation in CS survey effort explained by fixed-effect predictors in the top-ranked GLM and GLMMs, respectively (Nakagawa and Schielzeth 2013).

Results

We identified 205 freshwater CS programs, 150 of which provided coordinates. Sites (n = 181,622) covered 48 states and the District of Columbia, 2447 counties, and 1660 watersheds (Fig. 14). CS survey effort is spatially heterogeneous at all three scales of analysis (Fig. 15). Generally, coastal regions (Atlantic, Pacific, and Gulf Coasts), the Great Lakes region, and Texas were well-sampled compared to inland regions (Fig. 15). We provide an interactive web application to explore our database at https://tiny.utk.edu/fwCS.

CS programs more frequently targeted streams and rivers (77.6% of programs) compared to lakes and reservoirs (43.9%) (Fig. 16a), and more frequently sampled water quality (51.2%) and invertebrates (46.3%) relative to other variables (Fig. 16a). Riverine habitats showed longer program durations (median = 10 years, IQR = 23) compared to lakes (median = 5, IQR = 26) (Fig. 16b). Among variables, water quality (median = 25 years, IQR = 20) and invertebrate (median = 13.5, IQR = 23.5) programs showed the longest durations (Fig. 16c).

CS programs commonly reported watersheds (39.0% of programs) and states (38.0%) as spatial extents (Fig. 17). NGOs coordinated 40.5% of programs of aquatic CS programs, followed by independent projects (26.8%), government (22.9%), and university-affiliated programs (9.8%; Fig. 17). The spatial extent of programs varied among organizing entities. Most NGO programs (73.5%) organized at the watershed scale, whereas academic, government, and independent programs primarily sampled at the state extent (Fig. 17).

Among states, CS survey effort increased with increasing population density (β = 1.25, SE = 0.20, $|z|$ = 6.18; Fig. 18a) and forest land-cover (β = 0.47, SE = 0.17, $|z|$ = 2.77; Fig. 19a; R^2adjusted = 0.54).

Among counties, CS survey effort increased with increasing population density (β = 1.09, SE = 0.04, $|z|$ = 28.79; Fig. 18b), educational attainment (β = 0.33, SE = 0.03, $|z|$ = 12.14), college density (β = 0.07, SE = 0.03, $|z|$ = 2.12), forest (β = 0.29, SE = 0.04, $|z|$ = 7.20; Fig. 19b) and wetland land-cover (β = 0.08, SE = 0.03, $|z|$ = 2.61), and seasonal housing (β = 0.34, SE = 0.03, $|z|$ = 11.26), and decreased with increasing agricultural land-use (β = -0.09, SE = 0.04, $|z|$ = 2.51; R^2marginal = 0.42).

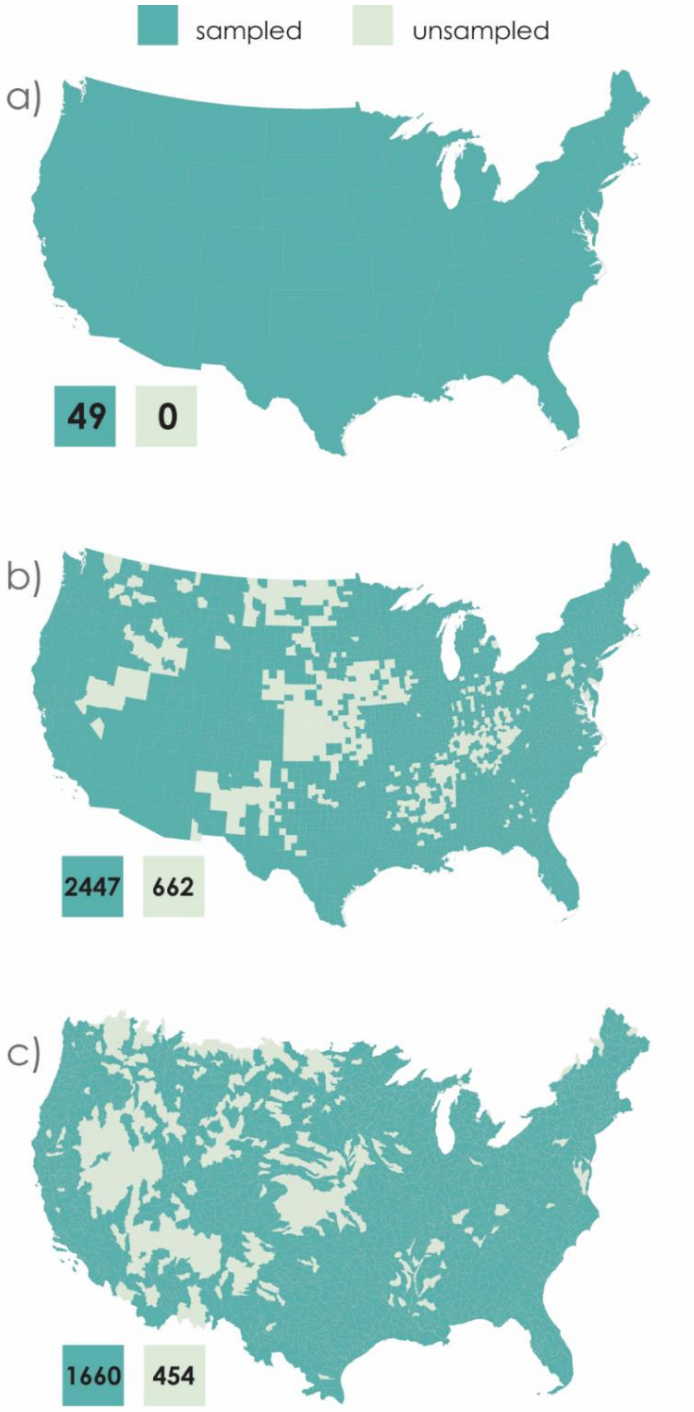

Figure 14. Presence or absence of freshwater community science surveys within (a) states, (b) counties, and (c) watersheds. Colors indicate sampled (dark green) and unsampled states, counties, and watersheds. The number of sampled and unsampled spatial units for each scale are indicated in the boxes below each map.

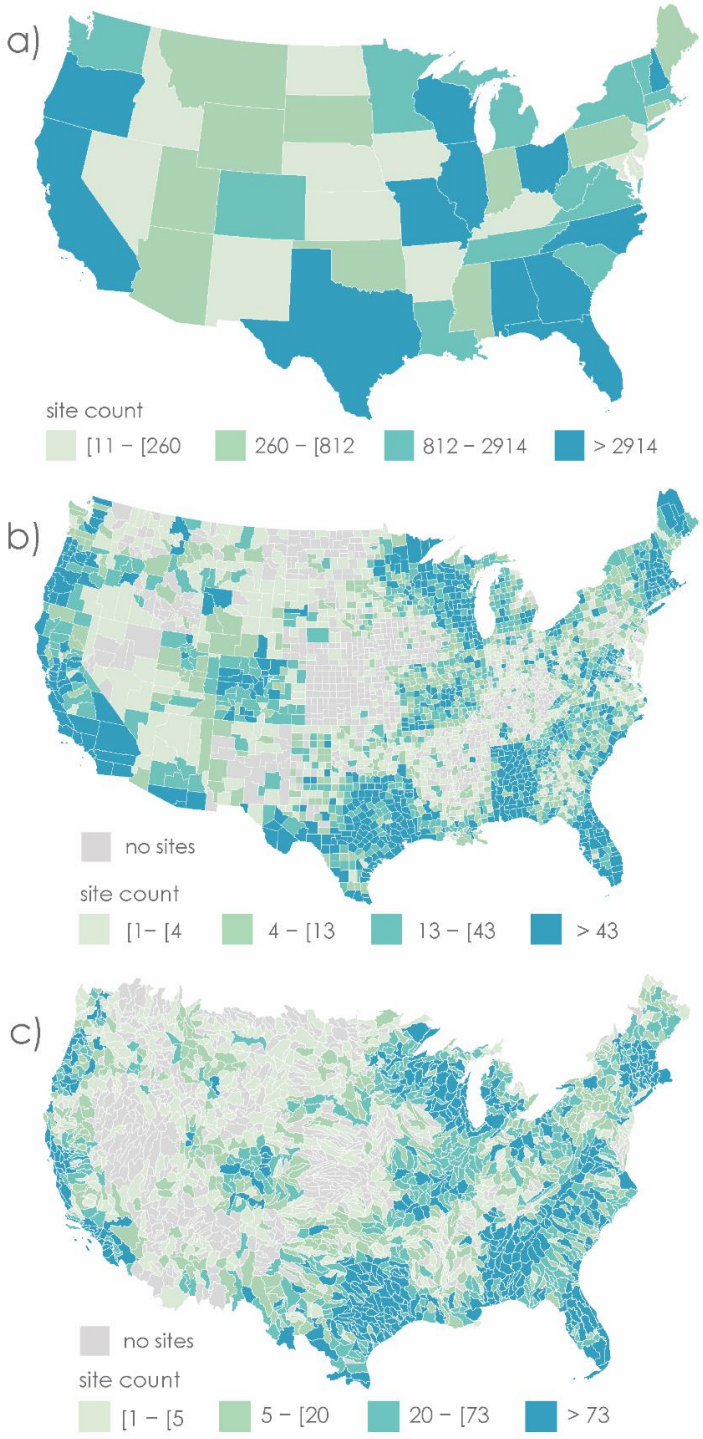

Figure 15. Freshwater CS survey effort across spatial scales. Maps indicate quantiles of CS site count in (a) states, (b) counties, and (c) watersheds (grey indicates no sites available).

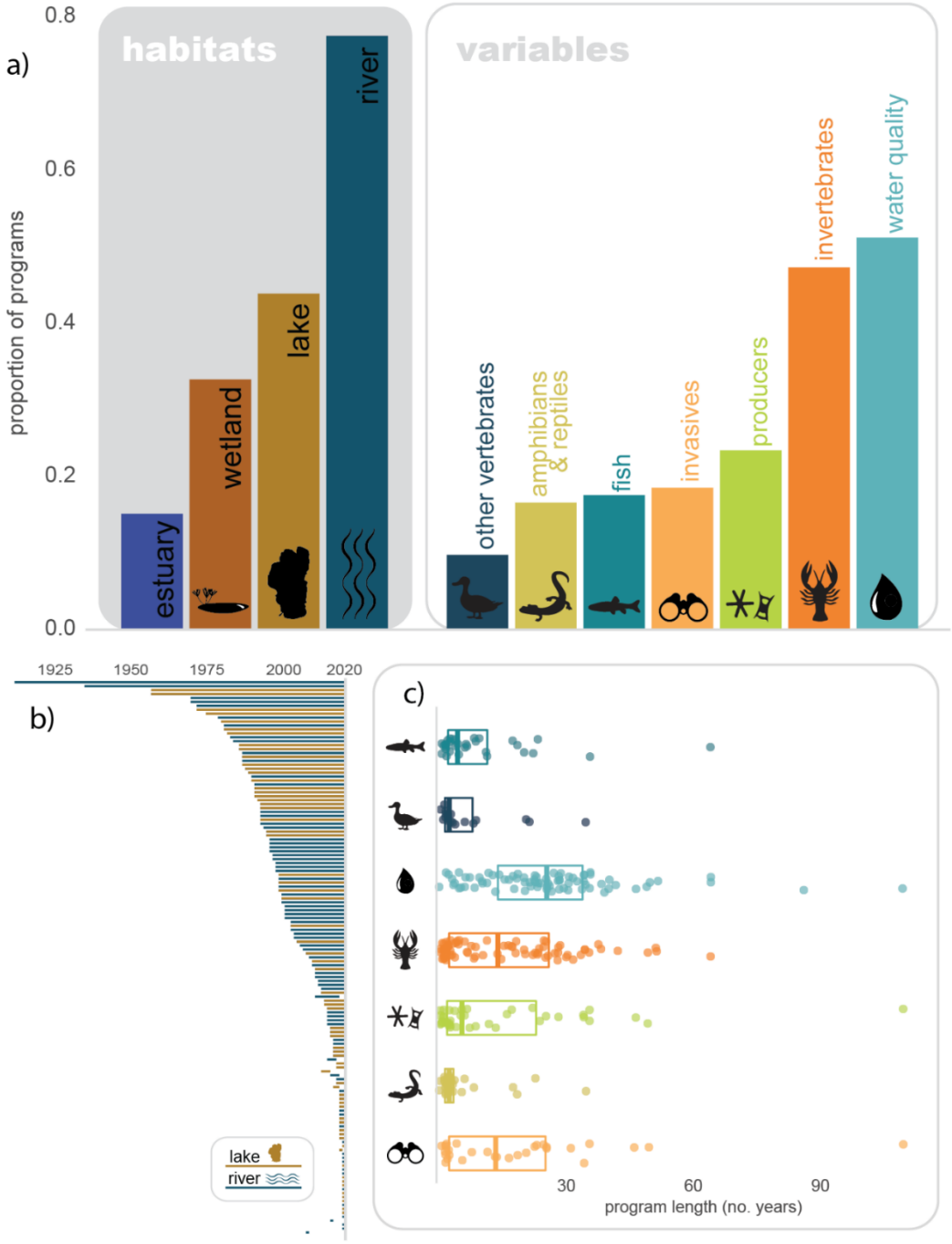

Figure 16. Program-level characteristics. (a) Proportion of programs sampling habitats (grey panel) and variables (white panel). (b) Program length of lentic (gold) and lotic (blue) CS programs. (c) CS program duration (number of years operating) for sampled variables with crossbars showing median and IQR.

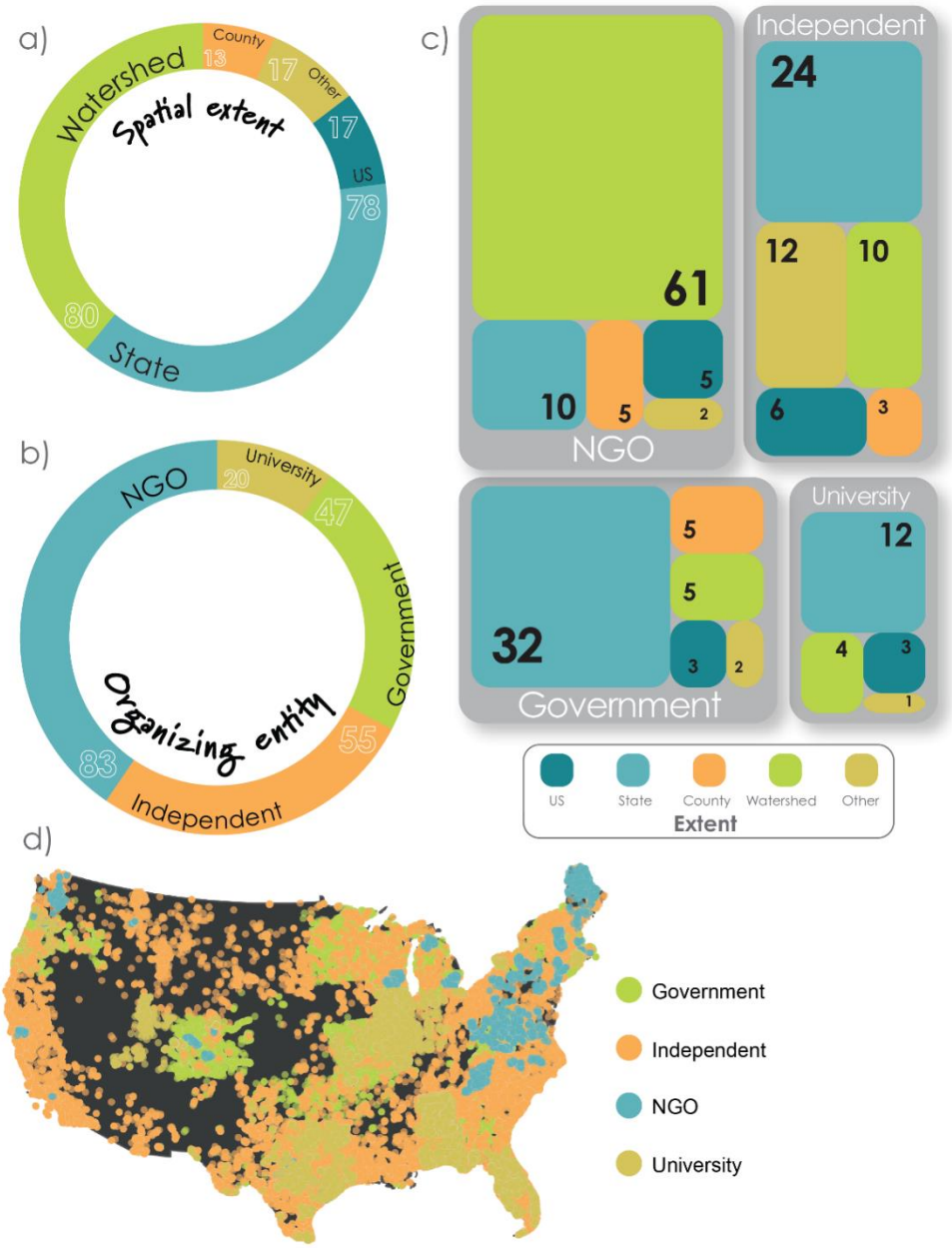

Figure 17. Program characteristics related to organizing entities and spatial extents. Plots showing the number of programs classified according to (a) spatial extents, and (b) organizing entities, with numbers indicating the number of programs within each group shown by bar colors. (c) Tree map showing the number of programs grouped by organizing entity and spatial extents. Different grey boxes show organizing entities according to labs. Within each grey box, rectangle colors indicate spatial extents with size representing the number of programs within organizing entities with spatial extents (larger size = larger number of programs indicated by the numbers in boxes). (c) Map of survey sites colored according to organizing entity of the program.

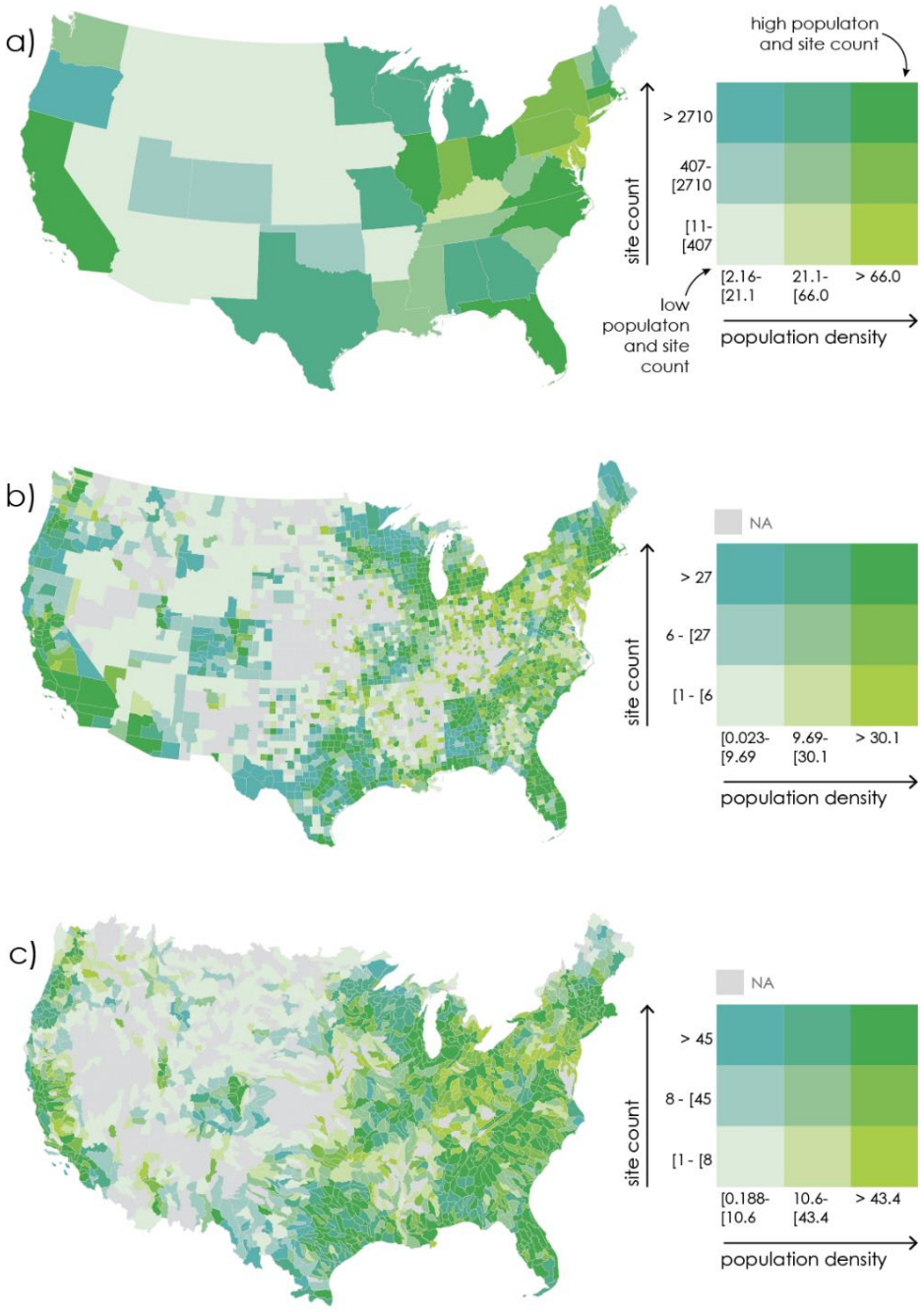

Figure 18. Maps of population density and CS site count across spatial scales. Bivariate color palettes correspond to one-third quantiles [low (0.0% – 33.3%), medium (33.3% – 66.7%), and high (66.7% – 100.0%)] for population density and CS site count within (a) states, (b) counties, and (c) watersheds. The nine color classes indicate the intersection of quantiles for population and site count (e.g., high population density and high site count, upper right) as indicated by labels on the state scale legend. Grey-colored counties and watersheds do not have CS sites.

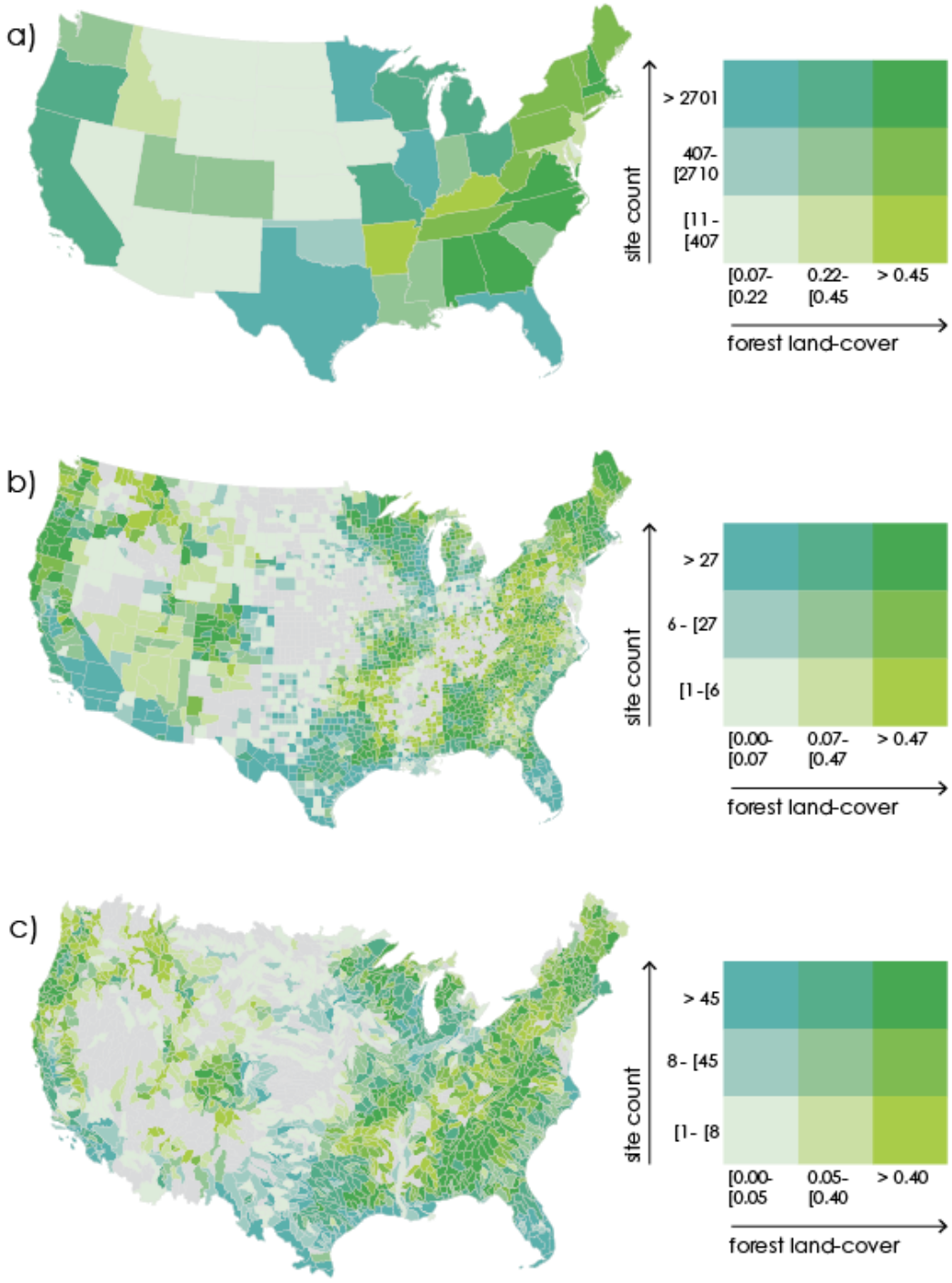

Figure 19. Maps of forest land-cover and CS site count across spatial scales. Bivariate color palettes correspond to one-third quantiles [low (0.0% – 33.3%), medium (33.3% – 66.7%), and high (66.7% – 100.0%)] for forested land-cover and CS site count within (a) states, (b) counties, and (c) watersheds. Grey-colored counties and watersheds do not have CS sites.

Among watersheds, CS survey effort increased with increasing population density (β = 1.09, SE = 0.05, |z| = 20.64; Fig. 18c), educational attainment (β = 0.24, SE = 0.04, |z| = 6.61), seasonal housing (β = 0.08, SE = 0.05, |z| = 1.60), forest (β = 0.58, SE = 0.05, |z| = 12.61; Fig. 19c), open water (β = 0.33, SE = 0.04, |z| = 8.85), and wetland (β = 0.12, SE = 0.04, |z| = 2.66) land-cover (R^2marginal = 0.64).

Discussion

Opportunities to leverage freshwater CS

Freshwater CS programs commonly collect invertebrates and water quality data likely because these metrics are relevant to public health (English et al. 2018) and are collected easily (Kosmala et al. 2016). These rapidly assessed variables also represent the earliest freshwater CS data; therefore, they can potentially be used to investigate global change impacts. For example, lentic CS datasets reveal long-term water quality trends at spatiotemporal scales unachievable with government datasets alone (Lottig et al. 2014). The quantity and temporal extent of riverine CS programs suggests an emerging opportunity for CS datasets to contribute to global change analyses in riverine systems. For example, macroinvertebrate CS data could augment recently standardized government databases and facilitate macroecological analyses for these traditionally data-poor taxa (Twardochleb et al. 2021).

The scope and scale of water quality CS surveys can further be leveraged to meet the needs of stakeholders including government agencies or nonprofits interested in preserving or improving water quality, and freshwater ecologists investigating large-scale patterns and drivers of aquatic biodiversity. Globally, water temperature and streamflow data are restricted to locations with maintained government gages and gage availability has been decreasing (Ruhi et al. 2018). Community-led monitoring could help close this data gap in regions lacking gages by providing critical data on freshwater resources (Buytaert et al. 2014). For example, CS provides hydrologic data in understudied contexts like intermittent (Allen et al. 2019) and sub-Saharan African (Walker et al. 2016) streams. Daily water temperature records submitted by local community members that regularly engage with water resources can be a relatively easy, safe, and low cost method to supplement gaging station datasets and parameterize hydrometeorological water temperature models (Pohle et al. 2019). National and international funding agencies should prioritize coordination and planning among programs to build water quality monitoring networks comprising sampling sites widely distributed across environmental and land-cover/use gradients. This allows comparable and standardized data to be collected across programs to provide critical information for water resource managers and researchers that require data at national to global scales.

States and watersheds are the most common spatial extents of CS programs. NGOs tend to sample within watersheds, whereas other entities commonly organize at larger extents, indicating that different entities complement one another in data collection. This also demonstrates the importance of NGOs in filling data gaps at locations unsampled by broader (e.g., state-level) programs.

Broadening coverage and participation in freshwater CS

One topical sampling gap in freshwater CS is the relative paucity of programs collecting fish data. Increasing CS fish survey effort could help fill temporal gaps created by government surveys which are typically conducted in the summer when hydrologic conditions permit electrofishing. Prioritizing non-summer fish CS observations can help address critical knowledge gaps on fish phenology, migration, and winter activity for these taxa (Shuter et al. 2012; Hampton et al. 2017; Woods et al. 2021). Employing newer sampling methods such as environmental DNA (Larson et al. 2020b) can reduce accessibility and safety barriers for public participation in sampling. This also presents an opportunity to engage recreational anglers whose sampling catch data or photographs can provide cost-effective, high-resolution data for fish conservation and management at relatively fine temporal grains (Karlsson and Kari 2020).

Population density and forest land-cover have consistent effects (i.e., they increase CS survey effort) across spatial scales. The range of environments characterized by high CS survey effort shows that these datasets can be leveraged to elucidate land-use/land-cover (LULC) impacts on freshwater resources. CS programs could incorporate activities that monitor LULC impacts on freshwater resources to engage local stakeholders in environments lacking high CS survey effort (e.g., agricultural areas). For example, a local-scale program in Ecuador monitored deforestation effects on water loss which increased support for fog forest conservation among community members (Becker et al. 2005). Such community-led initiatives often result in relatively prompt changes in conservation attitudes, behaviors, and management decisions relative to professional monitoring (Stepenuck and Green 2015). This interplay between public awareness and decision-making illustrates how CS can result in tangible management outcomes compared to sampling schemes lacking community engagement (McKinley et al. 2017). Therefore, CS could be an important avenue toward mitigating LULC impacts on freshwater resources considering the public health and food security services derived from these ecosystems.

Whereas state-level patterns are driven by differences in population density and land-use/land-cover (LULC), socioeconomic characteristics drive variation in CS programs among watersheds and counties. After controlling for population density, freshwater CS survey effort increases in areas with proportionally more college-educated residents, higher education facilities, and seasonal housing. Therefore, freshwater CS participants may represent a limited subset of the public with access to higher education and/or time and monetary resources for leisure activities (Church et al. 2019). This suggests that there is a need for CS programs to engage broader sectors of the public. Increasing engagement in communities where CS projects are currently underrepresented can help promote scientific skills, knowledge, and literacy which may in turn increase participants' interest in and behavior towards conservation (Schuttler et al. 2018). Additionally, broader public inclusion in CS can facilitate representation of different perspectives in decision making and ensure that benefits of conservation actions are more equitable (McKinley et al. 2017).

To broaden CS participation, programs could reduce barriers by incorporating multi-generational family-friendly activities and providing transportation to CS activities (Pandya 2012; Larson et al. 2020a). NGOs such as watershed conservation groups, which

tend to organize CS surveys at the watershed-scale, are well-placed to increase local participation through these activities. Larger-scale organizations such as governments, funding agencies, and universities can partner with local NGOs to organize programs that incorporative incentives and sampling procedures aligned with local communities' needs and availabilities (Buytaert et al. 2014). Such integrative approaches have led to successful participant recruitment in regions lacking prior CS programs, globally (Buytaert et al. 2014). For participant retention, we urge existing CS programs to provide public access to datasets, if possible, because impacting research can motivate continued CS participation (Larson et al. 2020a).

Conclusion

Our synthesis highlights opportunities to leverage existing CS datasets in freshwater research and identifies survey gaps that could be filled to expand the scope of freshwater CS. For water quality and macroinvertebrates, our analysis indicates that ample data relevant to global change, public health, and environmental justice are available. Emerging CS programs should consider collecting data on fish, streamflow, and water temperature to help fill spatial coverage gaps in academic, federal, and state surveys for these variables.

Our work reveals broad sampling gaps in freshwater CS survey efforts skewed toward accessible (densely populated) or attractive (forested or wetland) environments. We also identify local participation gaps reflecting disproportionate involvement of educated community members with time to engage in volunteer activities. Spatial survey gaps in freshwater CS can be bridged by broadening community participation of groups and locations that are currently underrepresented in CS, such as communities with proportionately fewer college graduates or agricultural areas. These findings also indicate a need for more research on what motivates and hinders public participation in CS, specifically in freshwaters. Meeting this goal will require coordination between community leaders and educators, local NGOs, and larger-scale academic and government entities.

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Appendix

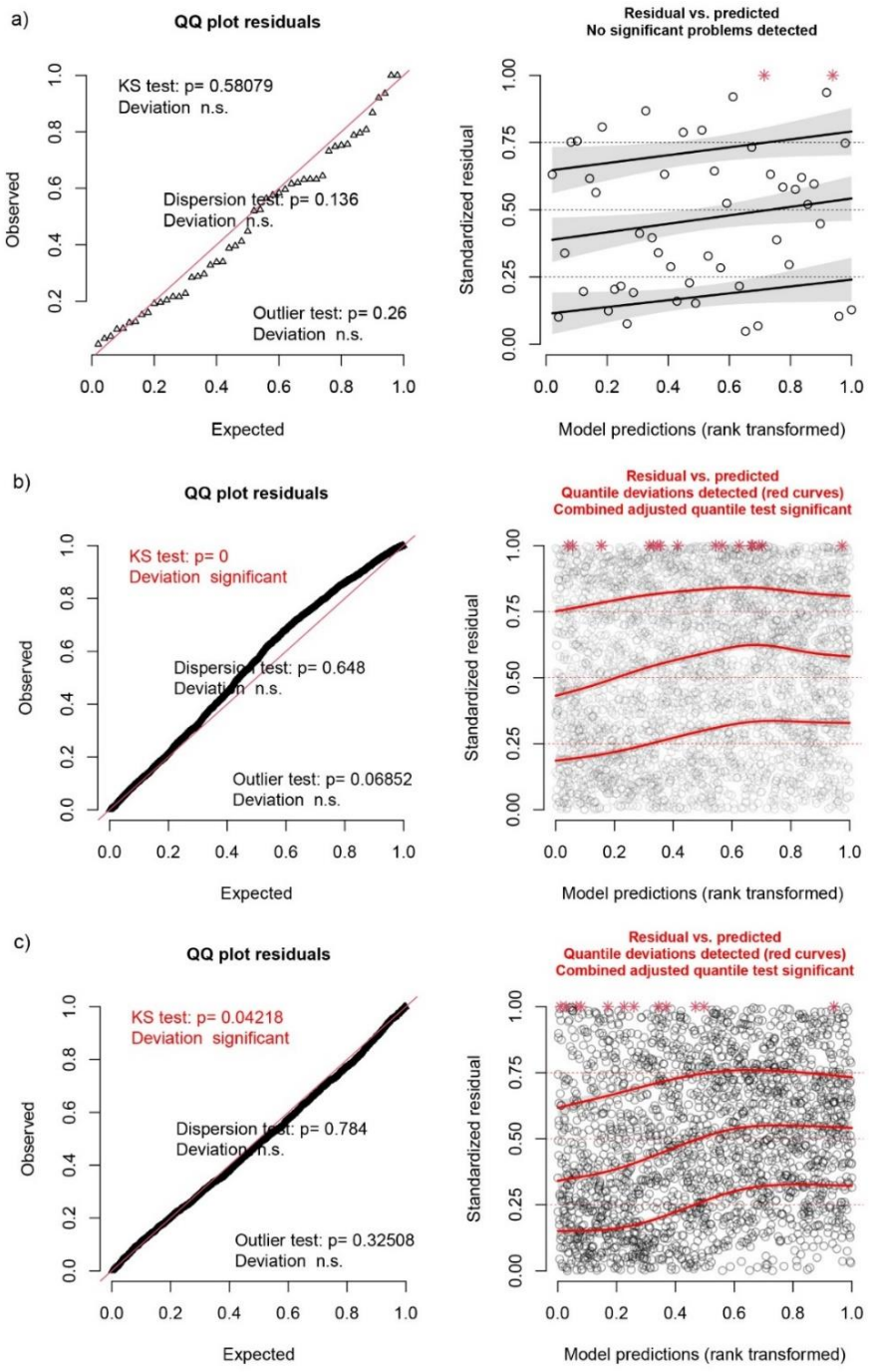

Figure 20. Model diagnostic plots. For the a) state, b) county, and c) watershed scale models, we show quantile-quantile (QQ) plots (left column) and plots of residuals versus predicted values (right column). Plots were interpreted for significant deviations from assumptions as described in the main text.

CHAPTER 4
UNIFYING PATTERNS AND MECHANISMS IN AQUATIC ECTOTHERM BODY SIZE ACROSS BIOLOGICAL SCALES

This chapter is currently in preparation for submission by Taylor Woods and Xingli Giam.

Taylor Woods and Xingli Giam conceptualized the project. Taylor Woods led the data collection, analysis and created figures with input from Xingli Giam. Taylor Woods led writing of the first draft and revisions, and Xingli Giam contributed to manuscript revisions and editing.

Abstract

Patterns and associated mechanisms in body size are the focus of much macroecological research. However, our understanding of these patterns and processes is incomplete for many taxa, especially ectotherms. Here, we aim to narrow knowledge gaps on proximate drivers underlying macroecological body size patterns in one such understudied ecological context, riverine fishes. Specifically, we use a comprehensive individual mass dataset and analyze patterns and mechanisms in body size across biological scales (assemblage, species, and populations). At each scale, we assess indirect geographic (latitude and elevation) mass patterns and identify underlying proximate environmental drivers (anthropogenic factors, area, climate, productivity, and seasonality) and intrinsic mechanisms (thermal traits) that mediate these patterns. Across scales, we find indirect positive patterns between mass and (absolute) latitude and elevation. These indirect patterns are strongly mediated by inverse relationships between environmental temperature and species critical thermal limits and body size.

Introduction

Body size underpins many ecological processes (e.g., metabolism; West et al. 1997) and properties (e.g., abundance; Damuth 1981). Because body size responds to proximate environmental factors (e.g., temperature; Daufresne et al. 2009), global change may affect ecosystem functioning via changes to body size. Therefore, elucidating drivers underlying contemporary body size patterns is a focus of macroecological research (Gaston & Blackburn 2000; Gaston et al. 2008). Generally, evidence supports a pattern of increasing body size with increasing absolute latitude and elevation (Blackburn & Ruggiero 2001; Meiri et al. 2007; Meiri 2011). However, notable exceptions also indicate negative relationships between body size and latitude or elevation (Geist 1987; Meiri et al. 2004). Therefore, size patterns may vary depending on the environmental or taxonomic context considered and thus warrant broad investigation to synthesize patterns and drivers among ecological contexts (Watt et al. 2010; Olalla-Tárraga 2011).

Many, potentially interacting, proximate drivers mediate indirect latitudinal and elevational (hereafter, ‘geographic’) size patterns. Larger-bodied organisms may require greater local habitat areas which can explain poleward increases in body size in the Northern hemisphere (Hawkins & Diniz-filho 2006; Rodríguez et al. 2008). But local habitat areas decrease at higher elevations, thus predicting inverse relationships between size and elevation if this area mechanism is invoked. Higher ecosystem productivity may relax energetic constraints on maximum achievable size, therefore larger sizes can be

expected in more productive lower latitudes or elevations (Rosenzweig 1968). In contrast, larger-bodied organisms may be more resistant to starvation in less productive environments which would predict indirect positive relationships between size and latitude or elevation (Lindstedt & Boyce 1985). Reduced growing seasons in more seasonal environments can limit development time which predicts indirect negative relationships between size and latitude or elevation (Mousseau 1997). Finally, larger body sizes may be advantageous in colder environments owed to greater mass-specific heat retention abilities which can predict positive patterns between size and latitude or elevation (Freckleton et al. 2003; Rodríguez et al. 2008; Blanchet et al. 2010; Brehm et al. 2018).

Body size patterns and drivers are particularly well-researched in terrestrial endotherms, especially for birds (Blackburn & Gaston 1996; Yom-Tov 2001; Ashton 2002; Meiri & Dayan 2003) and mammals (Ashton & Queiroz 2000; Freckleton et al. 2003; Rodríguez et al. 2008). However, size patterns in ectothermic organisms are also noteworthy because these species represent a disproportionate portion of Earth's biodiversity and may be more threatened by global change, relative to endotherms (Daufresne et al. 2009). Mechanisms underpinning ectothermic body size patterns may also differ from those established for endotherms (Zamora-Camacho et al. 2014). For example, a heat conservation mechanism cannot explain inverse relationships between body size and temperature in thermoconforming ectotherms. Instead, larger-bodied ectotherms may exhibit a greater thermal inertia than smaller-bodied species and may thus be better adapted to seasonal environments (Rohr et al. 2018). Ectothermic species with lower thermal limits may also exhibit counter-gradient growth (i.e., higher growth rates at higher latitudes) which could underlie inverse temperature-mass relationships in these taxa (Rypel 2014).

One group of ectothermic organisms whose macroecological body size patterns warrant further investigation is freshwater fishes. These taxa are an interesting study system owed to their remarkable biodiversity and substantial body size variation (Dudgeon et al. 2006). Prior research on size patterns for these species is inconclusive, perhaps owed to methodology discrepancies among studies. First, studies use differing biological scales to aggregate size and evaluate patterns, including assemblages (Knouft 2004; Blanchet et al. 2010; Griffiths 2013), species or higher taxonomic rank (e.g., family; Lindsey 1966), and populations (e.g., intraspecific; Belk & Houston 2002; Rypel 2014). These varying biological scales make it difficult to synthesize findings among studies. Second, size patterns are often investigated without consideration of proximate drivers that underlie them (Shelomi 2012). Robust analyses of size patterns for freshwater fishes should account for proximate drivers, especially those which are unique to the environmental context considered (e.g., streamflow). Finally, studies often base size patterns on literature estimates of species maximum total length (Blanchet et al. 2010; Griffiths 2013), but individual mass data may provide more rigorous assessments of body size.

Here, we seek to narrow these prior shortcomings with a robust assessment of macroecological body size patterns in contiguous United States (CONUS) riverine fishes. We do so with a comprehensive, standardized individual body size dataset to examine geographic patterns and underlying proximate drivers of mass across biological scales. We ask the following questions at the assemblage, species, and population scales: (1) how does body size vary along geographic (latitude and elevation) gradients, (2) what proximate

environmental drivers underlie body size patterns, (3) do thermal mechanisms explain these relationships, and (4) after controlling for proximate drivers and thermal mechanisms, is there evidence for additional factors or mechanisms contributing to geographic size patterns?

Methods

Data collection

Fish dataset cleaning and preparation

We obtained fish data from the US Geologic Survey's National Water-Quality Assessment (NAWQA; < https://aquatic.biodata.usgs.gov/ >). This program collects a representative sample of ichthyofauna at a given site in which species relative abundances reflect the actual relative abundances in the community (Moulton II et al. 2002). The data generated from this program is uniquely pertinent for examining patterns in size because it aims to characterize the body size distribution of each species in an assemblage by recording individual body length [total length (TL; mm)] and mass (g) of individual fish. All individuals of a species were measured if the sample comprised 30 or fewer individuals; for species with >30 individuals, 30 individuals representing the range of body lengths present in the sample were measured. This dataset therefore provides a standardized and accurate sample of body sizes within each assemblage, thus allowing comparisons across different species and locations. We removed records that lacked mass measurements and removed sampling events (n = 19) where size measures were submitted in aggregate among many individuals for at least one species. This occurred when small (< 1.0 g) individuals of a species were measured collectively (Moulton II et al. 2002). This step was necessary because aggregated mass measures would bias our estimates of body size statistics from individual-level data (see 'dataset aggregation and filtering').

We georeferenced NAQWA sites to stream reaches using the National Hydrography Dataset Version 2 Plus (NHD; McKay et al. 2012) accessed in the 'nhdR' R package (Stachelek 2019; R Core Team 2020; Fig. 1a). We removed sites on artificial stream segments (e.g., canals or ditches; Giam and Olden 2016) and referenced reaches to Watershed Boundary Dataset (USGS 2012) regions [2-digit hydrologic unit (HU2)] and basins [8-digit hydrologic unit (HU8)]. To prevent pseudoreplication, we kept only the most recent NAWQA survey from each stream reach. To minimize potential biases from sampling efficacy and selectivity of different gear types, we omitted surveys sampled by boat electrofishing in nonwadeable streams (Fig. 21a). Although this approach may omit the largest individuals in nonwadeable streams, boat electrofishing may not adequately provide area-standardized, representative samples of nonwadeable fish communities (Moulton II et al. 2002). Therefore, the remaining survey methods consisted of any combination of backpack electrofishing, towed barge, and seining methods along a specified length of stream reach and therefore represent area-standardized sampling methods in wadeable streams.

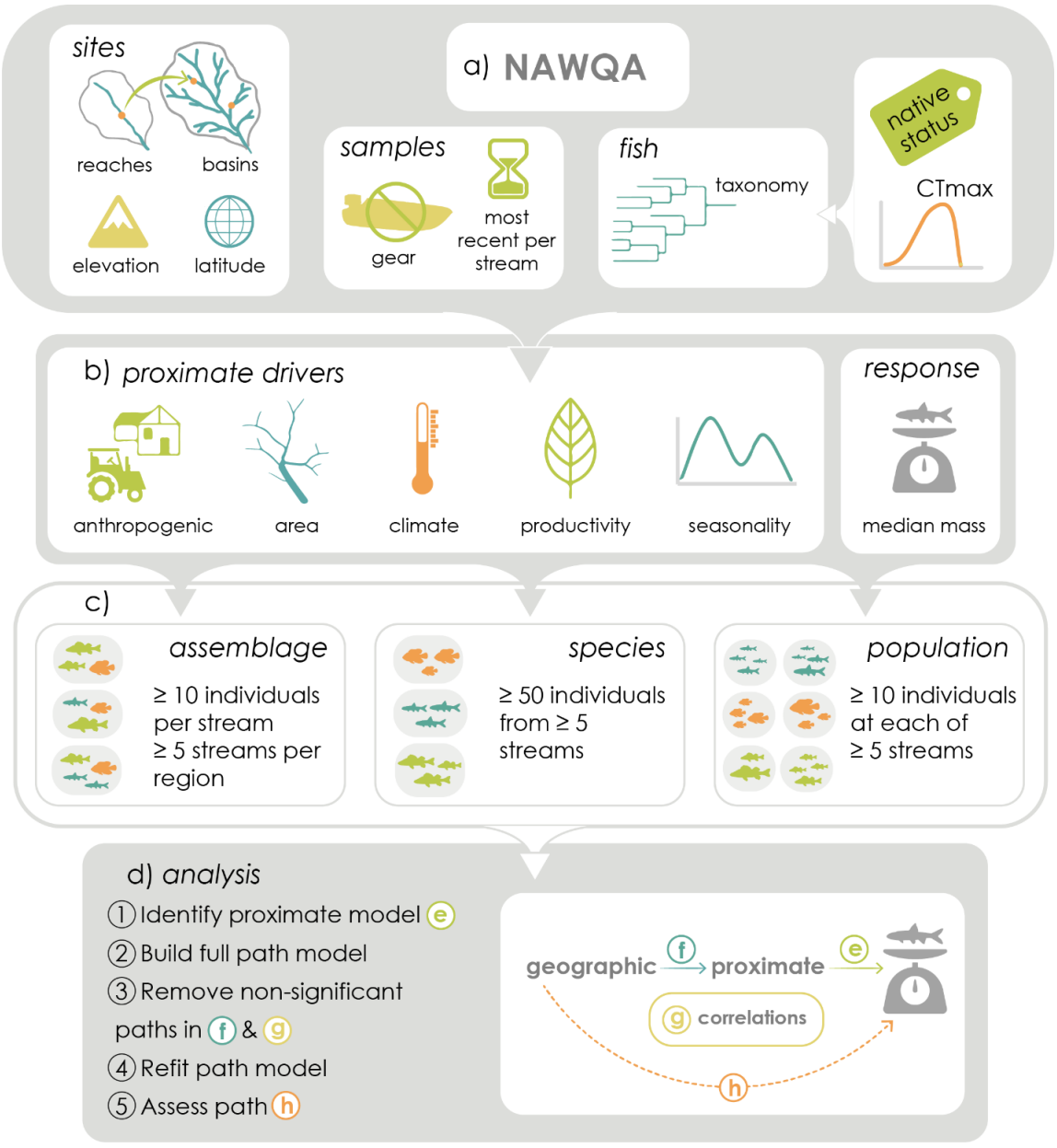

Figure 21. Methods flowchart. A visual summary of methods for a) fish dataset cleaning and preparation, b) data collection of proximate drivers, c) dataset aggregation and filtering, and d) data analysis as described in the main text. In c) colors represent different species and indicate how our individual mass dataset and environmental datasets were aggregated for differing biological scales of analysis.

We standardized taxonomy to valid species names in the Integrated Taxonomic Information System with the 'ritis' package (Chamberlain 2021) and removed occurrences without species-level identifications (Fig. 21a). We referenced species to a ray-finned fish phylogeny in the 'fishtree' package (Rabosky et al. 2018; Chang et al. 2019) and removed species not found in the phylogeny (n = 26 out of 388). These species were either beyond the scope of the phylogeny (e.g., lampreys, class Cephalaspidomorphi; n = 13 species) or from speciose families well-represented in our analysis (e.g., Cyprinidae, Catostomidae; n = 13 species). Therefore, removal of these occurrences was unlikely to influence our analysis.

We assigned native status ('native' or 'introduced') to each occurrence at the basin (HU8) scale using the NatureServe native fish distribution (NatureServe 2010) and US Geological Survey Nonindigenous Aquatic Species (NAS; U.S. Geological Survey 2019) databases (Fig. 21a). The NatureServe dataset contains distribution data for native (i.e., species native to the US) freshwater fish species at the HU8 scale. NAS contains data on introduced (native transplant and exotic) aquatic species occurrences from site (i.e., coordinates of introductions) to HU2 (i.e., regional introduced species lists) scales. First, we queried NAS and the NatureServe datasets to label species (n = 362) as 'native' (native to all basins in the US), 'native transplant' (native to the US, but introduced in at least one basin), or 'exotic' (introduced in all US basins of occurrence). Next, for species found in the NatureServe database (n = 352), we georeferenced coordinates to species' distributions and labelled these occurrences as native to the basin, or unknown (i.e., an occurrence beyond the extent of the NatureServe native range for that species). For the latter, we assumed unknown occurrences for native species were native and those for native transplants were introduced. For those species not in the NatureServe dataset (n = 10), we assigned all occurrences for exotic species (n = 3) as introduced and further queried NAS to label the remaining species occurrences as native or introduced at the HU8 scale.

We collected data on species critical thermal maxima (CTmax) to assess thermal mechanisms underlying body size patterns (Fig. 21a). We used an extensive dataset of modelled CTmax for marine and freshwater fishes from Comte & Olden (2017) and restricted this dataset to freshwater fishes found in the 'fishtree' phylogenetic dataset (n = 2169). We found high phylogenetic correlation in CTmax values for these species (Pagel's $\lambda = 0.97$, $p < 0.001$). Therefore, we used the 'Rphylopars' package (Goolsby et al. 2017, 2021) and performed phylogenetic imputation based on ancestral reconstruction for species in our dataset not found in the CTmax dataset (n = 51). This is an appropriate method for phylogenetic imputation of traits with strong phylogenetic signal (Johnson et al. 2021).

Proximate drivers

We formulated hypothesized geographic patterns and proximate drivers of riverine fish body size based on a review of literature and a priori knowledge of riverine ecosystems (Table 12). We identified proximate drivers of geographic patterns in body size as: anthropogenic factors, area, climate, productivity, and seasonality. Therefore, we collected information to summarize these aspects in riverine environments at the stream reach and associated catchment (terrestrial area directly draining into a reach) or watershed (upstream accumulated terrestrial catchments for a given reach) scales.

Table 12. Hypothesized relationships with body size. For each geographic, proximate, and thermal variable, we provide the abbreviation (following the main text), class of driver (area, anthropogenic, climate, geography, productivity, seasonality, and thermal), predictions (pred.) for the directional effect [(+) increase or (–) decrease] of each variable relative to increasing body size, and a description of our hypotheses from the literature or a priori knowledge of stream systems, with references, if applicable.

Variable	Abbrev.	Class	Pred.	Description
Catchment agricultural land-use	AGRCAT	Anthropogenic	+	Anthropogenic environments are characterized by larger-bodied generalists
Upstream watershed agricultural land-use	AGRWS	Anthropogenic	+	
Accumulated upstream catchment area	AREA	Area	+	Increasing habitat area allows larger-bodied species to establish
Community thermal index	CTI	Thermal	–	Low thermal limits allow ectotherms to reach large body sizes at higher latitudes or elevations
Critical thermal maximum	CTmax	Thermal	–	
Catchment reservoir volume	DAMSTOR	Anthropogenic	+	Larger-bodied species characterize reservoir environments
Mean catchment elevation	ELEV	Geography	+	Higher latitudes are characterized by larger-bodied species (Blackburn & Ruggiero 2001)
Catchment forested land-cover	FORCAT	Productivity	+	Greater allochthonous resources increase freshwater ecosystem productivity
Upstream watershed forested land-cover	FORWS	Productivity	+	
Latitudinal catchment centroid	LAT	Geography	+	Higher latitudes are characterized by larger-bodied species (Bergmann 1848)
Accumulated upstream stream length	LEN	Area	+	Increasing habitat area allows larger-bodied species to establish

Table 12 Continued

Variable	Abbrev.	Class	Pred.	Description
Mean catchment NDVI	NDVI	Productivity	+	Increasing productivity relaxes constraints on upper body size limits (Rosenzweig 1968)
Catchment NDVI CV	NDVICV	Seasonality	–	Greater resource seasonality limits larger body size
Discharge	Q	Area	+	Q estimates local area available to aquatic biota (McGarvey 2014)
CV of monthly discharge	QCV	Seasonality	–	More variable streamflow regimes are characterized by smaller-bodied opportunistic species (Mims & Olden 2012)
Mean catchment temperature	TMP	Climate	–	Larger-bodied ectotherms have greater thermal inertia (Rohr *et al.* 2018) and/or exhibit counter-gradient growth (Rypel 2014)
Catchment temperature CV	TMPCV	Seasonality	–	Shorter growing seasons favor smaller body sizes (Lindstedt & Boyce 1985)
Catchment urban land-use	URBCAT	Anthropogenic	+	Urbanized environments are often characterized by large, generalist species
Upstream watershed urban land-use	URBWS	Anthropogenic	+	

We used the NHD and assigned latitudes (LAT) as geographic catchment centroids. From the NHD, we also obtained the total upstream drainage area (km^2; AREA) and accumulated upstream stream length (km; LEN) for each reach. These variables represent variation in physical habitat variables along longitudinal stream gradients that determine the instream area accessible to aquatic biota [e.g., width, depth, and discharge (Table 12) (Vannote et al. 1980)]. We also collected gage-adjusted mean annual streamflow (Q), standard deviation of monthly flows (QSD), and coefficient of variation (CV) of monthly flows (QCV) for NHD reaches. We used Q to estimate local habitat area available to aquatic biota (McGarvey 2014) and QCV and QSD to characterize streamflow seasonality which can mediate fish size patterns via filtering of life history traits (Table 12) (Mims & Olden 2012).

We used the StreamCat dataset (Hill et al. 2016) and downloaded mean catchment elevation (meters; ELEV). We also used this dataset to characterize terrestrial land-use/land-cover (LULC) with catchment (CAT) and watershed (WS) percentages for agriculture (hay and crop; AGRCAT, AGRWS), forest (deciduous, coniferous, and mixed forests; FORCAT, FORWS), and urban (open, low, medium, and high intensity urban; URBCAT, URBWS) classes based on the 2011 National Land Cover Dataset (Table 12). From StreamCat, we also used the catchment volume of reservoirs listed in the National Inventory of Dams (DAMSTOR; m^3/km^2) to estimate anthropogenic influences on riverine environments via impoundment (Table 12).

We characterized climate using the PRISM dataset in the 'prism' package (Hart & Bell 2015) and calculated 1993–2018 (years of fish occurrences; see results) catchment mean and CV of temperature (TMP and TMPCV, respectively) (Table 12). We used the 'MODIStsp' package (Busetto & Ranghetti 2016) to access NASA MODIS monthly normalized difference vegetation index (NDVI) dataset and calculated mean catchment NDVI and CV (NDVICV) for the years 2000 (earliest year provided by NASA)–2018 (Table 12). Although our climate and productivity variables were terrestrial metrics, terrestrial climate variables provide adequate surrogates of instream variables (e.g., stream temperature) in macroecological analyses (McGarvey et al. 2018). Additionally, positive relationships between terrestrial and aquatic productivity (Guégan et al. 1998; Blanchet et al. 2010) indicate that NDVI can adequately infer instream resource availability, especially after controlling for factors that may cause instream productivity to deviate from this expected relationship (e.g., Q, temperature, forest land-cover; Bernhardt et al. 2018).

Dataset aggregation and filtering

We selected mass as our metric of body size over TL because mass reflects metabolic constraints and is more independent of potential geographic patterns in body shape (e.g., Allen's rule; Blackburn et al. 1999). We used median mass values, rather than mean values, to minimize potential bias introduced by the few very large individuals in assemblages, species, or populations (Blackburn & Gaston 1998; Blanchet et al. 2010). We used median mass as our response variable at three biological scales: assemblage (median mass per stream reach among all individuals of all species), species (median mass among all individuals of a species across all streams), and population (median mass among all individuals, within species, within streams; Fig. 21c). Across scales, we calculated median

mass from native records because introduced fishes represent a non-random selection of species aided by human translocations and may thus confound our inferences of natural size patterns (Blanchet et al. 2010).

We also summarized geographic variables, proximate drivers, and thermal mechanisms at each of the three biological scales for use as predictor variables (Table 12). For the assemblage and population analyses, we used predictor variable values at the stream reach, catchment, or watershed scale (as described in 'proximate drivers'). For the species analysis, we characterized conditions experienced across the species range by calculating mean values for predictors across all streams at which species occurred in our dataset as native occurrences (Velasco et al. 2020). To assess thermal mechanisms underpinning size patterns, we used species-specific CTmax at the species and population scales. For the assemblage analysis, we calculated the community thermal index (CTI) as the mean CTmax among species in an assemblage weighted by abundances (natural log-transformed; Comte et al. 2021).

We filtered our dataset to minimize potential biases from differing sample sizes among biological scales and ensured aggregate mass values were estimated from a minimum of ten individuals (Fig. 21c). We restricted our assemblage analysis to regions (HU2s) with at least five streams at which at least ten individuals were sampled (n = 627 streams among 15 regions). We restricted our species analysis to those with at least 50 individuals sampled among at least five streams (n = 145 species). For the population analysis, we used species observed in at least five catchments, each which at least ten individuals of the species sampled (n = 2398 populations of 98 species).

Data analysis

We natural log transformed mass, AREA, LEN, Q, ELEV, and TMP. For predictors containing zeros (DAMSTOR, AGRCAT, AGRWS, FORCAT, FORWS, URBCAT, and URBWS), we applied natural log transformations after adding the smallest non-zero value for each predictor. We further standardized (mean = 0, SD = 1) all variables. Following transformations, we examined correlation matrices and removed one variable from each pair of highly correlated (Pearson's $r \geq |0.70|$; Dormann et al. 2007) variables. We used AGRWS, DAMSTOR, FORWS, NDVI, Q, QCV, thermal limits (CTI or CTmax), TMP, and URBWS as uncorrelated predictors across scales.

We used a multi-step piecewise path analysis framework to disentangle indirect effects of geography (ELEV and LAT) versus proximate drivers (AGRWS, DAMSTOR, FORWS, NDVI, Q, QCV, TMP, and URBWS) and thermal mechanisms (CTI or CTmax) on median mass at each scale (Fig. 21d). First (1), we identified proximate drivers that related to body size and modelled median mass as a function of proximate drivers, thermal limits (CTI in assemblage analysis and CTmax in species and population analyses) and included an interaction term between thermal limits and TMP (Fig 21e). This interaction term tested the hypothesis that counter-gradient growth underpins temperature effects on body size. For example, a positive CTmax × TMP interaction would indicate that species with higher thermal limits (i.e., warmer-water fishes) show a less negative relationship between mass and TMP, in support of the counter-gradient growth hypothesis (Rypel 2014). We used multi-model inference based on small-sample corrected Akaike's

Information Criterion (AICc) to identify the top-ranked proximate driver model for statistical inference.

In the second step (2), we built a piecewise path model that incorporated: (i) the top-ranked proximate driver model identified above (hereafter 'proximate model'; Fig. 21e), (ii) models with each proximate driver from the proximate model explained by ELEV and LAT (hereafter 'geography models'; Fig. 21f), (iii) bidirectional correlations between all pairwise combinations of proximate drivers, and between ELEV and LAT (Fig. 21g). Third (3), we examined a summary of this path model to identify non-significant paths ($\alpha = 0.05$) in geography models or bidirectional correlations (Fig. 21f-g). Next (4), we refit the path model with these paths removed, if applicable. We based our inferences (5) on this revised path model and associated Fisher's *C* statistic and basis set (see Shipley [2009, 2016] for piecewise path analysis details). Briefly, a significant *C* statistic would reveal a missing path between ELEV and/or LAT with mass after accounting for proximate drivers (Fig. 21h), indicating alternative proximate drivers not accounted for in our analysis.

At each scale, the model structures for the proximate and geography models differed based on statistical factors that should be controlled for in assemblage, species, and population analyses. For the assemblage analysis, we used linear mixed-effects models (LMMs) for the proximate and geography models with random intercepts for region (HU2). A region intercept controlled for the potential that streams sampled within the same region may show more similar body size distributions or environmental conditions owed to regional species pools. For the species analysis, we used a phylogenetic generalized least squares (PGLS) regression model which controlled for the phylogenetic signal (Pagel's λ) in residuals to account for phylogenetic non-independence of mass values from closely-related species (Pagel 1999) which likely applied to our analysis because species body mass showed a strong phylogenetic signal ($\lambda = 0.89$, $p < 0.001$). We used generalized least squares regression models for geographic models in the species analysis. For the population proximate model, we compared the fit of two model structures: (1) a LMM with random intercepts for species (scientific names), and (2) a PGLS model. A comparison of AICc revealed the PGLS was a better fit (ΔAICc = 104.63), so we used this model for inference. We used LMMs with species as random intercepts to account for multiple species sampled from each stream for population geographic models, excluding the geographic model for CTmax which was built with a PGLS structure.

At each scale, we visually assessed quantile-quantile plots and residuals versus fitted values plots to assess potential substantial deviations from assumptions of normality of residuals. We used the R packages 'lme4' (Bates et al. 2015) for LMMs, 'nlme' (Pinheiro et al. 2020), 'fishtree' (Rabosky et al. 2018; Chang et al. 2019), and 'ape' (Paradis & Schliep 2019) for PGLS models, 'MuMIn' (Barton 2020) for multi-model inference model selection, and 'piecewiseSEM' (Lefcheck 2016) for path models.

Results

Our assemblage and population datasets spanned broad latitudinal (range = 20.9 decimal degrees), longitudinal (range = 52.7), and elevational (mean = 513.5 meters; SD = 608.1) gradients (Fig. 22a).

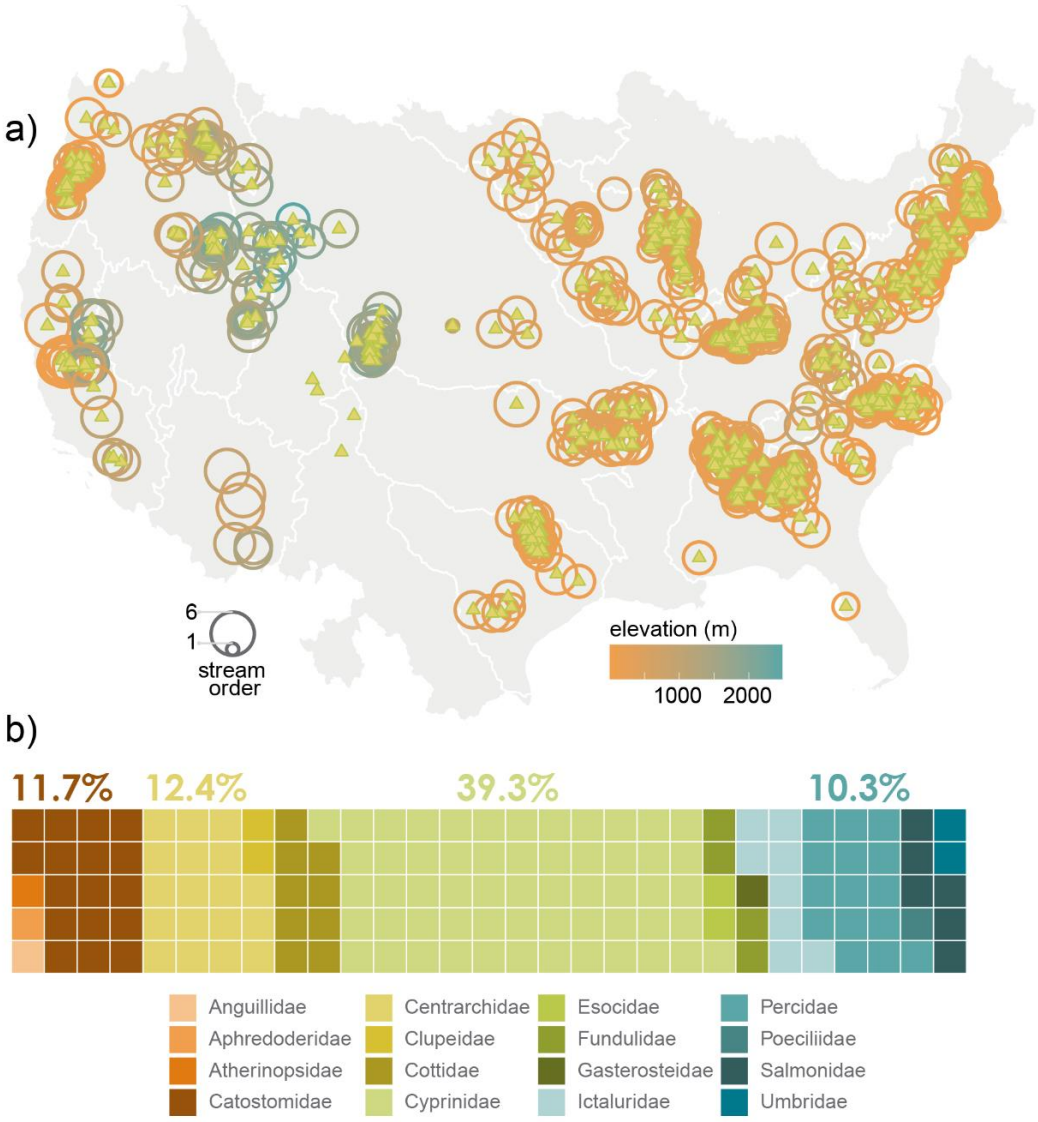

Figure 22. Dataset summary. Map a) shows the locations of assemblages (circles) and populations (triangles). Circle size indicates the Strahler stream order of each assemblage and color shows raw elevation in meters (m). Chart b) presents a taxonomic summary of the species scale dataset. Each square represents a species and is colored according to family. Percentages above the chart indicate the percentage of total species represented by the four most speciose families.

The 145 native species in our species scale analysis encompassed 16 families (Fig. 22b). Notably, these families included eight of the ten most specious North American fish families and ten of the 12 most speciose families in Atlantic drainages (see Smith et al. 2010). Therefore, our dataset broadly represented CONUS stream habitats and ichthyodiversity, thus enabling a robust analysis of body size patterns in CONUS riverine fishes.

At the assemblage scale, increasing watershed urbanization (β = 0.123, SE = 0.05) and temperature (β = 0.001, SE = 0.10) and decreasing CTI (β = -0.256, SE = 0.08) and NDVI (β = 0.10, SE = 0.05) increased median mass (Fig. 23a, Table 13). We also identified a positive interaction between CTI and temperature (CTI × TMP; β = 0.158, SE = 0.05, Fig. 23a, Table 13). This indicates that assemblages with higher CTI showed a less negative relationship between mass and temperature compared to those with lower CTI. CTI and CTI × TMP effects far exceeded those of TMP, indicating that thermal mechanisms outweighed those of environmental temperature (Fig. 24a). Proximate environmental variables and thermal mechanisms fully mediated geographic effects (C = 8.23, 8 *df*, p = 0.411, Table 19). Indirect effects showed positive relationships between ELEV and LAT and median assemblage mass (Fig. 24a). The indirect effect of LAT on mass was more than double that of ELEV (Fig. 24a) and was strongly mediated by direct effects of CTI on mass (Fig. 23a). The weaker ELEV effect may be explained by the negative indirect effect of ELEV on mass mediated by URBWS which opposed the overall positive effect of ELEV on mass (Fig. 23a). Although similar opposing indirect effects were observed for TMP, this weak effect was comparatively negligible on overall indirect patterns (Fig. 23a).

After controlling for phylogeny, decreasing temperature increased mass among species (β = -0.162, SE = 0.05, Fig. 23b, Table 14). Temperature fully mediated geographic effects (C = 1.63, 4 *df*, p = 0.803, Table 20). LAT and ELEV showed indirect positive relationships with mass, mediated by temperature but LAT showed a stronger indirect effect, relative to ELEV (Fig. 24b). This indicates that size variation among species is attributed to an indirect positive effect of LAT, mediated by environmental temperature. Although the top-ranked species model did not incorporate a thermal mechanism, model selection indicated that a model incorporating negative effects of CTmax and TMP on mass was within the family of best-fit models (ΔAICc = 0.14, Table 14). Therefore, a thermal mechanism may underlie the inverse relationship between mass and TMP among species.

Relative to assemblage and species models, a greater variety of proximate drivers affected population mass. Increasing URBWS (β = 0.055, SE = 0.02), AGRWS (β = 0.032, SE = 0.02), and FORWS (β = 0.037, SE = 0.02), and decreasing CTmax (β = -0.159, SE = 0.09), QCV (β = -0.063, SE = 0.02), TMP (β = -0.084, SE = 0.02), and NDVI (β = -0.038, SE = 0.02) increased mass (Fig. 23c, Table 15). However, these proximate variables did not fully mediate geography effects on mass (C = 93.72, 24 *df*, p < 0.001, Table 21). Specifically, the basis set revealed a significant missing path between LAT and mass, after accounting for proximate variables and thermal mechanisms (Table 21).

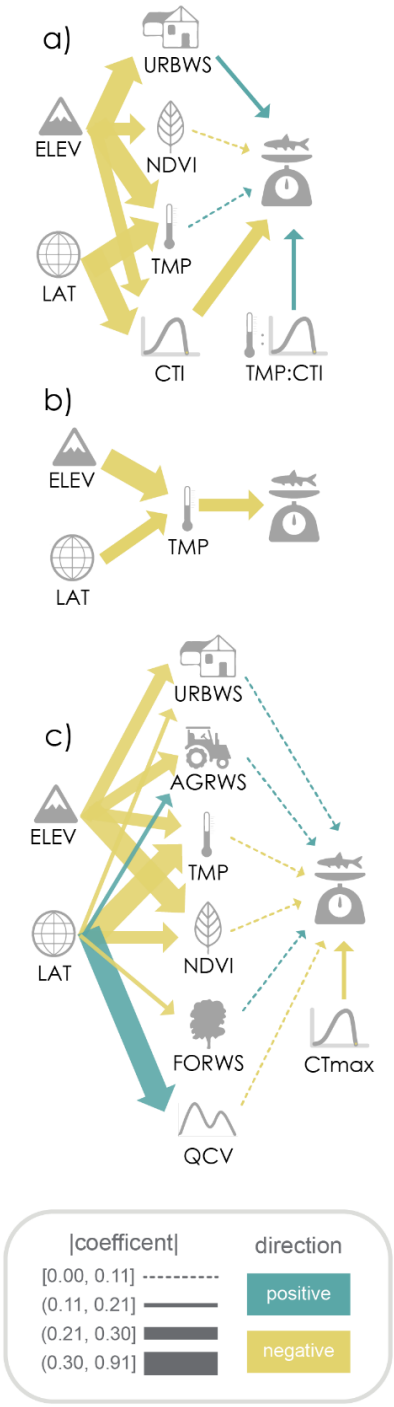

Figure 23. Path model results. For the a) assemblage, b) species, and c) population scales, we show the path model predicting mass as a function of geographic and proximate environmental variables. Line width indicates the absolute value of path coefficients binned into quartiles and color indicates the direction (positive or negative) of the effect. For clarity, bidirectional correlations are omitted but provided in Tables 16-18.

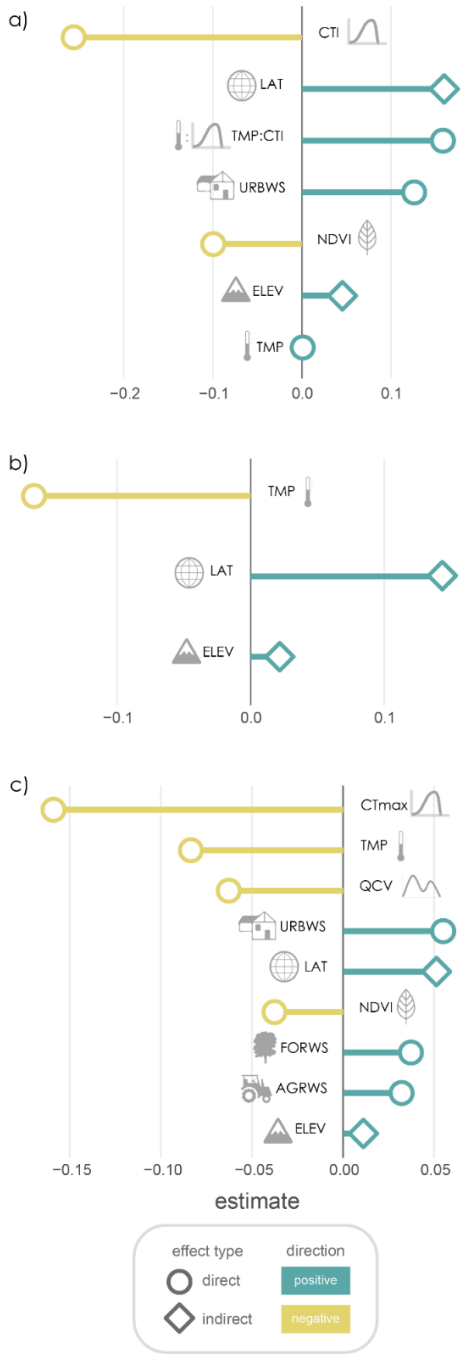

Figure 24. Direct and indirect effects. For the a) assemblage, b) species, and c) population scales, we show the direct effects of proximate environmental variables and indirect effects of geographic variables mediated by geographic variables, ordered by the absolute effect. Shape of the points indicates the type of effect (circles, direct; diamonds, indirect) and color indicates the direction (positive or negative) of the effect. Direct and indirect effects are estimated based on standardized path coefficients following Shipley (2016).

Indirect effects of ELEV and LAT via proximate drivers showed positive relationships with population mass (Fig. 24c). The indirect effect of LAT, which exceeded ELEV, was mediated by a relatively strong direct effect of TMP (Fig. 23c, Fig. 24c). Like assemblage results, we found that indirect effects of ELEV mediated by anthropogenic land-use (AGRWS and URBWS) opposed net positive effects of ELEV on mass (Fig. 23c). Indirect effects of LAT on mass mediated by QCV also opposed the overall positive indirect positive pattern between LAT and population mass (Fig. 23c).

Discussion

Across biological scales, increasing latitude and elevation indirectly increase mass in temperate riverine fishes and these patterns are stronger with respect to latitude, compared to elevation. Prior studies on latitudinal body size patterns in freshwater fish are inconclusive. For example, whereas interspecific patterns of increasing fish body size at higher latitudes are generally supported (Knouft 2004; Blanchet et al. 2010), support for the intraspecific pattern is not conclusive (Belk & Houston 2002; Rypel 2014). One reason we identify strong positive patterns between size and geographic variables across biological scales is the unique nature of the NAWQA dataset which provides methodological advantages to these prior studies. This standardized individual mass dataset at a large spatial extent facilitated a robust analysis of size patterns and thus was able to reveal patterns overlooked by prior datasets with coarser size measures (e.g., species maximum length) or limited spatial scopes. By incorporating data on proximate environmental factors, we are also able to infer mechanisms underlying these indirect latitudinal and elevational patterns.

We find that environmental temperature and thermal mechanisms are the strongest proximate drivers of body size across scales. Cooler environmental temperatures increase mass among species and populations. Additionally, assemblages and populations with lower thermal limits show larger masses, relative to those with higher thermal limits. This suggests larger-bodied ectotherms with lower thermal maxima may be more adapted to cooler environments, relative to smaller-bodied species with higher thermal limits. Rypel (2014) found that cold-water fishes exhibit counter-gradient growth which can explain inverse temperature size relationships for these taxa. Larger-bodied ectotherms may also have greater thermal inertia and may, therefore, exhibit slower cooling rates in seasonally cold environments (Zamora-Camacho et al. 2014; Rohr et al. 2018). Finally, due to higher metabolic rates in warmer environments, ectotherms may mature faster and at smaller sizes at higher temperatures, leading to larger body sizes in colder environments (Atkinson & Sibly 1997). Ultimately, identifying thermal mechanisms underpinning inverse temperature-size relationships in ectotherms will require replicated laboratory experiments along latitudinal and/or elevational gradients (Villeneuve et al. 2021). Regardless, our results provide conclusive evidence that poleward patterns of increasing size arise via thermal responses to environmental temperature in riverine ectotherms across biological scales.

Mass also increases with increasing watershed anthropogenic land-use at the population and assemblage scales. Contrary to overall positive indirect effects of elevation, indirect effects of elevation on mass mediated by land-use variables indicate inverse

patterns between body size and elevation. This may be because environmental conditions in streams in human-modified, lowland landscapes select for larger-bodied, generalist species. For example, larger, generalist fishes may require larger habitat areas (Giam & Olden 2018) which may be more prevalent in lowland, channelized, urban streams. However, we accounted for stream size with discharge which is highly collinear with upstream area and accumulated upstream stream length which accounts for potential area effects. Alternative environmental features such as stream habitat or resource homogenization indirectly measured by watershed land-use metrics may benefit generalist fishes, thus driving partial indirect negative relationships between elevation and mass. One other anthropogenic stressor unaccounted for in our analysis that may impact fish body size patterns is recreational fishing pressure. Drivers of recreational fishing pressure may differ from those of anthropogenic land-uses and this metric could be considered by future research on freshwater fish body size (Davis and Darling 2017).

Terrestrial productivity metrics also mediate geographic size patterns. Negative effects of NDVI on mass, in part, explain positive indirect relationships between elevation and mass. Greater starvation resistance can select for larger body sizes among mammals in low resource environments (Lindstedt & Boyce 1985). In freshwater fishes, larger body sizes across thermal guilds exhibit dampened lipid cycling, relative to smaller body sizes, which can better enable these species to survive on acquired energy stores over periods of nutrient depletion (Fernandes & McMeans 2019). In contrast to negative relationships between NDVI and mass, increasing watershed forest land-cover increases population mass. This may indicate forest land-cover indirectly affects body size via differences in stream thermal regimes caused by riparian shading. For example, Ilha et al. (2018) found that streams in deforested landscapes were warmer and showed reduced fish body sizes, relative to forested reaches. Although we controlled for terrestrial environmental temperatures, forest land-cover may create cool-water thermal refugia at finer scales not captured by our catchment-scale metric. Thus, our work indicates an urgent need for future research to disentangle potential interactions between climate and deforestation on stream fish body size under global change.

At the population scale, decreasing monthly variation in streamflow increased fish body size. Smaller bodied opportunistic species often characterize hydrologically variable streams because their life history characteristics are well-suited to cope with frequent environmental disturbances (Mims & Olden 2012, 2013). However, streamflow variability increased at higher latitudes thus opposing overall positive indirect latitude-size patterns. Mechanisms through which streamflow affects body size may differ from those commonly associated with positive size-latitude patterns. While lower temperatures at higher latitudes may influence mass via metabolic rates (Gillooly et al. 2001), streamflow may impose size constraints via altered fish morphology. For example, fish populations in hydrologically stable streams are often deeper-bodied relative to more streamlined forms from hydrologically variable streams (Andres et al. 2019). Therefore, inverse latitudinal mass patterns mediated by streamflow variability may indicate morphological filtering of body forms among populations from less to more hydrologically variable environments.

In summary, we find indirect positive relationships between latitude and elevation and mass across biological scales. However, proximate drivers and associated mechanisms

underlying these patterns varied among scales. Mechanisms through which lower thermal limits in larger bodied organisms are advantageous in cooler environments likely apply across biological scales. Decreasing productivity also consistently increased body size, indicating that starvation resistance mechanisms underlie positive relationships between mass and elevation in seasonal environments. Although latitude and elevation show overall positive indirect effects across biological scales, we identify circumstances in which proximate environmental variables oppose these patters. For example, generalist species may show inverse elevation-mass relationships mediated by anthropogenic land-use. These results indicate a need for nuanced considerations of the way in which global change stressors impact aquatic ectotherm body size.

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Appendix

Table 13. Top 10 models for the assemblage scale proximate model identified by multi-model inference model selection based on AICc.

Rank	Int.	DAM STOR	CTI	NDVI	AGRWS	FORWS	URBWS	Q	TMP	CTI: TMP	ΔAICc
1	-0.06		-0.26	-0.10			0.13		0.00	0.16	0.00
2	-0.07		-0.27	-0.10	0.06		0.13		-0.02	0.18	0.64
3	-0.06		-0.25	-0.10			0.12	-0.03	0.01	0.16	1.42
4	-0.06		-0.25	-0.10		0.01	0.13		0.00	0.16	2.01
5	-0.07		-0.27	-0.10	0.06		0.12	-0.03	-0.01	0.18	2.03
6	-0.06	0.00	-0.26	-0.10			0.13		0.00	0.16	2.05
7	-0.06		-0.26	-0.10			0.13		0.00	0.16	2.06
8	-0.05		-0.22				0.15		-0.05	0.18	2.23
9	-0.07		-0.27	-0.11	0.06	0.02	0.13		-0.01	0.17	2.52
10	-0.07	0.01	-0.27	-0.10	0.06		0.13		-0.01	0.18	2.68

Table 14. Top 10 models for the species scale proximate model identified by multi-model inference model selection based on AICc.

Rank	Int.	CTmax	DAMSTOR	AGRWS	URBWS	Q	TMP	CTmax:TMP	ΔAICc
1	0.43						-0.16		0.00
2	0.43	-0.16					-0.13		0.14
3	0.40	-0.17			0.14	0.10	-0.15		0.89
4	0.42	-0.17			0.07		-0.15		1.05
5	0.42				0.06		-0.19		1.07
6	0.40				0.13	0.10	-0.18		1.08
7	0.42	-0.17		0.04			-0.10		1.68
8	0.36	-0.15			0.15	0.13	-0.15	0.07	1.76
9	0.42			0.03			-0.15		1.77
10	0.43		-0.02				-0.16		1.91

Table 15. Top 10 models for the population scale proximate model identified by multi-model inference model selection based on AICc.

Rank	Int.	CTmax	NDVI	AGRWS	FORWS	URBWS	Q	QCV	TMP	ΔAICc
1	0.49	-0.16	-0.04	0.03	0.04	0.05		-0.06	-0.08	0.00
2	0.49	-0.15				0.05		-0.06	-0.09	0.71
3	0.49	-0.16		0.02		0.05		-0.06	-0.09	0.82
4	0.47		-0.04	0.03	0.04	0.05		-0.06	-0.09	1.24
5	0.49	-0.15				0.06	0.02	-0.05	-0.09	1.34
6	0.49	-0.15	-0.03		0.03	0.05		-0.06	-0.08	1.49
7	0.49	-0.16		0.03	0.02	0.06		-0.06	-0.10	1.59
8	0.47					0.05		-0.06	-0.10	1.66
9	0.49	-0.16	-0.04	0.03	0.03	0.06	0.01	-0.06	-0.08	1.77
10	0.49	-0.16		0.02		0.06	0.02	-0.05	-0.09	1.81

Table 16. Assemblage piecewise path model coefficients.

Response	Predictor	Estimate	SE	df	|*t*|	*p*
Mass	TMP	0.001	0.10	131.94	0.00	0.993
Mass	CTI	-0.256	0.08	446.18	10.59	0.001
Mass	NDVI	-0.100	0.05	532.93	4.29	0.039
Mass	URBWS	0.126	0.05	599.86	6.80	0.009
Mass	TMP:CTI	0.158	0.05	395.17	8.16	0.005
URBWS	ELEV	-0.335	0.04	564.80	61.99	< 0.001
TMP	ELEV	-0.352	0.01	621.35	615.59	< 0.001
TMP	LAT	-0.729	0.03	430.80	447.07	< 0.001
CTI	ELEV	-0.246	0.02	620.38	113.32	< 0.001
CTI	LAT	-0.626	0.06	468.98	122.67	< 0.001
NDVI	ELEV	-0.250	0.04	624.77	38.83	< 0.001
~~ELEV	~~LAT	0.203		625	5.19	< 0.001
~~URBWS	~~TMP	0.453		627	12.67	< 0.001
~~URBWS	~~CTI	0.177		627	4.50	< 0.001
~~URBWS	~~NDVI	-0.132		627	3.33	0.001
~~TMP	~~CTI	0.142		627	3.58	< 0.001
~~TMP	~~NDVI	0.249		627	6.41	< 0.001
~~CTI	~~NDVI	-0.164		627	4.15	< 0.001

Table 17. Species piecewise path model coefficients.

Response	Predictor	Estimate	SE	*df*	|*t*|	*p*
Mass	TMP	-0.162	0.05	145	3.00	0.003
TMP	ELEV	-0.135	0.03	145	4.56	< 0.001
TMP	LAT	-0.885	0.03	145	30.02	< 0.001
~~ELEV	~~LAT	0.398		143	5.18	< 0.001

Table 18. Population piecewise path model coefficients.

Response	Predictor	Estimate	SE	*df*	|*t*|	*p*
Mass	Ctmax	-0.159	0.09	2398.00	1.80	0.072
Mass	QCV	-0.063	0.02	2398.00	4.07	< 0.001
Mass	TMP	-0.084	0.02	2398.00	3.73	< 0.001
Mass	NDVI	-0.038	0.02	2398.00	1.90	0.058
Mass	URBWS	0.055	0.02	2398.00	3.18	0.002
Mass	AGRWS	0.032	0.02	2398.00	1.87	0.062
Mass	FORWS	0.037	0.02	2398.00	1.96	0.051
QCV	LAT	0.401	0.02	675.75	275.36	< 0.001
TMP	ELEV	-0.256	0.01	2394.72	1604.29	< 0.001
TMP	LAT	-0.914	0.01	2320.43	13906.29	< 0.001
NDVI	ELEV	-0.338	0.02	2235.71	265.80	< 0.001
NDVI	LAT	-0.246	0.02	1646.48	101.32	< 0.001
URBWS	ELEV	-0.262	0.02	2236.09	153.65	< 0.001
URBWS	LAT	-0.116	0.02	1647.34	21.43	< 0.001
AGRWS	ELEV	-0.264	0.02	2385.20	160.93	< 0.001
AGRWS	LAT	0.159	0.03	2173.67	40.37	< 0.001
FORWS	LAT	-0.213	0.03	1538.60	62.15	< 0.001
~~ELEV	~~LAT	0.179		2396.00	8.92	< 0.001
~~QCV	~~URBWS	-0.044		2398.00	2.13	0.017
~~QCV	~~AGRWS	0.108		2398.00	5.31	< 0.001
~~QCV	~~FORWS	-0.037		2398.00	1.81	0.035
~~TMP	~~URBWS	0.283		2398.00	14.45	< 0.001
~~TMP	~~AGRWS	0.094		2398.00	4.63	< 0.001
~~TMP	~~FORWS	-0.234		2398.00	11.78	< 0.001
~~NDVI	~~URBWS	-0.220		2398.00	11.03	< 0.001
~~NDVI	~~FORWS	0.529		2398.00	30.48	< 0.001
~~URBWS	~~AGRWS	-0.111		2398.00	5.45	< 0.001
~~URBWS	~~FORWS	-0.264		2398.00	13.39	< 0.001
~~URBWS	~~Ctmax	0.050		3934.00	3.13	0.001
~~AGRWS	~~FORWS	-0.183		2398.00	9.09	< 0.001
~~FORWS	~~Ctmax	0.028		3934.00	1.73	0.042

Table 19. Assemblage scale d sep test.

Independence claim	***p***
(ELEV, Mass) | {TMP×CTI, TMP, CTI, NDVI, URBWS}	0.337
(LAT, Mass) | {TMP×CTI, TMP, CTI, NDVI, URBWS}	0.885
(LAT, NDVI) | {ELEV}	0.187
(LAT, URBWS) | {ELEV}	0.292
C	8.231
Overall p-value ($\chi^2_{df=8}$)	0.411

Table 20. Species scale d sep test.

Independence claim	***p***
(LAT, Mass) | {TMP}	0.464
(ELEV, Mass) | {TMP}	0954
C	1.633
Overall p-value ($\chi^2_{df=4}$)	0.803

Table 21. Population scale d sep test.

Independence claim	***p***
(CTmax, QCV) | {LAT}	0.667
(CTmax, TMP) | {LAT, ELEV}	0.001
(CTmax, NDVI) | {LAT, ELEV}	0.019
(CTmax, AGRWS) | {LAT, ELEV}	0.000
(LAT, Mass) | {CTmax, QCV, TMP, NDVI, URBWS, AGRWS, FORWS}	0.001
(ELEV, QCV) | {LAT}	0.266
(ELEV, FORWS) | {LAT}	0.058
(ELEV, Mass) | {CTmax, QCV, TMP, NDVI, URBWS, AGRWS, FORWS}	0.079
(QCV, TMP) | {LAT, ELEV}	0.715
(QCV, NDVI) | {LAT, ELEV}	0.114
(TMP, NDVI) | {LAT, ELEV}	0.639
(NDVI, AGRWS) | {LAT, ELEV}	0.359
C	93.72
Overall p-value ($\chi^2_{df=24}$)	< 0.001

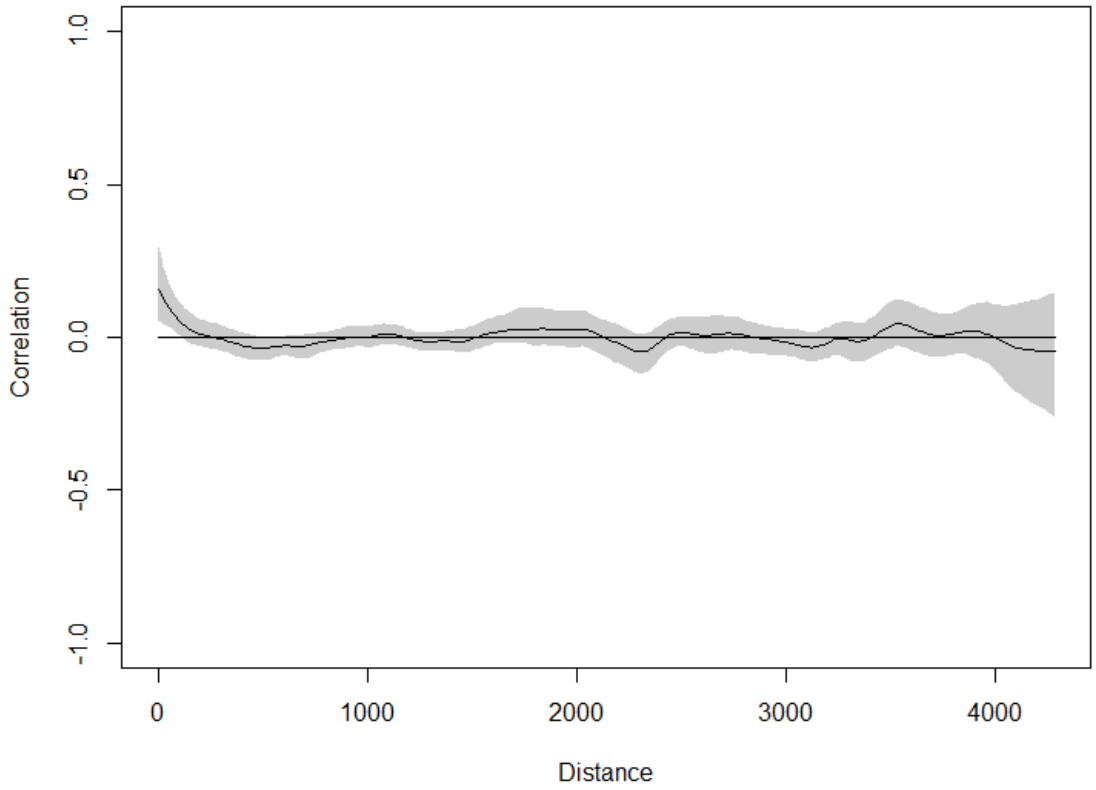

Figure 25. Moran's correlogram at the assemblage scale. Moran's correlogram to assess spatial autocorrelation in model residuals in the top-ranked assemblage model.

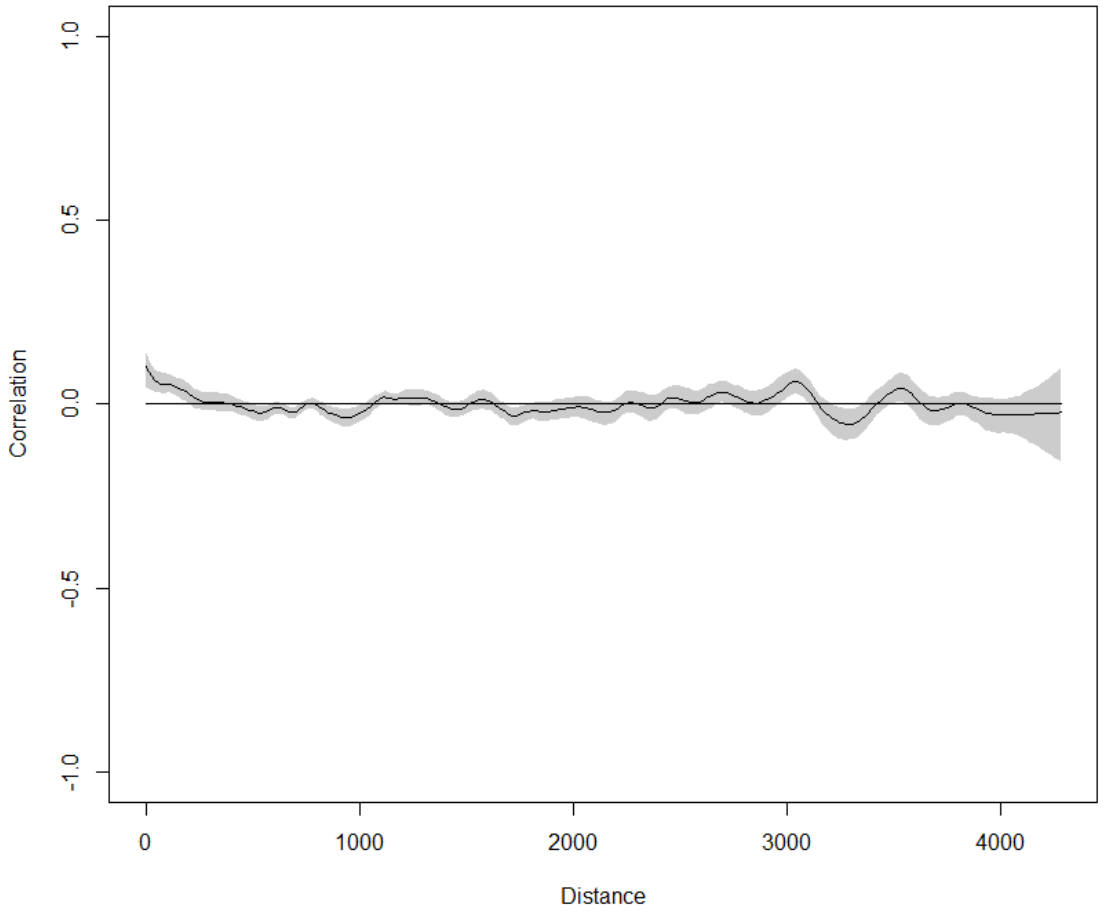

Figure 26. Moran's correlogram at the population scale. Moran's correlogram to assess spatial autocorrelation in model residuals in the top-ranked population model.

CONCLUSION

This dissertation makes substantial contributions to freshwater macroecology. The chapters are unified by a focus on three common macroecological responses to global change: shifts in phenology, biodiversity, and body size. Although well studied in terrestrial environments, these responses are less studied in freshwater contexts owed to data limitations.

In chapter I, primary literature is surveyed to assess key environmental cues, intrinsic traits, and biotic interactions associated with freshwater phenology. I find that freshwater phenology events are cued by temperature, resource, and hydrology regimes. Therefore, shifts in the timing of freshwater phenology are likely to be widespread owed to global change impacts on these key environmental cues. However, I identify broad knowledge gaps in intrinsic traits and biotic interactions associated with phenology. These gaps limit our ability to generalize findings among taxa and understand implications of shifting phenology on community structure and functioning.

In chapter II, I document the biodiversity-ecosystem functioning relationship in riverine ecosystems. This finding is important because it indicates that ongoing freshwater biodiversity loss can decrease stream fish community biomass. Additionally, these results indicate potential impacts of global change on the many ecosystem services provided by stream fish communities (e.g., nutrient cycling, food resources).

In chapter IV, I assess geographic patterns and proximate drivers in fish assemblage body mass across biological scales. Across biological scales, I find that decreasing temperature and increasing watershed urbanized land-use increase fish body size. These results indicate that shifts body size distributions in freshwater may be pervasive responses to ongoing global change.

Beyond these novel contributions to the freshwater macroecology research, each chapter demonstrates how different data sources can be leveraged to overcome knowledge gaps in traditionally under sampled freshwater environments. Chapter I uses a rich dataset on environmental cues and freshwater phenology obtained from published literature. Chapters II and IV use standardized government sampling monitoring programs in France and the United States, respectively. Chapter III extends upon these chapters and analyzes freshwater community science datasets to understand how these emerging data sources may aid in more robust assessments of freshwater biodiversity responses to global change.

In chapter III, I synthesize spatial biases and gaps in freshwater community science (CS) survey effort. CS is often advertised as a novel tool to overcome data limitations created by more traditional standardized biodiversity datasets. However, I identified broad spatial biases and participation gaps in these datasets. There are many opportunities for CS data to provide information to freshwater macroecology, but these data should be used in consideration of the associated biases.

Each chapter used different dataset(s) and equipped me with advanced skills in data cleaning, combination, and processing datasets from disparate sources. I also honed project planning and time management skills required for independent research. Finally, my technical writing skills have improved immensely through the course of my dissertation research.

VITA

Taylor Woods was raised in South City St. Louis, MO. She received a BSc degree in Environmental Biology from Tulane University in 2011 and a MSc in Environmental Studies from Virginia Commonwealth University in 2018 before starting a PhD in Ecology and Evolutionary Biology at the University of Tennessee.