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The Influence of Spatial Structure and Trophic Interactions on Ecological Communities

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The Influence of Spatial Structure and Trophic Interactions on Ecological Communities

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by

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September 2022

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Much of the inspiration for my dissertation research was grounded both in an inherent interest in the theory of community ecology and also in spending ample time

wandering in the high alpine mountains of Western North America. I was particularly fascinated by the high alpine lakes littered throughout the landscape in their stark contrast with steep facing mountains and the diversity of aquatic habitats and organisms within these systems. I was determined in finding out what maintains diversity in these particularly fascinating systems with the hope of spending more time there and understanding these systems better. This field system and ideas also translated into much of the inspiration in my laboratory protist microcosm research. This dissertation is thus dedicated to the wild, high mountains of North America and their charismatic critters, long may they live free and be a place of inspiration!

Some of the most important aspects I learned during my PhD were agnostic to my dissertation research, but rather a greater understanding of my personal self: past, present, and future. For this, I am grateful for my friends, family, and mentors along the way who helped me prioritize my personal self and those around me who helped me form a true community.

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ABSTRACT OF THE DISSERTATION

The Influence of Spatial Structure and Trophic Interactions on Ecological Communities

by

Matthew Douglas Green

Doctor of Philosophy, Graduate Program in Evolution, Ecology, and Organismal Biology
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Dr. Kurt E. Anderson, Chairperson

The central theme of my dissertation is the influence of spatial structure and trophic interactions on ecological community dynamics and subsequent patterns of community diversity. I studied this phenomenon in different ecological contexts. In a synthesis of protist microcosm experiments, I studied how spatial network structure influenced predator-prey persistence (chapter 1). Subsequently, I shifted my focus to Sierra Nevada, CA high elevation aquatic systems. In high elevation lake-stream networks, I investigated whether patterns of macroinvertebrate diversity matched predictions from established stream ecology frameworks and the underlying processes driving these diversity patterns (chapter 2). Lastly, in order to understand how spatial structure and trophic interactions interactively structure communities, I studied how macroinvertebrate and zooplankton communities in Sierra Nevada streams and lakes are structured along spatial gradients and as a function of the presence of fish (chapter 3).

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Introduction

Ecological communities exist in spatially structured landscapes and the processes that regulate communities and ecosystems are modified by the underlying spatial arrangement of habitats. Ecologists' subjectivity in defining spatial and temporal scales has led some to conclude that the community concept should be abandoned, because drawing generalities contingent on arbitrarily defined scales has caused much confusion and debate (Lawton 1999, Ricklefs 2008). From my perspective, community ecologists have not yet adequately addressed the pervasive influence of scale, despite a legacy of spatial perspectives (Gause 1934, Huffaker 1958, MacArthur 1958, Hutchinson 1959) and widespread recognition of its fundamental importance (Wiens 1989, Levin 1992, Leibold and Chase 2018).

A major goal of community ecology is to generalize the processes responsible for generating variation in biodiversity along spatial and environmental gradients. System-specific frameworks have been one avenue for explaining biodiversity responses to environmental gradients. However, system-specific frameworks have been largely context dependent and difficult to generalize, which requires new frameworks that focus on core ecological processes structuring biodiversity across ecosystems. Recent syntheses in community ecology propose that four major processes structure biodiversity: dispersal (the movement of individuals through space), speciation (the formation of new species), niche selection (changes in species relative abundances owing to abiotic and biotic conditions that give rise to deterministic fitness differences between species), and ecological drift (changes in species relative abundances that are random with respect to species identities; Vellend 2010, 2016, Leibold and Chase 2018, Leibold et al. 2020). Syntheses based around these four mechanisms are collectively known as the Theory of Ecological Communities (TEC; Vellend 2010, 2016), which has been demonstrated as a useful approach to linking patterns in biodiversity with processes (Siqueira et al. 2020, Leibold et al. 2020). Importantly, ecologists are now faced with the task of generalizing the TEC framework by disentangling the relative importance of the four constituent processes in structuring communities (Chase and Myers 2011) and linking these four processes to system specific frameworks of community assembly.

Multiscale frameworks in community ecology (e.g., metacommunity ecology, community assembly, and the theory of ecological communities) integrate ecological processes across scales. These frameworks largely emphasize the “horizontal” structure of communities, or species interactions (e.g., competition) within a guild, with little attention given to food webs and the “vertical” structure of communities, or trophic interactions (e.g., predation and mutualism) among different guilds (Holt 2009, Gravel et al. 2011, Leibold and Chase 2018). The incorporation of food webs into multiscale frameworks demonstrate that trophic interactions can modify the relative importance of ecological processes and community structure (Huffaker 1958, Piechnik et al. 2008, Chase et al. 2009, Stier et al. 2013, Fahimipour and Anderson 2015, Livingston et al. 2017).

Food webs are a basic organizational unit for ecologists, yet until recently consideration of how food webs interact across spatial scales has been largely absent from the literature (Schoener 1989, Holt 1993, Polis et al. 1997, Holt and Hoopes 2005).

Classical studies in ecology have demonstrated the importance of spatial and environmental heterogeneity on predator-prey persistence, where persistence is defined as the duration of a species in a community before local or regional extinction occurs (Elton 1927, Nicholson 1933, Huffaker 1958, Pimentel et al. 1963). Local variability of trophic dynamics can lead to increased stability at regional scales through a variety of mechanisms such as rescue effects and dispersal, and thus increased persistence of food webs (Leibold and Chase 2018). Increasingly, ecologists have incorporated spatial perspectives from metacommunity ecology (Leibold and Chase 2018) and network theory (Holland and Hastings 2008a, Gross et al. 2020) to mechanistically understand the importance of spatial, environmental, and biotic factors on food web dynamics (Holyoak and Lawler 1996, Holyoak 2000a, 2000c, Laan and Fox 2020). Despite progress, theoretical studies of spatial trophic dynamics far surpass our empirical understanding. Importantly, we currently lack experimental tests and/or syntheses of how multiple spatial and environmental factors work in concert to influence predator-prey dynamics and persistence.

The incorporation of trophic dynamics into multiscale community ecology framework not only displays the influence of spatial structure on species persistence and biodiversity, but also how trophic interactions can modify the relative importance of ecological processes structuring communities (Chase and Leibold 2003, Leibold and Chase 2018). The presence of predators in a metacommunity of prey species modifies the effects of prey dispersal by either selectively feeding on a competitively dominant species, resulting in increased prey diversity (Paine 1966, Kneitel and Miller 2003, Cadotte et al. 2006) or by reducing overall prey abundance and diversity (Shurin 2001, Chase et al. 2010). Predators alter the strength of environmental selection (Vellend 2010), but the magnitude of predator effects may depend on how predators are influenced by the environment. Predators can also influence community size and thereby increasing the likelihood of extinction and ecological drift. Alternatively, predators feeding selectively can act as an ecological filter which increases more deterministic processes. The relative importance of ecological processes structuring communities is thus dependent on predator and prey life history traits, habitat heterogeneity, and spatial structure.

In natural systems, the influence of spatial structure is generally studied in concert with environmental factors to tease apart processes structuring biodiversity patterns (Brown et al. 2017). Beta (β) diversity, or community dissimilarity, links local (α) and regional (γ) scale diversity to reflect compositional turnover of species among communities (Anderson et al. 2011). Species turnover, or β-diversity along environmental gradients, is also an indicator of the strength of different forms of selection in driving species composition and maintaining diversity at the regional scale (Anderson et al. 2011). Species diversity and turnover along environmental gradients in space or time have the potential to buffer or magnify the impact environmental change on ecosystem functioning. Turnover in zooplankton species composition among Sierra Nevada lakes maintains community biomass in the face of fish introduction at high elevation but not at low elevation (Symons and Shurin 2016). The prevalence of different assembly mechanisms should result in different patterns of β-diversity along environmental, spatial, and temporal gradients, although the link has not been clearly established, especially in freshwater systems and multitrophic communities.

Explicitly incorporating food webs into multiscale frameworks in community ecology is a pressing need moving forward, and authors have suggested that multitrophic interactions might be one of the great sources of unexplained variation in many metacommunity and assembly studies (Leibold and Chase 2018). Linking theoretical and experimental findings with natural systems will provide the most thorough and convincing evidence to understand the effects of spatial structure and trophic interactions in structuring complex ecological communities. My dissertation aims to contribute to the aforementioned gaps in the literature.

The main theme of my dissertation is understanding the role that space and trophic interactions plays in maintaining species persistence and structuring community diversity. I will address the following three aims: (1) to examine the role spatial structure, productivity, and trophic interactions play in determining predator and prey persistence in experimental microcosms; (2) to investigate whether patterns of macroinvertebrate diversity matched predictions from established stream ecology frameworks and the underlying processes driving these diversity patterns; and (3) to understand how spatial structure and trophic interactions interactively structure aquatic communities.

Overall, the present dissertation links ecological theory to empirical studies allowing for a better understanding the role space and trophic interactions play in determining community persistence and diversity. Empirical test of theoretical models in spatial trophic ecology are needed, as our theoretical understanding far surpasses our empirical understanding. Although such multiscale and large spatial experimental studies can be logistically challenging and difficult to synthesize, my hope is that the present extension of spatial community ecology research will inspire researchers to expand upon this work and tackle empirically many unresolved theoretical ideas in spatial food web ecology.

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Chapter 1: Productivity and Trophic Interactions Alter Spatial Benefits of Metacommunity Persistence Across Network Sizes and Structures

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Abstract

Predator-prey systems are notoriously extinction prone in isolated and controlled habitats, but spatial and environmental heterogeneity can enhance predator-prey persistence. Metacommunity and food web theory predicts that aspects of spatial heterogeneity (i.e., metacommunity size and spatial connectivity) and environmental variability (i.e., productivity) influence predator-prey persistence through a variety of mechanisms such as statistical stabilization, colonization-extinction dynamics, and trophic interactions. However, we currently lack explicit tests of how these spatial factors act in concert across different spatial networks configurations and sizes. Such investigations are required to understand the robustness of predictions across a range of spatial systems, environmental variation, and predator-prey systems. Here, we synthesized data from protist predator-prey microcosm experiments to ask how: 1) metacommunity size, 2) spatial connectivity, 3) productivity, and 4) predator identity influence predator-prey persistence, measured through extinction times, colonization/extinction dynamics, and occupancy patterns of both predators and prey. We found that time to prey extinction increased with productivity and decreased with both metacommunity size and connectivity, contrary to predictions. Consistent with theoretical predictions, metacommunity size and productivity positively affected prey occupancy and contrary to predictions, connectivity negatively influenced prey occupancy. For predator persistence, both patterns of occupancy and time to predator extinction responded similarly to spatial and environmental factors. Productivity showed a hump shaped relationship with predator persistence and both spatial factors had positive effects on predator persistence. Further, metacommunity size and connectivity had positive effects on predator occupancy, and productivity showed a hump-shaped relationship with predator occupancy. From our analyses of mechanisms, trophic interactions drove variation in spatial occupancy patterns, where the strength and direction of predator-prey occupancy relationships varied among productivity levels and predator-prey combinations due to differences in the importance of top-down and bottom-up effects. Observed predator occupancy patterns matched expectations derived from metacommunity theory, while prey occupancy patterns were better explained by its relationship with predator occupancy and thus trophic interactions. Taken together, these results highlight that spatial network structure has a complex, spatially contingent relationship with predator-prey persistence and mechanisms have detectable and important roles across a range of spatial networks and conditions.

Introduction

Classical studies in ecology have demonstrated the importance of spatial and environmental heterogeneity on predator-prey persistence, where persistence is defined as the duration of a species in a community before local or regional extinction occurs (Elton, 1927; Huffaker, 1958; Nicholson, 1933; Pimentel et al., 1963). Increasingly, ecologists have incorporated spatial perspectives from metacommunity ecology (Leibold & Chase, 2018) and network theory (Gross et al., 2020; Holland & Hastings, 2008) to mechanistically understand the importance of spatial, environmental, and biotic factors on food web dynamics (Holyoak, 2000a, 2000b; Holyoak & Lawler, 1996; Laan & Fox, 2020). Despite progress, theoretical studies of spatial trophic dynamics far surpass our empirical understanding. Importantly, we currently lack experimental tests and/or syntheses of how multiple spatial and environmental factors work in concert to influence predator-prey persistence, highlighting the importance of this synthesis. In this paper, we synthesized data from protist predator-prey microcosm experiments to ask how: 1) metacommunity size, 2) spatial connectivity, 3) productivity, and 4) predator identity influence predator-prey persistence (measured through extinction times, colonization/extinction dynamics, and occupancy patterns of both predators and prey) along with a study of the mechanisms (spatially explicit occupancy models and trophic dynamics) promoting persistence.

Metacommunity size as well as local habitat area have some of the best documented positive effects on predator-prey persistence (Burkey, 1997; Crowley, 1978; Hassell et al., 1991; Luckinbill, 1974; Wang et al., 2021). Mechanistically, metacommunity size is positively related to species persistence through the role of colonization-extinction dynamics. Extinction probabilities are hypothesized to increase as area decreases (Chase, Blowes, et al., 2020; He & Hubbell, 2011; Hubbell, 2001; MacArthur & Wilson, 1967; Pimm et al., 2014; Pimm & Askins, 1995) because smaller habitats may restrict population sizes (Bender et al., 1998; Fahrig, 1998; Foley, 1997; Hanski et al., 2013). In addition to total metacommunity size, variation in local habitat size influences species persistence and the role of one large metacommunity versus many smaller habitats has been a subject of great debate in conservation biology (Diamond, 1975; Fahrig et al., 2022; Simberloff & Abele, 1976). However, variation in local habitat size does not have strong effects on persistence and biodiversity patterns relative to connectivity (Carrara et al., 2014) and it remains an open question of whether total metacommunity size or variation in local habitat size has a stronger influence on species persistence (Fahrig et al., 2022).

Spatial structure is largely defined by the degree of spatial connectivity between patches, which directly affects species dispersal. Spatial connectivity is generally hypothesized to have positive effects on species persistence (Adler & Nuernberger, 1994; Fahrig & Merriam, 1985; Hanski, 1998; MacArthur & Wilson, 1967), although dispersal surplus and dispersal limitation of either prey or predator species can cause instability (Leibold & Chase, 2018). In particular, prey populations can be negatively influenced by surplus predator dispersal (Baggio et al., 2011; Salau et al., 2012), especially when more highly connected, regular networks increase dispersal and synchronization of patch dynamics (Holland & Hastings, 2008). In contrast, predator-prey persistence tends to be supported in networks with variation in connectivity, where prey are able to colonize less-connected patches that allow them to avoid high predator densities (Covich et al., 2009; Pillai et al., 2011). These more isolated patches typically vary independently and have higher variability due to lower dispersal (Finn et al., 2011; Green et al., 2022), which can provide stabilizing effects to regional community persistence (Anderson & Hayes, 2018).

Aside from spatial processes, environmental factors, such as productivity, are a major driver of persistence and stability in food webs (Carpenter et al., 1985; Rosenzweig & MacArthur, 1963; Schoener, 1989). Low productivity systems often exhibit smaller food chain length, which may drive higher variability and extinction rates among secondary consumers (Oksanen et al., 1981; Post, 2002). Alternatively, increased productivity can destabilize trophic dynamics via the paradox of enrichment, where higher instability occurs due to increased production (Laan & Fox, 2020; Rosenzweig, 1971). Despite the destabilizing effects of very low and very high productivity on local food webs, spatial variation in productivity is hypothesized to be stabilizing at the regional scale where source-sink dynamics maintain persistence (Donahue et al., 2003; Zhang et al., 2017). Productivity has a spatially contingent relationship with biodiversity, hump-shaped relationship at small spatial scales and positive at larger scales (Chase & Leibold, 2002). Such spatial contingency may extend to the influence of productivity on spatial trophic dynamics, although research on this topic is still needed (Leibold & Chase, 2018).

Importantly, the above mentioned spatial (i.e., connectivity and metacommunity size) and environmental (i.e., productivity) factors interact in natural metacommunities to influence predator-prey persistence. Most of the emphasis on the interactions among these variables has focused on food chain length, rather than the temporal dynamics, stability, or persistence of communities, underlining the importance of this synthesis. For example, productivity has a positive effect on food chain length when resources are limiting and ecosystem size also has positive effects on food chain length (Post, 2002; Post et al., 2000; Sabo et al., 2009; Vander Zanden & Fetzer, 2007). These effects may vary across ecosystems due to underlying differences in the strength of species interactions and the spatial habitat structure (Anderson & Hayes, 2018; Shurin et al., 2002, 2006). Despite progress in understanding how spatial and environmental factors interact to influence food webs, gaps remain in our understanding of how these factors interact to influence predator-prey persistence and temporal dynamics.

Occupancy patterns have long been used in theoretical and empirical spatial ecology to explore population and community dynamics (Hastings, 1980; Levins, 1969; Levins & Culver, 1971; May & Nowak, 1994; Wang et al., 2021). Metapopulation theory posits that regional persistence of species and/or communities is reflected in occupancy patterns, where local occupancy is maintained by a balance of colorizations and extinctions (Mouquet & Loreau, 2003). Extensions of occupancy models have expanded to be spatially explicit (Hanski & Ovaskainen, 2000; Pillai et al., 2010; Wang et al., 2021), which show that variation in the underlying spatial structure alters predicted occupancy patterns, where, for example, more spatially heterogeneous networks maintain higher metapopulation persistence in comparison to regular lattice structures (Arancibia & Morin, 2022; Gilarranz & Bascompte, 2012). Furthermore, recent efforts to incorporate food web interactions in spatially explicit occupancy models (Pillai et al., 2010; Wang et al., 2021) and synthesis of trophic metacommunity dynamics (Beger et al., 2010; Gravel et al., 2011; Guzman et al., 2019; Holt, 2002; Pillai et al., 2011) are critical, because species on different trophic levels often respond to space differently (Leibold & Chase, 2018). Spatial structure and the loss or fragmentation of habitat affect species on higher trophic levels more strongly (Pillai et al 2011; Barter and Gross 2016; Liao et al 2017; Ryser et al. 2019). The importance of colonization and extinction dynamics and metacommunity predictions in explaining predator-prey occupancy may vary depending on the importance of top-down or bottom-up effects (Holyoak 2000).

Here, we tested whether spatial structure (metacommunity size and connectivity) and productivity have consistent and detectable effects on predator-prey persistence across a range of spatial networks structures, productivities, and predator identities. We synthesized data from predator-prey protist microcosm experiments manipulating spatial structure and productivity from publicly available sources (Holyoak, 2000a; Holyoak & Lawler, 1996) along with new experiments (M. Green et al., 2022). We measured predator-prey persistence using species occupancy patterns, time to extinction, and colonization/extinction dynamics. We explored the importance of mechanisms including spatially explicit occupancy models and trophic interactions in determining observed occupancy patterns. Based on the ecological theory and empirical evidence reviewed above, we hypothesized that higher occupancy and longer time to extinction results from 1) larger metacommunity size as extinction probabilities decrease with area (Crowley, 1978; MacArthur & Wilson, 1967), 2) increased connectivity due to increased colonizations with connectivity (Cadotte & Fukami, 2005; Holyoak, 2000a; Holyoak & Lawler, 1996), 3) lower and intermediate productivity due to the paradox of enrichment effects at high productivity (Rosenzweig, 1971), and 4) *Euplotes* treatments as *Euplotes* has a lower attack rate than *Didinium* (Carrara et al., 2015; Jiang & Morin, 2005; Miller-ter Kuile et al., 2022).

Methods

We conducted a data synthesis on experimental studies that manipulated aspects of spatial structure and measured this effect on predator-prey persistence. We focused our study on predator-prey protist microcosm experiments that were conducted in spatially connected metacommunities that allowed for active dispersal of protozoa (rather than passive dispersal via pipetting) and sampled at high temporal frequencies. We utilized a suite of previously unpublished experiments from our laboratory (M. Green et al., 2022) and also from publicly available data (Holyoak, 2014; Holyoak & Lawler, 2014) for a total of 22 experiments representing 16 unique spatial network structures (Fig. 1; Table 1).

Experimental Methods. Full details of methods conducted for the data used in this synthesis can be found in the original papers and data repository (M. Green et al., 2022; Holyoak, 2000a; Holyoak & Lawler, 1996), but we summarize them below. We included data from the predator-prey dynamics of three groups of predators and prey in a spatial context: 1) *Euplotes eurystomus* and *Tetrahymena pyriformis*, 2) *Didinium nasutum* and *Colpidium striatum*, 3) *Didinium nasutum* and *Paramecium aurelia*. *Euplotes* is an omnivorous ciliated protist that feeds on smaller protozoa species as well as bacteria (Naeem & Li, 1998). *Tetrahymena* is a smaller (~50μm) ciliated protist that naturally feeds on bacteria and grows approximately logistically in the absence of other ciliates (Doerder & Brunk, 2012). *Didinium* is a voracious predator that naturally feeds on both *Colpidium* and *Paramecium* in natural systems (Holyoak, 2000a; Veilleux, 1979). All these protist species naturally co-occur and interact in aquatic environments (McGrady-Steed et al. 1997).

Individual protist microcosms were either 175mL or 32mL polypropylene Nalgene bottles, depending on the experiment, that were linked by silicon rubber tubing that allowed for natural, active movement of materials and individuals among connected bottles. Each network had its own unique design and connections, but were generally attached using 11cm tube lengths except when geometric constraints prevented this in the ring lattice treatment (Fig. 1k). For all experiments, each network had four replicates. The protist medium used in experiments varied from higher to lower productivity medium and was used as an explanatory factor in statistical analyses of species persistence. Medium was composed of 1000mL of water, 0.1g of Reptivite, and either 1) 1.28g (high productivity), 2) 0.76g (medium productivity), or 3) 0.56g (low productivity) of protozoan pellet. Twenty-four hours after autoclaving the protist medium, three freshwater species of bacteria were inoculated in this medium: *Bacillus subtilis*, *Bacillus cereus*, and *Serratia marcescens*.

Each Nalgene bottle was filled with 50mL (for 175mL microcosms) or 30mL (for 32mL microcosms) of protist medium with associated bacteria species and one boiled wheat seed, which provides a slow release of ample nutrients to bacteria throughout the experiment. Prey species were initially added to the experiment from a stock culture at carrying capacity. After two days, predator species were added in low densities from a stock culture at carrying capacity to all bottles. Sampling of experiments followed standard protist microcosm procedures (Altermatt et al., 2015) and consisted of mixing the community, pipetting five to ten 20μl drops (~0.032 mL/drop) of the community, weighing the sample, and counting the total number of each species under a microscope. For studies involving *Didinium*, 3mL of the community was sampled for predator densities. Sampling of protist microcosms occurred three times per week throughout the duration of each experiment. Due to differences in experimental length among different studies, we cut off experimental data at day 75, as all experiments ran for this length at a minimum. Each week, sterile medium (without bacteria) was replaced in each microcosm to remove waste buildup, replenish carbon supply, and replace sampled medium.

Spatial Metrics. Connectivity was determined as nearest neighbors' connectivity, which was defined for each focal bottle as the average number of connections for directly connected neighbors (Gilarranz & Bascompte, 2012; Melián & Bascompte, 2002). Metacommunity size was determined as the total number of bottles per spatial network. Although the volume varied among experimental treatments from 50mL or 32mL in local communities, the difference is similar enough that it did not influence outcomes (Fig. B.3). Total number of bottles was highly correlated with total volume ($r = 0.87$) and total number of bottles is more reflective of the metrics commonly used in the literature. We transformed metacommunity size using the natural log +1 to meet assumptions of normality in subsequent analyses.

Variable Descriptions. We evaluated the effects of spatial structure and productivity on predator-prey persistence using time to extinction and total extinction time as response variables. At the local level (i.e., individual bottle), time to extinction was defined as the day when prey or predator densities first experienced density = 0. At the metacommunity level, time to prey or predator extinction was defined as the day when prey or predator densities among all bottles in a replicate first experienced density = 0.

We also evaluated prey and predator occupancy to understand the influence of productivity and spatial structure on predator and prey persistence at both the individual bottle and metacommunity level. Occupancy was defined as a binomial variable, where 0 indicated no occupancy (density = 0) and 1 indicated occupancy (density > 0). Mean occupancy was calculated as the average occupancy for each individual bottle or metacommunity replicate throughout the entire experiment.

In order to understand patterns of predator-prey occupancy, we looked at how spatial structure and productivity influenced colonization and extinction probabilities (Hanski & Ovaskainen, 2000; Holyoak, 2000a). Colonization was determined as the probability a species is present where it was absent from a previous time step. Similarly, extinction probability was determined by the probability a species is absent at a location where it was present in a previous time step. We calculated these metrics individually for each bottle, spatial network, and replicate through time.

In order to mechanistically understand how consistently spatial structure and observed colonization-extinction dynamics predict observed occupancy patterns, we compared observed patterns to those predicted by metapopulation theory (Wang et al., 2021). We used the spatially explicit metapopulation model of Hanski and Ovaskainen (2000) to predict metapopulation, regional scale occupancy proportions ${p^*}_N$ and the local scale occupancy probabilities ${p^*}_B$ from observed extinction *e* and colonization *c* probabilities for each species. At the metapopulation level, ${p^*}_N = 1 - \left(\frac{e_N}{c_N \lambda_m}\right)$ and λ_m is the leading eigenvalue of the network adjacency matrix, whereas at the local scale, ${p^*}_B = \frac{c_B}{c_B e_B}$. We used these spatially explicit occupancy models to predict predator and prey occupancy at both the regional and local scale, and explored how colonization and extinction probabilities explained predator and prey occupancy.

To understand the influence of trophic relationships, we explored predator-prey occupancy relationships. These analyses were done separately for each unique predator-prey combination and productivity level, to understand the roles of top-down and bottom-up effects in driving persistence. All analyses were done at the local community scale and done separately for each species combination and productivity level.

Model Creation. For analyses including time to extinction, average occupancy, and colonization and extinction dynamics, we assessed the effects of spatial and environmental factors on time to extinction using generalized linear models (GLMs) in the 'stats' package (R Development Core Team, 2022). Occupancy, colonization, and extinction were modeled by fitting GLMs with binomial error distributions (McCullagh & Nelder, 1989) and for time to extinction we fit GLMs with Poisson error distributions. The most-parameterized model included the effect of productivity level as a factor, predator identity as a factor, spatial connectivity, metacommunity size, and all additive combinations of these variables, with other models being nested subsets. We teased out predator identity effects by treating predator identity as a factor, because predators have different effects on prey based on predator attack rate, movement rate, and other life history traits (Carrara et al., 2015; Jiang & Morin, 2005; Miller-ter Kuile et al., 2022).

For the predicted occupancy analyses, we used beta regression models using the 'betareg' package (Cribari-Neto & Zeileis, 2010). Because binomial GLMs cannot handle proportion data well without weights, we instead used beta regression models, which can handle data measured on a continuous scale and restricted to the interval 0-1 (Cribari-Neto & Zeileis, 2010), to analyze predicted occupancy models. For this analysis, we modeled observed occupancy as a function of predicted occupancy for predators and prey separately to determine how well theoretical models predict observed dynamics at both local and regional scales. We also modeled colonization and extinction probabilities as a function of observed occupancy for predators and prey separately to understand the importance of colonization and extinction dynamics in explaining occupancy. For the predicted occupancy analyses, all candidate models were compared to a null model.

For analysis of trophic relationships, we fit GLM models with binomial error distributions (McCullagh & Nelder, 1989). Models included prey occupancy as a response variable and predator occupancy as the predictor for all predator and productivity combinations separately to understand the importance of trophic relationships in driving occupancy. These candidate models were compared to a null model.

Model Selection. We implemented an information-theoretic approach for model selection and inference (Burnham & Anderson, 2002). Our model selection approach involved creating a list of a priori candidate models describing the dependence of the response variables on the different levels of the predictor variables. For each analysis separately, candidate models were ranked and weighted by Akaike information criterion (AIC) using the ‘bbmle’ package (Bolker, 2020). This method allowed us to make robust inferences about the data from several models and avoided overfitting. In this study, weights and AIC scores for best supported models were very clear and we only report weights and R^2 in the text, but the full model tables can be found in the Supplement. Pseudo R-squared values for all models were determined by first subtracting the null deviance from the model deviance and then dividing that value by the model null deviance. We confirmed the absence of multicollinearity in all analyses, by exploring correlation coefficients among predictor variables and the variance inflation factor of all models using the “check_collinearity” function in the “performance” package (Lüdecke et al., 2021). To visualize relationships for time to extinction, local and regional occupancy, and colonization and extinction dynamics, we plotted the raw data points and used best fit lines from individual single factor GLMs with appropriate distributions. We plotted single factor GLM models because the best fit models were generally the most parametrized model with all four predictors and there is substantial difficulty in visualizing models with four predictors variables. All analyses and data visualizations were carried out using R version 4.0.2 (R Development Core Team, 2022).

Results

Prey went extinct in 20% (135/690) of local communities across all experiments with 0 (0/114) regional extinctions (Fig. A.1a, c). For predators, local extinctions occurred in 49% (336/690) of local communities and in 8% (9/114) of regional metacommunities (Fig. A.1b, d). Because of this high prey and predator persistence at the regional scale, we focused subsequent analyses of extinction at the local scale.

Time to prey extinction, the first day an extinction of prey occurred locally, was best explained by the full model including the additive effects of productivity, predator identity, metacommunity size, and connectivity ($w_{time\ prey\ ext.} = 1$, $R^2 = 0.59$; Fig. 1.2a-d; Table A.1). Productivity increased with time to prey extinction. Time to prey extinction did not differ strongly among predator species, although *Didinium* had greater variability. Metacommunity size and connectivity decreased with time to prey extinction. Time to predator extinction was best explained by the full model including the additive effects of productivity, predator identity, metacommunity size, and connectivity ($w_{time\ pred\ ext.} = 1$, $R^2 = 0.26$; Fig. 1.2e-h; Table A.1). Time to predator extinction did not differ among predator species and showed a unimodal relationship with productivity, where time to predator extinction was highest in intermediate productivity (Fig. 1.2e-h). Metacommunity size and connectivity were positively associated with time to predator extinction.

At the local scale, prey occupancy was best explained by the full model including productivity, predator identity, metacommunity size, and connectivity ($w_{prey\ occup.} = 1$, $R^2 = 0.45$; Fig. 1.3a-d; Table A.2). Both productivity and metacommunity size showed a positive correlation with prey occupancy, while connectivity had a negative relationship with prey occupancy. Prey occupancy was highest in treatments with *Euplotes*. Predator occupancy was also best explained by the full additive model of productivity, predator identity, metacommunity size, and connectivity ($w_{pred.\ occup.}$ = 0.72, R^2 = 0.61; Fig. 1.3e-h; Table A.2). Predator occupancy showed a hump-shaped relationship with productivity, where occupancy was maximized at intermediate productivity. Predator occupancy increased with metacommunity size and connectivity and did not vary among predator identities.

At the metacommunity scale, prey occupancy was best explained by the full additive model of productivity, predator identity, metacommunity size, and connectivity ($w_{prey\ occup.}$ = 1, R^2 = 0.48; Fig. A.2a-d; Table A.2). Prey occupancy increased with productivity and metacommunity size. Prey occupancy decreased with connectivity and was higher in *Didinium* treatments. Predator occupancy was also best explained by the full model of productivity, predator identity, metacommunity size, and connectivity ($w_{pred.\ occup.}$ = 1, R^2 = 0.71; Fig. A.2e-h; Table A.2). Predator occupancy showed a hump shaped relationship with productivity, decreased with metacommunity size, increased with connectivity, and was higher in *Euplotes* treatments than in *Didinium* treatments.

Prey colonization was best predicted by the additive model of productivity, predator identity, and connectivity ($w_{prey\ col.}$ = 0.64, R^2 = 0.33; Fig. 1.4a-d; Table A.3). The full additive model of productivity, predator identity, metacommunity size, and connectivity also was well supported ($w_{prey\ col.}$ = 0.36, R^2 = 0.33; Fig. 1.4a-d; Table A.3). Prey colonization increased with connectivity and metacommunity size, was higher in *Didinium* treatments, and showed a hump shaped relationship with productivity. Predator colonization was best predicted by the full additive model ($w_{pred.\ col.}$ = 0.86, R^2 = 0.44; Fig. 1.4e-h; Table A.3). Predator colonization increased with metacommunity size and connectivity, was highest in intermediate productivity relative to the low and high productivity treatments, and did not vary among predator identities.

Extinction dynamics of prey were best predicted by the full additive model ($w_{prey\ ext.}$ = 0.92, R^2 = 0.44; Fig. 1.5a-d; Table A.3). Prey extinction was also moderately supported by the model including productivity, predator identity, and connectivity ($w_{prey\ ext.}$ = 0.08, R^2 = 0.44; Fig. 1.5a, b, d; Table A.3). Prey extinction decreased with productivity, did not differ strongly among predator identities, and increased with metacommunity size and connectivity. Predator extinction was best predicted by the full additive model of productivity, predator identity, metacommunity size, and connectivity. Predator extinction decreased with metacommunity size and connectivity, showed an inverse hump shaped relationship with productivity, and did not differ among predator identities ($w_{pred.\ ext.}$ = 0.8, R^2 = 0.51; Fig. 1.5e-h; Table A.3). Predator extinction was moderately supported by the model of productivity, predator identity, and connectivity ($w_{pred.\ ext.}$ = 0.14, R^2 = 0.5; Fig. 1.5e-h; Table A.3). Lastly, predator extinction was weakly supported by the additive model of productivity, predator identity, and metacommunity size ($w_{pred.\ ext.}$ = 0.07, R^2 = 0.5; Fig. 1.5e-h; Table A.3).

At the network scale, spatially explicit metapopulation models showed a positive relationship with predator observed occupancy as a function of predator predicted occupancy, as well as the model for prey observed occupancy as a function of prey predicted occupancy ($w_{prey\ obs.\ occup.}$ = 1, R^2 = 0.8; $w_{pred.\ obs.\ occup.}$ = 1, R^2 = 0.85; Fig. 1.6a, b; Table A.4). Predator and prey observed occupancy at the local scale also increased with predator and prey predicted occupancy ($w_{prey\ obs.\ occup.} = 1$, $R^2 = 0.85$; $w_{pred.\ obs.\ occup.} = 1$, $R^2 = 0.93$; Fig. 1.6c, d; Table A.4). The proportion of explained variation from colonization and extinction determining observed occupancy varied among species, where colonization and extinction explained more variation for predators than for prey. At the local scale, prey and predator colonization increased with prey and predator observed occupancy, respectively ($w_{prey\ col.} = 1$, $R^2 = 0.51$; $w_{pred.\ col.} =1$, $R^2 = 0.84$; Fig. 1.6e, f; Table A.4). At the local scale prey extinction and predator extinction were negatively related to observed prey and predator occupancy, respectively ($w_{prey\ ext.} =1$, $R^2 = 0.47$; $w_{pred.\ col.} =1$, $R^2 = 0.68$; Fig. 1.6g, h; Table A.4).

The strength and direction of predator and prey occupancy relationships varied among productivity levels and predator-prey combinations. In spatial systems with *Euplotes* and *Tetrahymena*, prey occupancy increased with predator occupancy in the low productivity treatment, whereas at higher productivity no relationship existed as prey occupancy was high across bottles regardless of predator occupancy (Low productivity: $R^2= 0.28$; High productivity: $R^2= 0$; Fig. 1.7; Table 1.2). In spatial systems with *Didinium* and *Colpidium* at intermediate productivity, prey occupancy increased with predator occupancy ($R^2= 0.32$; Fig. 1.7; Table 1.2). In both low and high productivity treatments with *Didinium* and *Paramecium*, prey occupancy decreased with predator occupancy, and this negative relationship was strongest in low productivity environments (Low productivity: $R^2= 0.5$; High productivity: $R^2= 0.28$; Fig. 1.7; Table 1.2).

Discussion

Empirical and modeling studies have shown that species in spatially connected food webs have higher persistence than isolated ones, but these previous studies have been limited in scope, typically manipulating one or two spatial or environmental factors across a limited range (Carrara et al., 2012; Gross et al., 2020; Holyoak, 2000a). In this synthesis, we accounted for multiple facets of spatial structure and trophic interactions in promoting persistence. We showed that spatial factors robustly predict occupancy dynamics and time to extinction across experiments. Rarely have all these spatial factors and mechanisms been explored in concert empirically, highlighting the importance of this synthesis. Our study revealed that extinction-prone predator-prey systems persist in spatial networks due to the additive effects of connectivity, metacommunity size, productivity, and predator-prey identities, and that prey and predator persistence respond differently to these factors. At the regional scale, predator and prey communities rarely went fully extinct, whereas at the local scale predators went extinct in around 50% and prey went extinct in around 20% of local communities. As predicted by metacommunity theory, both predator and prey local occupancy increased with metacommunity size. However, prey occupancy decreased with connectivity contrary to predictions, whereas predator occupancy increased with connectivity, suggesting an apparent trophic effect, where predators are forcing prey into less favorable, less connected communities. Taken together our synthesis highlights that metacommunity theory was robust in predicting predator-prey persistence across a range of spatial network sizes and configurations and that the strength of responses vary with top-down (i.e., predator identity) or bottom-up (i.e., productivity) effects.

Results from this synthesis suggest that the effect of spatial structure on prey populations was less pronounced because of trophic dynamics. Trophic interactions appeared to drive variation in the way both species were spatially structured; predators had higher occupancy in more connected bottles in larger metacommunities, which appeared to force prey to communities that were more spatially isolated in smaller metacommunities. Studies have shown that spatial structure affects species on higher trophic levels more strongly than their prey (Barter & Gross, 2016; Gilbert et al., 1998; Liao et al., 2016; Pillai et al., 2011; Ryser et al., 2019), which then drives spatial variation in prey dynamics as seen in our synthesis empirically. Furthermore, predator colonization and extinction dynamics were well explained by predator occupancy, which in turn followed patterns among bottles and network types predicted by metacommunity theory (Fig. 6). For prey, colonization and extinction probabilities did not explain as much variation in observed occupancy patterns and were much weaker, relative to predators.

While predator persistence better matched predictions derived from metacommunity theory, prey persistence responded more to the dual influences of top-down (predation) and bottom-up (productivity) effects. In our synthesis, productivity had a strong positive effect on time to prey extinction, whereas for predators, productivity had weaker effects where intermediate productivity maximized time to extinction. Luckinbill (1974) found that higher productivity increased prey and time to predator extinction in non-spatial systems and Holyoak (2000b) found no strong differences in prey or time to predator extinction among spatial systems varying in productivity. These contradictory results could reflect differences in the spatial structures used and the importance of spatial refugia for prey. Similar patterns of productivity emerged in occupancy relationships at both local and regional scales, where productivity had a positive effect on prey occupancy, and intermediate productivity maximized predator occupancy. Our results conflict with those of Laan and Fox (2020) which showed a negative relationship with productivity and predator persistence. This could reflect fundamental differences among the experiments' predator-prey combinations, spatial structures, or dispersal laboratory techniques, but most likely reflects differences among the experiments' productivity levels. In our synthesis, productivity showed a hump shaped relationship with predator and prey colonization probabilities, where colonization was highest in intermediate productivity treatments. Further, extinction probabilities of prey and predators decreased with productivity. This suggests predators were affected by the paradox of enrichment and prey were simply responding positively to increased productivity, but this relationship was dependent on the particular predator-prey and productivity combination.

Predator-prey occupancy relationships additionally varied in direction and strength depending on the strength of predator-prey interactions (Fig. 7). When predator-prey interaction strengths were strongest (*Didinium-Paramecium*), prey occupancy decreased with predator occupancy consistent with the role of top-down effects predicted by spatial food web theory (Gravel et al., 2011; Guzman et al., 2019; Holt, 2009). This top-down effect was strongest in low productivity environments, a result predicted by other modeling and empirical studies (Chase, 2003; Galiana et al., 2021) and alternative theory and findings support an opposite pattern, in which top-down effects are strongest in high productivity environments (Abrams, 1993; Leibold, 1989, 1996; Oksanen et al., 1981). This discrepancy between these two predictions may rest in their focus on the effects of prey diversity and diverse food webs as well as mismatches between time averaged data and equilibrium predictions (Laan & Fox, 2020). Lastly, in our trophic analysis we found some support for the paradox of enrichment, which predicts that coexistence should be maximized in lower and intermediate productivity treatments, where top-down effects should be dampened (Rosenzweig, 1971).

Bottom-up effects appeared stronger in the lowest (*Euplotes*-*Tetrahymena)* and intermediate (*Didinium*-*Colpidium*) predator-prey interaction strengths, where predator-prey occupancy relationships were positive. However, in the *Euplotes*-*Tetrahymena* high productivity treatment no predator-prey occupancy relationship emerged, as prey occupancy was high across bottles regardless of predator occupancy. In these low to intermediate predator-prey interaction strength systems, bottom-up effects appear to drive spatial food web patterns, potentially due to high prey reproductive rate and carrying capacity outpacing the ability of predators to capture prey (Rosenzweig & MacArthur, 1963). Alternatively, competition for bacteria, rather than predation, could be responsible for the *Euplotes*-*Tetrahymena* occupancy relationship. *Euplotes* exhibits omnivorous tendencies in that it can persist, albeit temporarily, on just bacteria alone (Zubkov & Sleigh, 1996). However, *Euplotes* strong preference for *Tetrahymena* over bacteria (C.W.

personal observation) and there is no empirical evidence of omnivory in *Didinium*, making bottom-up effects the more likely driver of these predator-prey occupancy patterns.

Conclusions. Our synthesis of spatial predator-prey persistence highlights how different aspects of spatial structure and productivity influence variation in species persistence and adds to recent body of research of trophic dynamics in metacommunity theory (Gravel et al., 2011; Guzman et al., 2019; Holt, 2002; Pillai et al., 2011). Additional complexities to trophic metacommunity dynamics not accounted for in this current study include differences in life history traits such as dispersal and body size that differ among and within trophic levels. Such differences can lead trophic levels to experience the environment at different spatiotemporal scales (Anderson & Fahimipour, 2021; McCann et al., 2005). Thus, the loss of top predators can have significant and unexpected consequences on food web stability due to their disproportionately large top-down effects on lower trophic levels (Woodward et al., 2012).

Understanding how spatial structure influences the persistence of ecological communities is a pivotal goal of both fundamental and applied ecology (Chase, Jeliazkov, et al., 2020; da Silva et al., 2021; Leibold & Chase, 2018; Patrick et al., 2021). Our study demonstrates that maintaining connectivity and, importantly, variation in connectivity, appears particularly necessary given that species on different trophic levels maintain persistence by utilizing habitats differently. Additionally, this study shows that preserving variation in habitat sizes is important, as prey species persisted longer in smaller metacommunities and predators in larger metacommunities. Moving forward, consideration of the effects of environmental heterogeneity and life history traits on spatial food web dynamics will improve our understanding of these systems and how to effectively manage them.

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Figures and Tables

Table 1.1: Summary of data used in this synthesis. Structure code (Code) correspond to letters in Figure 1. Source refers to the corresponding data specific citation. Productivity (Prod) was determined by the weight (g) of protist pellets, a food resource for bacteria, used in the experiment. Metacommunity size (Meta) is the total number of bottles in each experiment. Connectivity (Conn) is the average nearest neighbor's connectivity. Bottle size (Bottle) is the size of bottles (mL) and volume (Vol.) is the amount of medium (mL) used in experiments.

Code	Source	Predator	Prey	Prod	Meta	Conn	Bottle	Vol
A	(Holyoak, 2014)	*Didinium*	*Colpidium*	0.76	2	1	32	30
B	(Holyoak, 2014)	*Didinium*	*Colpidium*	0.76	3	2	32	30
C	(Holyoak, 2014)	*Didinium*	*Colpidium*	0.76	3	1.67	32	30
D	(Holyoak, 2014)	*Didinium*	*Colpidium*	0.76	3	2	32	30
E	(Holyoak, 2014)	*Didinium*	*Colpidium*	0.76	3	2	32	30
F	(Holyoak, 2014)	*Didinium*	*Colpidium*	0.76	4	3	32	30
G	(Holyoak, 2014)	*Didinium*	*Colpidium*	0.76	4	1.75	32	30
H	(Holyoak, 2014)	*Didinium*	*Colpidium*	0.76	4	2	32	30
I	(Holyoak, 2014)	*Didinium*	*Colpidium*	0.76	4	4	32	30
J	(M. Green et al., 2022)	*Euplotes*	*Tetrahymena*	1.28	7	2.52	175	50
K	(M. Green et al., 2022)	*Euplotes*	*Tetrahymena*	1.28	7	4	175	50
L	(M. Green et al., 2022)	*Euplotes*	*Tetrahymena*	1.28	7	1.86	175	50
J	(M. Green et al., 2022)	*Didinium*	*Paramecium*	1.28	7	2.52	175	50
K	(M. Green et al., 2022)	*Didinium*	*Paramecium*	1.28	7	4	175	50
L	(M. Green et al., 2022)	*Didinium*	*Paramecium*	1.28	7	1.86	175	50
J	(M. Green et al., 2022)	*Didinium*	*Colpidium*	1.28	7	2.52	175	50
K	(M. Green et al., 2022)	*Didinium*	*Colpidium*	1.28	7	4	175	50

L	(M. Green et al., 2022)	*Didinium*	*Colpidium*	1.28	7	1.86	175	50
M	(M. Green et al., 2022)	*Didinium*	*Colpidium*	0.56	8	3	175	50
N	(M. Green et al., 2022)	*Didinium*	*Colpidium*	0.56	8	3	175	50
O	(Holyoak & Lawler, 2014)	*Didinium*	*Colpidium*	0.76	9	5.24	32	30
P	(M. Green et al., 2022)	*Euplotes*	*Tetrahymena*	1.28	15	2.6	175	50
Q	(M. Green et al., 2022)	*Euplotes*	*Tetrahymena*	1.28	15	3.1	175	50
R	(Holyoak & Lawler, 2014)	*Didinium*	*Colpidium*	0.76	25	6.3	32	50

Table 1.2: Results from GLMs analyzing the effects of trophic dynamics. Response variables focus on mean prey occupancy (prey.oc) as a function of mean predator occupancy (pred.oc) at the local scale. Each model was compared to a null model. Models are ranked by ΔAIC separately for each predator-prey and productivity combination. Each model is presented with AIC, the degrees of freedom, Akaike weights w_i, and the fraction of null deviance (R^2) explained.

Predator-Prey	Productivity	Response	Model	ΔAIC	*df*	w_i	R^2
Euplotes-Tetraymena	Low	prey.oc	~pred.oc	0	2	0.9938	0.28
			~1	10.2	1	0.0062	0.00
Euplotes-Tetraymena	High	prey.oc	~1	0	1	0.73	0.00
			~pred.oc	2	2	0.27	0.01
Didinium-Colpidium	Medium	prey.oc	~pred.oc	0	2	1	0.32
			~1	71.7	1	<0.001	0.00
Didinium-Paramecium	Low	prey.oc	~pred.oc	0	2	1	0.50
			~1	48.9	1	<0.001	0.00
Didinium-Paramecium	High	prey.oc	~pred.oc	0	2	0.997	0.28
			~1	11.6	1	0.003	0.00

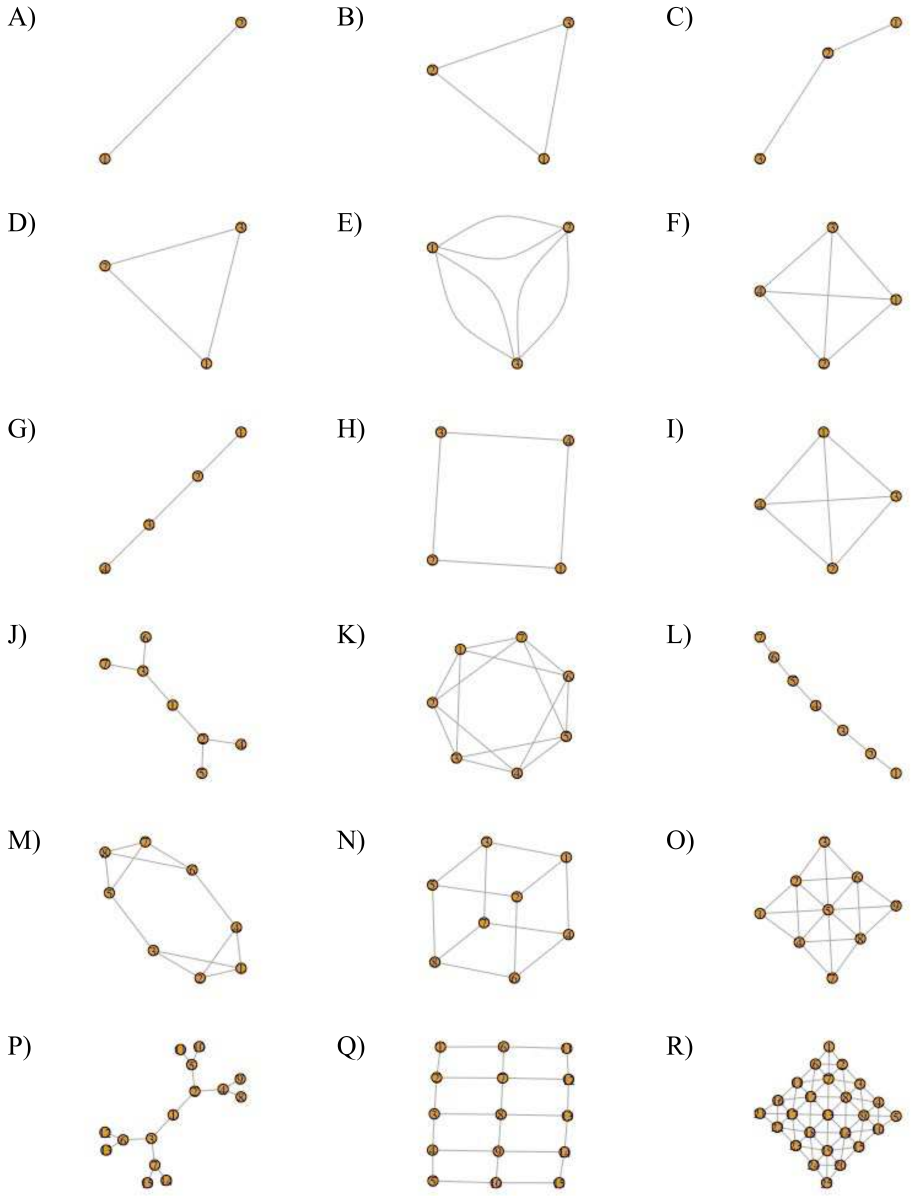

Figure 1.1: The spatial network structures used in this data synthesis. Each circle represents a microcosm community with predators and prey. The lines connecting bottles represent direct dispersal connections that allow microorganisms to actively disperse throughout the metacommunity. The labels correspond to Table 1 Structure Codes.

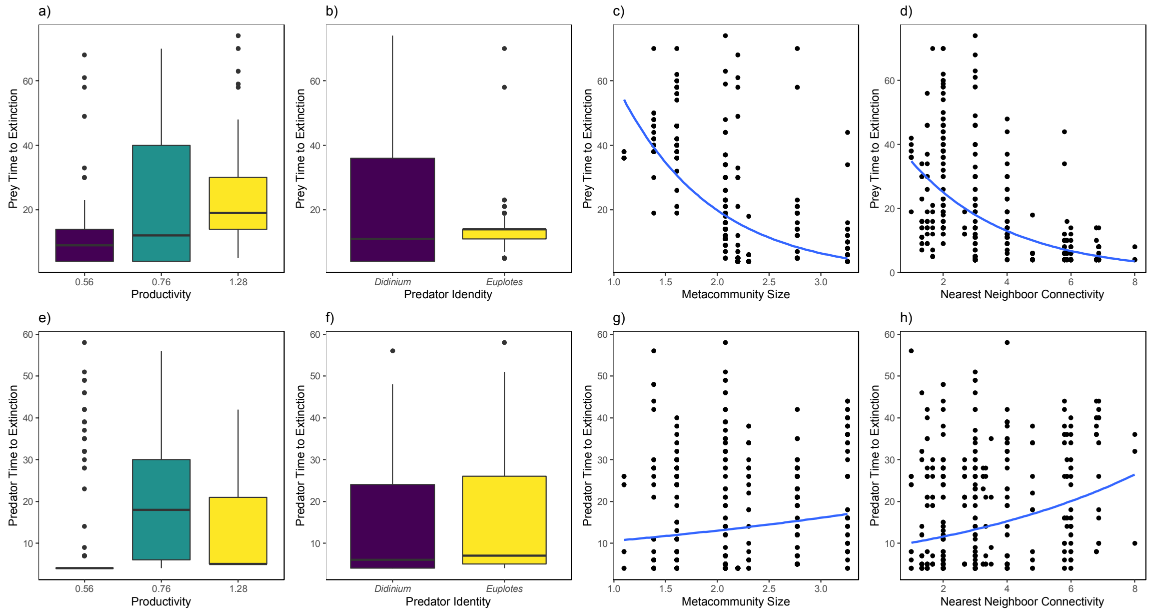

Figure 1.2: Local time to extinction for prey (a-d) and predators (e-h) as a function of productivity (a, e), predator identity (b, f), metacommunity size (c, g), and connectivity (d, h). Best fit lines are shown as GLMs for individual predictor variables.

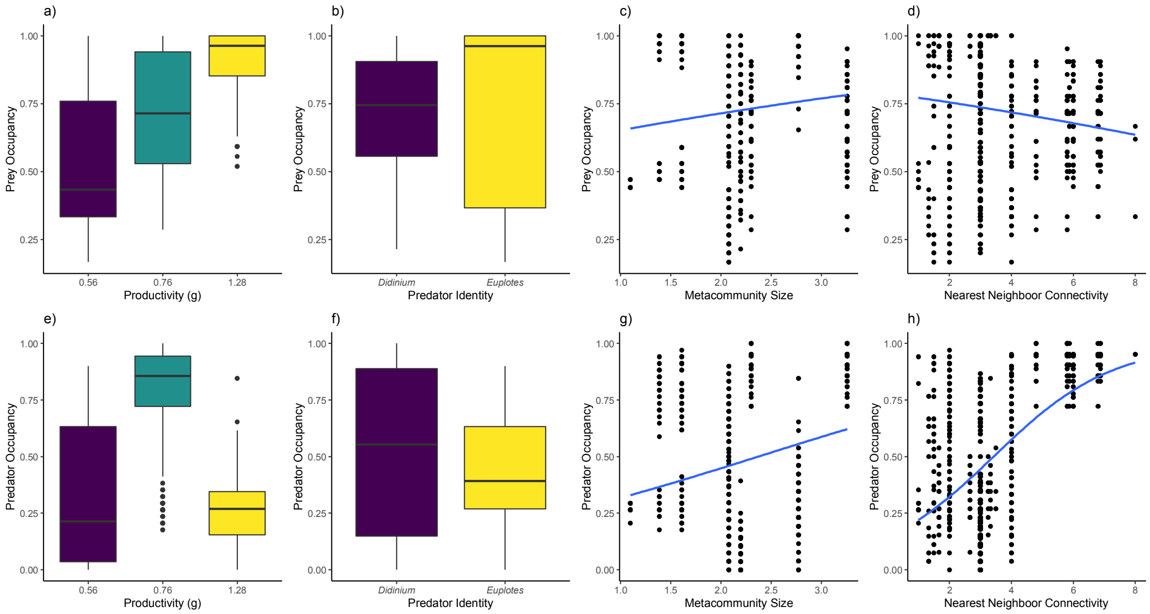

Figure 1.3: Local occupancy dynamics for prey (a-d) and predator (e-h) species as a function of productivity (a, e), predator identity (b, f), metacommunity size (c, g), and connectivity (d, h). Best fit lines are shown are plotted as GLMs for individual predictor variables.

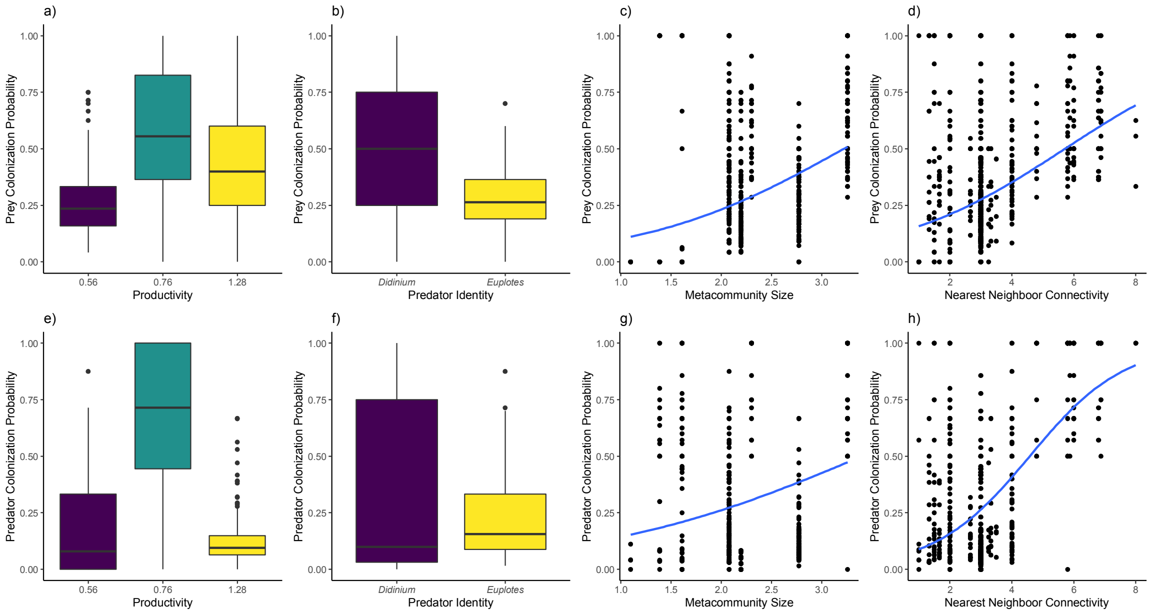

Figure 1.4: Colonization probabilities at the local scale of prey (a-d) predator (e-h) species as a function of productivity (a, e), predator identity (b, f), metacommunity size (c, g), and connectivity (d, h). Best fit lines are shown as GLMs for individual predictor variables.

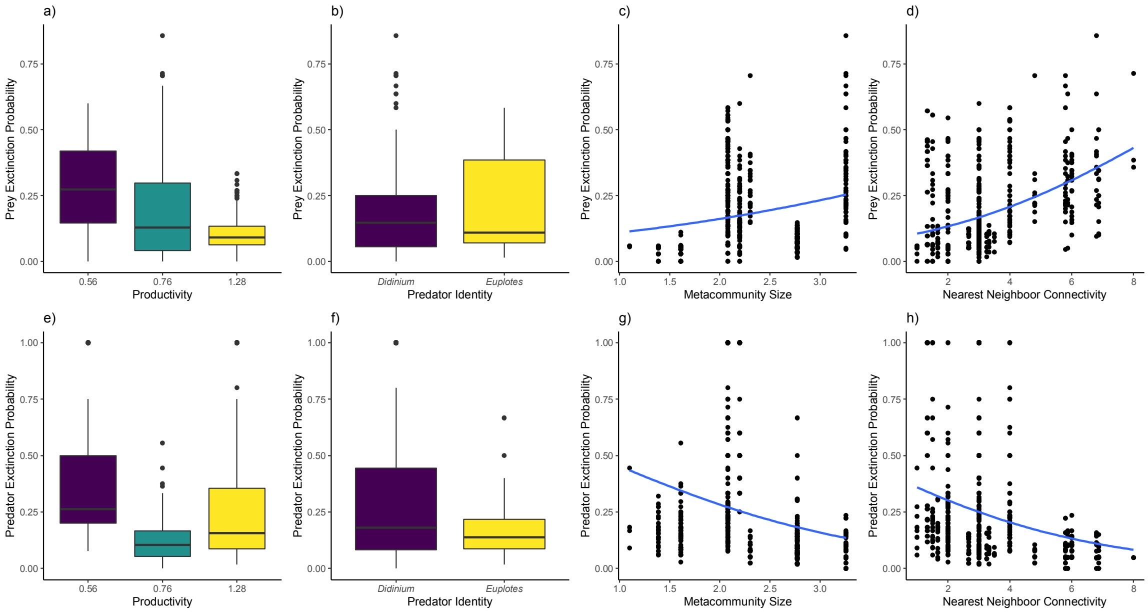

Figure 1.5: Extinction probabilities at the local scale of prey (a-d) predator (e-h) species as a function of productivity (a, e), predator identity (b, f), metacommunity size (c, g), and connectivity (d, h). Best fit lines are shown as GLMs for individual predictor variables.

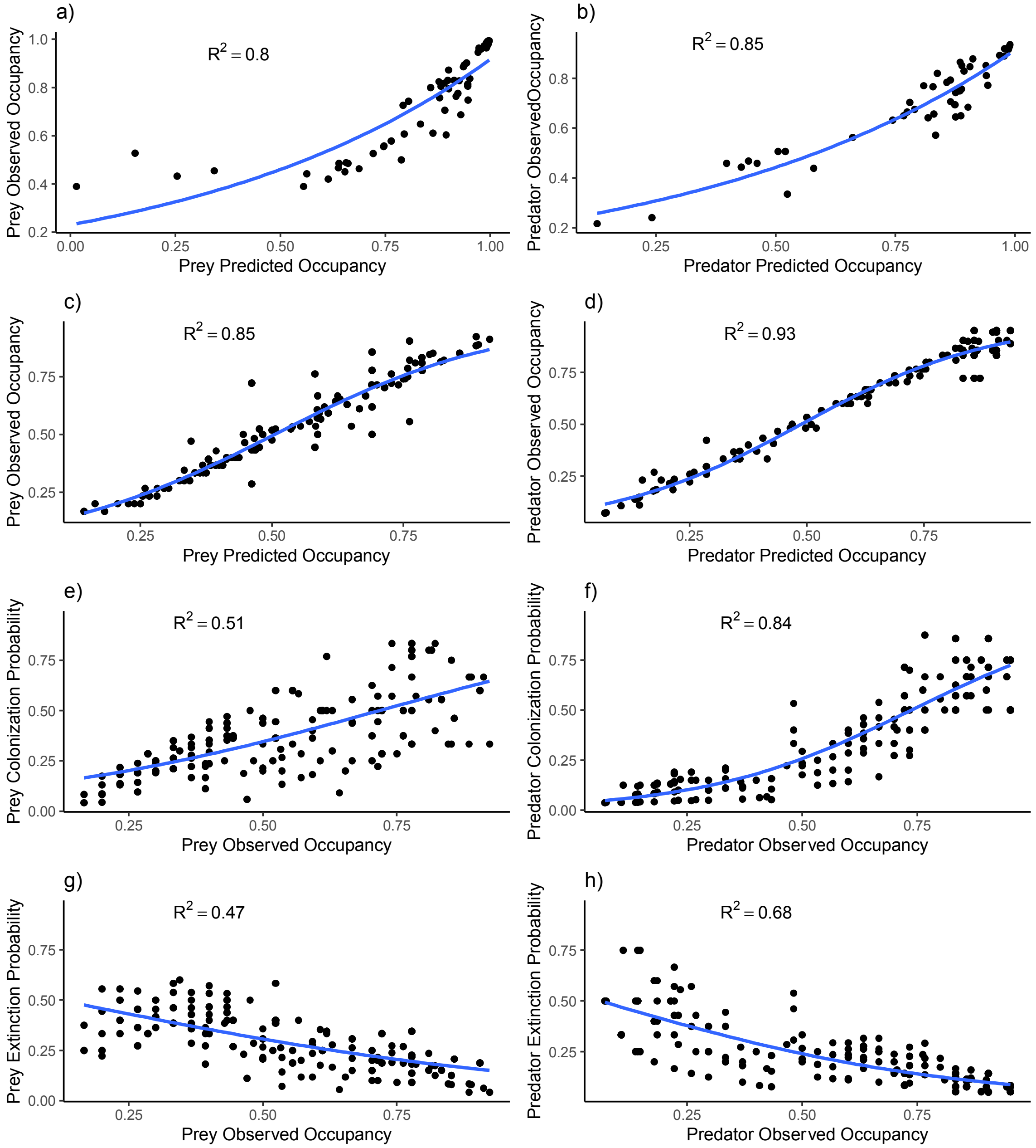

Figure 1.6: Drivers of occupancy, extinction, and colonization dynamics for predators and prey. Network wide observed occupancy patterns ${p^*}_N$ are strongly related to predicted prey (a) and predator (b) predicted occupancy patterns across spatial structures. Predator (c) and prey (d) observed occupancy at the local scale ${p^*}_B$ is also strongly related to predicted occupancy. Colonization probabilities by prey (e) and predator (f) of individual bottles show positive relationships with observed network wide occupancy. Extinction probabilities for prey (g) and predators (h) in individual bottles are negatively related to observed occupancies at the network level.

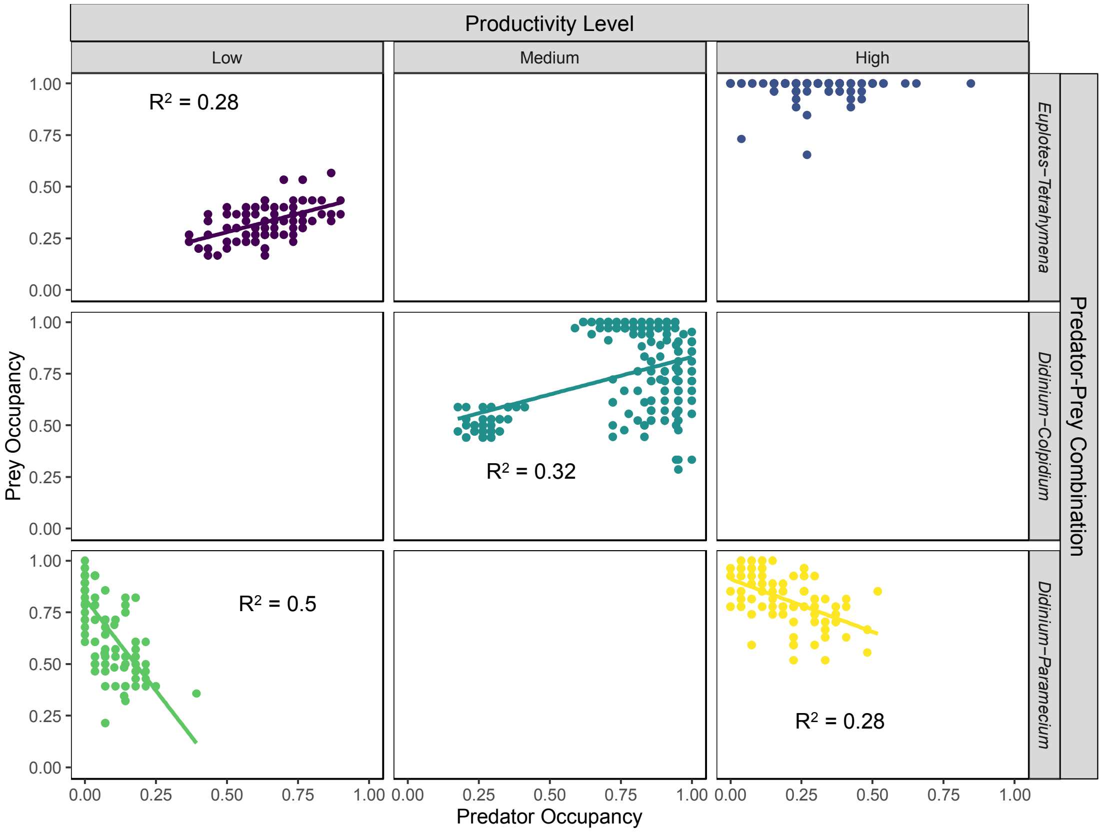

Figure 1.7: Predator-prey occupancy relationships as a function of productivity level (low, medium, and high) and predator-prey species combinations (*Euplotes-Tetrahymena*, *Didinium-Colpidium*, *Didinium-Paramecium*). Significant relationships are shown with plotted regression lines and R^2 values.

Chapter 2: Rethinking Biodiversity Patterns and Processes in Stream Ecosystems

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Abstract

A major goal of community ecology is understanding the processes responsible for generating biodiversity patterns along spatial and environmental gradients. In stream ecosystems, system specific conceptual frameworks have dominated research describing biodiversity change along longitudinal gradients of river networks. However, support for these conceptual frameworks has been mixed, mainly applicable to specific stream ecosystems and biomes, and these frameworks have placed less emphasis on general mechanisms driving biodiversity patterns. Rethinking biodiversity patterns and processes in stream ecosystems with a focus on the overarching mechanisms common across ecosystems will provide a more holistic understanding of why biodiversity patterns vary along river networks. In this study, we apply the Theory of Ecological Communities (TEC) conceptual framework to stream ecosystems to focus explicitly on the core ecological processes structuring communities: dispersal, speciation, niche selection, and ecological drift. Using a unique case study from high elevation networks of connected lakes and streams, we sampled stream invertebrate communities in the Sierra Nevada, CA to test established stream ecology frameworks and compared them to the TEC framework. Local diversity increased and β-diversity decreased moving downstream from the headwaters, consistent with the *river continuum concept* and the *small but mighty* framework of mountain stream biodiversity. Local diversity was also structured by distance below upstream lakes, where diversity increased with distance below upstream lakes, in support of the *serial discontinuity concept*. Despite some support for the biodiversity patterns predicted from the stream ecology frameworks, no single framework was fully supported, suggesting “context dependence”. By framing our results under the TEC, we found species diversity was structured by niche selection, where local diversity was highest in environmentally favorable sites. Local diversity was also highest in sites with small community sizes, countering predicted effects of ecological drift. Moreover, higher β-diversity in the headwaters was influenced by dispersal and niche selection, where environmentally harsh and spatially isolated sites exhibit higher community variation. Taken together our results suggest that combining system specific ecological frameworks with the TEC provides a powerful approach for inferring the mechanisms driving biodiversity patterns and provides a path toward generalization of biodiversity research across ecosystems.

Introduction

A major goal of community ecology is to generalize the processes responsible for generating variation in biodiversity along spatial and environmental gradients. Recent syntheses in community ecology propose that four major processes structure biodiversity: dispersal (the movement of individuals through space), speciation (the formation of new species), niche selection (changes in species relative abundances owing to abiotic and biotic conditions that give rise to deterministic fitness differences between species), and ecological drift (changes in species relative abundances that are random with respect to species identities) (Vellend 2010; 2016; Leibold and Chase 2018; Leibold et al. 2020). Syntheses based around these four mechanisms are collectively known as the Theory of

Ecological Communities (TEC; Vellend 2010, 2016), which has been demonstrated as a useful approach to for linking patterns in biodiversity with processes (Siqueira et al. 2020; Leibold et al. 2020). Importantly, ecologists are now faced with the task of generalizing the TEC framework by disentangling the relative importance of the four constituent processes in structuring communities (J. M. Chase and Myers 2011) and linking these four processes to system specific frameworks of community assembly.

Special attention has been devoted to the ecology of stream communities due to their directional connectivity and strong environmental gradients that influence patterns of biodiversity (Brown and Swan 2010; Carrara et al. 2012). Indeed, much of the generation and maintenance of biodiversity in stream ecosystems is thought to be driven by their inherent spatial structure (Townsend 1989; Tedesco et al. 2012; Dias et al. 2014; Oberdorff et al. 2019). As a result, stream ecology has a long history of system specific frameworks for explaining biodiversity responses to environmental gradients. However, support for these frameworks has been largely context dependent and difficult to generalize. One potential reason for the lack of transferability is that assembly mechanisms can shift in importance either in different spatial locations within a stream and/or across stream ecosystem types (Brown and Swan 2010), which are not consistently accounted for in established stream ecology frameworks. In addition, stream ecology frameworks emphasize different ecological processes and scales of diversity responses, without accounting for all community assembly processes and scales of diversity (Table 2.1). Here, we review three major conceptual frameworks in freshwater ecology describing biodiversity patterns and then integrate these frameworks with the TEC framework to disentangle the processes structuring diversity.

Biodiversity Frameworks in Stream Ecology

Perhaps one of the most well-known and longstanding conceptual frameworks in stream biodiversity is the *river continuum concept* (RCC; Doretto et al. 2020). The RCC describes a linear view of streams, where the change in physical stream characteristics from headwaters longitudinally to mainstems drives a unimodal distribution of local diversity, with a peak diversity in mid-order stream reaches (Vannote et al. 1980). Because small streams (i.e., 1st-4th order) have been studied more extensively, the upper half of this unimodal biodiversity response predicts a pattern of increasing local (α) diversity moving downstream from the headwaters (Fig. 2.1a; Finn et al. 2011). Despite the majority of studies finding positive relationships between local diversity and downstream distance, many studies found the opposite or no patterns at all, calling into question the generality of the RCC (see Vorste et al. 2017 for a full review). Importantly, the RCC focuses on how niche selection influences local community diversity, without accounting for the role of dispersal, speciation, or ecological drift in determining local diversity, or how all four processes influence beta (β) diversity (spatial variation in biodiversity among communities within a region) and gamma (γ) diversity (regional variation in biodiversity) (Table 2.1).

In order to understand how species composition changes spatially, Finn et al. (2011) proposed the *mighty headwaters hypothesis* (MHH), which posits that β-diversity should be highest in headwaters and decrease moving downstream, showing an inverse relationship with local diversity (see also Brown and Swan 2010, Carrara et al. 2012, Schmera et al. 2018; Fig. 2.1a). Due to the spatially isolated nature of headwaters, high environmental heterogeneity among headwaters, and their abundance relative to the total stream length, headwaters are hypothesized to contribute strongly to overall γ-diversity through high β-diversity. Evidence for the MHH is mixed, with evidence for higher β-diversity in headwaters (Clarke et al. 2008; Finn et al. 2011; Jamoneau et al. 2018), humped shaped patterns of β-diversity (Wang et al. 2020), and no pattern (Harrington, Poff, and Kondratieff 2016; Tonkin et al. 2016). The MHH posits that dispersal and niche selection influence β-diversity (Table 2.1; Finn et al. 2011) and there is empirical support that dispersal and niche selection (Brown and Swan 2010; Schmera et al. 2018) as well as ecological drift resulting from small community sizes (Siqueira et al. 2020) influence β-diversity in stream ecosystems.

In contrast to traditionally studied perennial streams, many streams throughout the world flow intermittently or have damns, natural lakes, or impoundments that modify connections between upstream and downstream communities. The *serial discontinuity concept* (SDC) describes the effects of dams on downstream ecosystems and predicts that local diversity increases with distance below upstream dams due to the dams' disturbance of environmental conditions (Fig. 2.1b; Ward and Stanford 1983). The few empirical tests of the SDC lend support to the concept (Voelz and Ward 1991; Lucy Eunsun Ellis and Jones 2013; L. E. Ellis and Jones 2016; Mwedzi et al. 2016; Guzy et al. 2018), but longitudinal diversity studies downstream from lakes are still rare. In this paper, we extend the SDC to understand how lakes influence community variability. Lake-outlet communities, those closest downstream of lakes, are dominated by filter feeding species with low species richness and low turnover (Richardson and Mackay 1991). These communities are replaced by more typical stream communities increasingly downstream (Robinson and Minshall 1990), therefore increasing community turnover with distance downstream. Once this community resembles a more typical stream community, β-diversity should decrease. We predict that β-diversity should show a unimodal relationship moving downstream from lakes, with peak β-diversity midway downstream from lakes (Fig. 2.1b). The SDC focuses on how dispersal and niche selection drive local community diversity and now through this paper, community variability (Table 2.1).

A challenge to generalizing the RCC, MHH, and SDC is that, across biomes and stream types, lotic systems vary contextually along their longitudinal range from the headwaters to mainstems. For example, headwaters in deciduous biomes present more favorable environmental conditions with high inputs of allochthonous materials, and greater nutrient availability in comparison to downstream sites (Vannote et al. 1980). In alpine streams, environmental conditions are typically harshest in headwaters, where headwater sites have low temperatures, shorter growing seasons, and are spatially isolated from mainstem and downstream dispersal pathways (Hotaling et al. 2017). Further, in streams with discontinuities (i.e., intermittency, lakes, or dams), environmental gradients do not necessarily change continuously with distance downstream. In intermittent streams, headwater segments vary both spatially and temporally in habitat area and spatial connectivity, and have dynamic changes in water chemistry and nutrient dynamics in response to water availability (Datry et al. 2017; Gómez et al. 2017; von Schiller et al. 2017; Herbst et al. 2019). Thus, longitudinal variation may vary too much across stream biomes to be generalizable, which requires new conceptual frameworks for mechanistically understanding drivers of biodiversity.

Applying the Theory of Ecological Communities Framework

Because the RCC, MHH, and SDC all predict biodiversity to change along spatial and environmental gradients, we aim to shift the focus of stream ecology towards more integrative analyses of spatial and environmental gradients that can apply across river ecosystem types and link diversity patterns to general community assembly processes. The theory of ecological communities (TEC) lays out four core ecological processes structuring communities. Here, we outline how dispersal, speciation, niche selection, and ecological drift (Vellend 2010; 2016) give rise to observed patterns of biodiversity in stream ecosystems. In our case study, we leave out speciation as a process in our analysis because of the spatial and temporal scope of our study (Vellend 2016), and the similarity of the regional pool and historical events shaping our study region, the Sierra Nevada Mountains, CA (Mazor et al. 2016).

Dispersal is notoriously difficult to measure and ecologist rely on proxies for dispersal such as spatial gradients of isolation and connectivity (Vellend 2016). In stream ecosystems, spatial gradients may include variables such as elevation, stream size, distance below lakes, and distance from headwaters, among others. Species diversity is predicted to increase with increasing dispersal or spatial connectivity (MacArthur and

Wilson 1967; Vellend 2016), although this relationship has also been shown theoretically (Mouquet and Loreau 2003) and empirically (Cadotte 2006) to be hump shaped with diversity maximized at intermediate rates of dispersal. In this paper, we focus on the linear relationship as the majority of observations occur in the range where the relationship is positive (Cadotte 2006; Myers and Harms 2009). Compositional dissimilarity is predicted to decrease with increasing dispersal due to mixing (Fig 2a; Hubbell 2001, Mouquet and Loreau 2003).

Species are added to the regional species pool not only by dispersal, but also by speciation (Ricklefs 1987; Vellend 2016). Speciation can drive local community structure even at small spatial scales, especially when local diversity is limited by the number of species in the regional pool that have evolved to persist under particular environmental conditions (Vellend 2016). If speciation is driving variation in community structure, both local diversity and β-diversity should increase with increasing regional pool size (Fig. 2.2b; Cornell 1985, Srivastava 1999, Chase 2003, Kraft et al. 2011, Cornell and Harrison 2014). Importantly, local scale processes (competition, niche partitioning) can also create opportunities for speciation over longer time scales (Mittelbach and Schemske 2015).

Environmental gradients have a long history in ecology to explain local control of community structure, hereafter referred to as niche selection. In stream ecosystems, environmental gradients should include relevant environmental variables that stream biota respond to such as water chemistry, light and nutrient availability, substrate composition, and other habitat and landscape characteristics. If niche selection and species sorting is driving diversity patterns, local diversity should increase, and β-diversity should decrease with increasing environmental favorability (Fig. 2.2c; Chase and Leibold 2003, Chase and Myers 2011).

Lastly, community structure can be altered by ecological drift, primarily when communities have low species richness and small community sizes. We define community size as the density (individuals/m^2) within local communities (Orrock and Watling 2010). If ecological drift is important, local diversity should increase and community dissimilarity should decrease with increasing community size (Fig. 2.2d) through mechanisms such as neutral dynamics and demographic stochasticity (Hubbell 2001). We use community size as a proxy for ecological drift potential, because small communities have few individuals per unit area and thus random birth and death events are more likely to alter community composition (Orrock and Watling 2010; Siqueira et al. 2020).

Case Study in Alpine Lake-Stream Networks

Here, we explored predictions from stream ecology frameworks and from the TEC framework (Table 2.1) using landscape biodiversity patterns from macroinvertebrate stream communities across a series of high elevation lake-stream networks in Sierra Nevada, CA. Lake-stream networks (also referred to as stream-lake networks), a series of lakes connected by streams, provide a spatially explicit landscape for studying ecological patterns across spatial scales and ecosystems (Jones 2010; Baker et al. 2016). In lakes, landscape limnologists have demonstrated the importance of landscape position, or the sequential spatial position in lake-chains (Soranno et al. 1999), and landscape cover on biogeochemistry, bacteria diversity, and ecosystem functioning (Soranno 1999; Nelson, Sadro, and Melack 2009; Sadro, Nelson, and Melack 2012). Stream ecology perspectives in lake-stream networks have been limited to local effects of lakes on downstream communities, where these lake outlet communities are dominated by filter feeding assemblages (Richardson and Mackay 1991). Landscape biodiversity patterns in lake-stream networks are poorly understood due to lack of available data, but can provide important insights into how biodiversity is structured across connected ecosystems and spatial scales.

In this study, we sought to understand the processes responsible for generating patterns of α- and β-diversity in stream macroinvertebrate in connected alpine lake-stream networks located in the Sierra Nevada, CA. We first tested the predictions from stream ecology theories, (e.g., RCC, MHH, and SDC) in lake-stream networks and then integrate these perspectives with the TEC framework to understand the processes structuring biodiversity patterns. We tested predictions from stream ecology frameworks by analyzing biodiversity patterns as a function of distance downstream from the headwaters, distance below upstream lakes, and the interaction between the two spatial gradients as multiple ecological gradients can simultaneously structure biodiversity (Fig. 2.1). To test the influence of the core ecological processes structuring biodiversity, we analyzed the relationships between dispersal connectivity, environmental variability, community size, and all pairwise interactions among these variables, as multiple ecological processes can structure biodiversity (Fig. 2.2).

Methods

Study Area. The study area was located in the Sierra Nevada Mountains of eastern California (USA) and encompasses portions of Inyo National Forest and Sequoia-Kings Canyon National Park. Over the ice-free seasons (June-September), we sampled five distinct lake-stream networks, where each network was within a spatially distinct catchment and were treated as independent replicate systems (Fig. 2.3). The Kern (n=24) and Bubbs (n=26) networks were sampled in 2011, the Evolution (n=21) and Cascades (n=11) networks in 2018, and Rock Creek (n=36) in 2019. For each lake-stream network, streams were sampled throughout the network along a spatial gradient from headwaters downstream as well as along a spatial gradient downstream from lakes. Because the spatial distances of the river networks and the distance separating lakes naturally vary among networks as well as backcountry sampling constraints, the number of sites sampled along the distance from headwaters gradient varied (n=11 to n=36) and the downstream lake gradient varied (n=1 to n=9). This field system and the data collected naturally provide spatial gradients relevant to test stream ecology theories. In addition, this data is ideal for testing TEC processes because of the naturally varying gradients of community size, connectivity, and environmental heterogeneity present in our sampling design.

Field Methods. At each sampling location, we established transects in riffle sections of streams. At five equally spaced points along transects we measured stream depth and current velocity at mid-depth using a portable flow meter (Marsh-McBirney Flow Mate

2000). We then calculated stream discharge as the sum of the product of average depth x current velocity x width/5 over all transect points (Gordon et al. 2010; Herbst et al. 2018). A calibrated YSI multiparameter device was placed above transects to measure temperature, dissolved oxygen, conductivity, and pH. Benthic chlorophyll data was collected by scrubbing the entire surface area of three randomly selected cobble sized rocks (64-255 mm) of benthic algae (periphyton) with a toothbrush for 60 seconds (Herbst and Cooper 2010). Chlorophyll measurements were taken using a handheld fluorometer (Turner Designs Aquafluor), which measures raw fluorescence units. Florescent measurements were calibrated to chlorophyll concentration using a known concentration of Rhodamine. We standardized chlorophyll measurements by accounting for both the surface area of rocks and volume of water used to remove algae.

Eight to twelve macroinvertebrate samples at each site were collected using a D-frame kick net (250 μm mesh, 30cm opening, 0.09m^2 sample area) in riffle habitats, depending on the density of macroinvertebrate samples collected. We took samples by placing the net on the streambed, then turning and brushing all substrate by hand in the sampling area (30cm x 30cm) immediately above the net, with dislodged invertebrates being carried by currents into the net. All macroinvertebrate samples were preserved in 75% ethanol within 48 hours of sampling. Samples were sorted, identified, and counted in the laboratory. Taxa were identified to the finest taxonomic level possible, usually to genus or species for insects (excluding Chironomidae) and order or class for non-insects (Merritt, Cummins, and Berg 2019). The replicate samples taken at each site were pooled together and divided by the number of replicates and the area sampled to determine the density of invertebrate communities.

Spatial Data. Stream distance measurements were taken using the R package “riverdist”, which utilizes data from the USGS National Hydrological Dataset Flowline in order to determine pairwise distances from sampling sites along the river network (Tyers 2020). We determined distance below upstream lakes, with the closest upstream lake location being the outlet of the lake determined by the USGS Watershed Boundary Dataset. For sites where multiple upstream lakes were draining into streams, we defined the upstream lake as the closest upstream lake to sites that was also along the mainstem of the flowline. We determined distance from headwaters as the streamwise distance from sites to the uppermost portion (headwaters) of the mainstem of streams, where the headwaters of streams was determined by the endpoint (beginning) of the flowline in the USGS NHD Flowline Dataset (U.S. Geological Survey 2016). In cases where multiple headwater stream reaches corresponded to downstream sites, we defined the headwaters as the particular reach that accounted for the most discharge which was determined using USGS Flowline Dataset. Upstream lake area and perimeter measurements were determined using the USGS Watershed Boundary Dataset. Land-cover proportions were computed using the 2016 USGS National Land Cover Database (Jin et al. 2019).

Stream Ecology Frameworks Analysis. To test how macroinvertebrate community diversity is structured in lake-stream networks, we modeled community diversity metrics as a function of distance below upstream lakes (SDC) and distance from the headwaters (RCC and MHH) using generalized linear mixed models (GLMMs). For this analysis, we removed 5 sites that were in the headwaters, upstream to any of the lakes in our study system. We used species (Shannon) diversity to quantify α-diversity and local contribution to beta diversity (LCBD) to quantify β-diversity. We quantified Shannon diversity for each site using the exponential of the diversity function in the vegan package (Oksanen et al. 2019). LCBD was calculated using the “adespatial” package (Dray et al. 2020) for each network separately. LCBD quantifies the relative contribution of local sites to the total metacommunity diversity, and whether individual sites have a high contribution to overall β-diversity (Legendre and Cáceres 2013). We calculated the total beta diversity for each network (BD_{Total}) which was estimated as the variance of the Hellinger-transformed community data matrix, and was later decomposed into the relative contributions of individual sites, called LCBD (Legendre and Cáceres 2013). We regressed species diversity as a function of distance below upstream lakes to test the SDC and regressed species diversity as a function of distance from the headwaters to test the RCC (Fig. 2.1). We also regressed LCBD values against distance from the headwaters and distance below upstream lakes to test both the MHH, and the SDC, respectively (Fig. 2.1).

We fit GLMM’s using the “glmmTMB” package with Gaussian error distributions for local diversity and beta error distributions for LCBD to identify spatial drivers of local and beta diversity (M. E. Brooks et al. 2017). We verified that these response variables met all appropriate assumptions of these distributions prior to analyses. Multicollinearity was not an issue for this data analysis, as there was a low degree of correlation between the two spatial variables (r=0.19). We also used the "check_collinearity" function in the "performance" package to detect for multicollinearity by calculating variance inflation factors (VIF) of models, all of which were less than 1.31, where values of 1 indicate no correlation and values above 5 indicate high degrees of correlation (Lüdecke et al. 2021). We ran all models with the random effect of river network, a null model, two single factor models with either spatial predictor, and an interaction model with both spatial predictors. We used these spatial metrics and excluded the local environment as predictors for biodiversity to explicitly test stream ecology frameworks, which assume these spatial metrics are proxies for environmental and/or spatial processes. We used a model selection approach by assessing delta AIC of all models to determine best fit models via the "AICtab" function in the "bbmle" package (Bolker 2020).

Applied TEC Framework Analysis. To test how dispersal, niche selection, and ecological drift structure local diversity and β-diversity we applied the TEC framework (Fig. 2.2). We removed sites from this analysis where environmental data was missing or incomplete, dropping all Kern sites and 10 sites from the Bubbs network. Community diversity metrics were calculated in the same manner as previously described (*Methods: Stream Ecology Frameworks*).

To estimate the effect of dispersal, we used a spatial gradient ranging from spatially isolated to connected sites. We ran a principal components analysis (PCA) for each network separately on our spatial variables of elevation, streamwise distance from headwaters, streamwise distance below upstream lakes, and upstream lake area. Upstream lake area can strongly influence dispersal throughout a river network, as the majority of larval species may not be able to move through large and deep lakes (Bagge 1995; A. J. Brooks et al. 2017; Parisek 2018; Kurthen et al. 2020). Distance from headwaters, distance below upstream lakes, and elevation all loaded on the first PC axis which explained 60% of the spatial variation on average for all networks (Evo: 53%, Cascade: 66%, Bubbs: 45%, Rock: 75%) and described a gradient from spatially isolated sites, which were typically found high in the headwaters and close to larger, upstream lakes, to spatially connected sites, which were typically found downstream from the headwaters and downstream from lakes with smaller areas. (Appendix B: Table B.1, B.2).

To estimate the effect of niche selection, we used an environmental gradient ranging from environmentally favorable to environmentally harsh sites. We ran a principal components analysis (PCA) for each network separately on environmental variables of dissolved oxygen, chlorophyll, pH, temperature, discharge, conductivity, and land cover metrics. Dissolved oxygen, temperature, discharge, chlorophyll, and pH all loaded on the first PC axis which explained 40% on average for all networks (Evo: 30%, Cascade: 40%, Bubbs: 46%, Rock: 43%) of the environmental variation and described a gradient from environmentally harsh sites with low temperatures and low productivity to environmentally favorable sites with higher temperatures and productivity (Appendix B: Table B.3, B.4).

To estimate the effect of ecological drift on communities, we used community size as a proxy for the effect of ecological drift (Orrock and Watling 2010, Velland 2016, Siqueira et al. 2020). Community size was determined by the total community density in each stream site, calculated as the total number of individuals across all species per unit area (individuals/m^2). We transformed this metric by taking the logarithm of community size to meet assumptions of normality and homogeneity of variances.

In order to test the importance of dispersal, niche selection, and ecological drift on community diversity (α-diversity and β-diversity), we ran GLMMs to understand individual and interactive effects of these processes. We ran all models with the random effect of river network, a null model, all single factor models, all possible two-way interaction models, and left out three-way interactions due to the difficulty in interpreting three-way interaction models. We used a model selection approach in the same manner as previously described (*Methods: Stream Ecology Frameworks*). Multicollinearity was not an issue for this TEC analysis. Although, there was a moderate degree of correlation between the Dispersal and Environmental gradients (r=0.47), we had low degrees of correlation between the Environmental and Drift gradient (r=0.13), as well as between the Dispersal and Drift gradients (r=0.09). We also used the "check_collinearity" function in the "performance" package to detect for multicollinearity by calculating VIF of models, all of which were less than 1.45 (Lüdecke et al. 2021). All analyses and data visualizations were carried out using R version 4.0.2 (R Development Core Team 2021).

Results

Species Diversity. The regional (γ) diversity of stream macroinvertebrates from this study was 140 taxa. Among lake-stream networks, species richness varied where the Bubbs Lakes Network (Bubbs) had 88 taxa, the Cascade Lakes Network (Cascade) had 47 taxa, the Evolution Lakes Network (Evo) had 39 taxa, the Kern Lake Network (Kern) had 56 taxa, and the Rock Creek Lakes Network (Rock) had 67 taxa. Overall, total beta diversity (BD_{Total}) varied among the four networks, where the Kern watershed had the highest β-diversity (BD_{Total}= 0.70), followed by Bubbs (BD_{Total}= 0.63), Evo (BD_{Total}= 0.55), Cascade (BD_{Total}= 0.55), and lastly, β-diversity was lowest in the Rock Creek watershed (BD_{Total}= 0.52).

Biodiversity Patterns Predicted from Stream Ecology Frameworks. Model selection favored the model that local diversity was structured interactively by distance from the headwaters and distance from upstream lakes, where local species diversity was lowest in the headwaters and increased moving downstream, but only when those downstream sites were not close to upstream lakes (weight=0.91, ΔAIC=0, Fig. 2.4e, Table 2.2). In sites that were downstream from the headwaters, but close to upstream lakes, that pattern disappeared. Model selection provided moderate support that local species diversity increased solely with distance below upstream lakes (weight=0.09, ΔAIC=4.6, Fig. 2.4a, Table 2.2) and little to no support with the effect of headwater distance alone (weight=0.0017, ΔAIC=12.6, Fig. 2.4c, Table 2.2).

Model selection strongly favored the model that β-diversity was structured interactively by distance from the headwaters and distance from upstream lakes, where β-diversity was highest in the headwaters but only when headwater sites were not close to upstream lakes. In headwater sites that were close to upstream lakes, that pattern disappeared, and beta diversity decreased (weight= 0.99, ΔAIC=0, Fig. 2.4f, Table 2.2). Model selection provided less support that β-diversity was highest in headwaters and declined moving downstream (weight=0.0021, ΔAIC=12.3, Fig. 2.4d, Table 2.2).

Biodiversity Patterns and Processes from Applied TEC Framework. Model selection determined that local diversity was structured interactively along the environmental and community size gradients (weight=1, ΔAIC=0, Fig. 2.5a, Table 2.3). Local community diversity increased with environmental favorability and small community sizes as well as in environmentally harsh sites with large community sizes. In environmentally harsh sites with small community sizes and in sites with environmentally favorable conditions and large community sizes, local diversity was low (weight=1, ΔAIC=0, Fig. 2.5a, Table 2.3). All other models of local diversity had low degrees of support (weight= <0.001; Fig. 2.5; Table 2.3).

The best performing model for β-diversity showed that community variability was structured interactively along the spatial and environmental gradients, where community dissimilarity was highest in spatially isolated and environmentally harsh sites and decreased with environmental favorability and spatial connectivity (weight=0.98, ΔAIC=0, Fig. 2.6e, Table 2.3). All other models of β-diversity had low degrees of support (weight = <0.01; Fig. 2.6; Table 2.3).

Discussion

Our study of stream communities in alpine lake-stream networks highlights how multiple ecological processes simultaneously structure biodiversity. By combining established stream ecology frameworks with the Theory of Ecological Communities (TEC) we were able to better elucidate the processes structuring biodiversity patterns. Specifically, we showed how the mechanisms hypothesized by stream ecology frameworks to structure diversity were only partially supported and in other cases found no support (Table 2.4). We found that local diversity increased with distance below upstream lakes and with distance from the headwaters, in support of the SDC and RCC, respectively, but that niche selection was not solely responsible for driving these patterns. Over larger scales, we found that headwaters promote increased β-diversity in stream invertebrate communities, supporting the MHH and as found in many well-studied biomes. β-diversity was also structured by the interaction between the two spatial gradients, where β-diversity is highest in the headwaters and downstream from lakes.

Despite support for the predicted biodiversity patterns from the RCC, MHH, and SDC, the mechanisms hypothesized to structure biodiversity by each framework were only partially supported. Overall, niche selection and ecological drift were the primary ecological processes influencing local community structure, indicating local diversity patterns are largely explained by a combination of local environmental filtering and changes in species relative abundances that are random with respect to species identities. These processes driving local diversity are consistent with patterns posited in the RCC and SDC, because local diversity was highest in environmentally favorable sites, which are typically downstream from the headwaters, and sites with small community size, which are found further downstream from the highly subsidized sites near lake outflows (Appendix B: Fig. B.1). However, local diversity was highest in sites with small community sizes, countering predicted effects of ecological drift. High β-diversity in the headwaters is primarily influenced by dispersal and niche selection, as higher community variation was seen in these more spatially isolated and environmentally harsher sites. In sites that were spatially connected and environmentally favorable, which tended to be downstream from the headwaters and downstream from upstream lakes, β-diversity was lowest. Moreover, we also found support for the MHH mechanisms, that dispersal and niche selection structure β-diversity. Thus, our results highlight the challenge of using individual stream ecology frameworks as none are fully supported and leaving our only option to invoke “context dependency”. Instead by focusing on the TEC, we are agnostic to the limitations of any one framework allowing for a broader focus on mechanisms (speciation, dispersal, ecological drift, niche selection) which can lead to greater generalization. We further discuss the role of each TEC process in structuring biodiversity patterns in relation to the stream ecology frameworks.

Dispersal

Contrary to our prediction that local diversity should increases with increasing spatial connectivity (Fig. 2.2a), dispersal was not the primary process structuring local diversity in our study. The pattern of local diversity increasing with dispersal is widely supported (MacArthur and Wilson 1967; Cadotte 2006; Kalmar and Currie 2006), although there are studies that show a hump-shaped relationships (Mouquet and Loreau 2003; Cadotte 2006) and where dispersal had no effect (Warren 1996; Shurin 2000). Our study occurred at the landscape scale and this scale may not fully capture the dispersal and local diversity relationship as strongly as studies measuring this relationship at larger scales (Jonathan M. Chase et al. 2018). The spatial gradient we used to test dispersal is a proxy, being a representation of spatial connectivity and isolation that is commonly used, but future experimental studies are needed to directly manipulate dispersal and test its effects with this framework. Further, we aimed to sample linearly along the river network gradient rather than focusing our sampling design on the dendritic branching network, where spatial connectivity may play a stronger role in structuring local diversity (Clarke et al. 2008; Brown and Swan 2010). In addition, incorporating further metrics such as overland distance metrics and dispersal traits may provide more support in explaining the influence of dispersal (Brown and Swan 2010; Tonkin et al. 2018). Lastly, local species richness in areas of low diversity may not be limited by dispersal, but processes occurring at smaller scales such as niche selection and ecological drift.

At larger spatial scales, dispersal influenced β-diversity, where β-diversity was highest in spatially isolated areas and decreased with increasing spatial connectivity. This supports the MHH and associated mechanisms that dispersal limitation influences these patterns, as some species may not be able to reach suitable habitat. Dispersal is influenced by the branching organization of river networks, with varying connectivity and dispersal between sites depending on their position along the network (Tonkin et al. 2018). Headwater reaches are more isolated than downstream due to their small size, isolation in the network, and directional dispersal downstream, making headwaters potentially less open to the arrival of new individuals (Brown and Swan 2010).

We did not find evidence that lakes alone influence β-diversity, contrary to our predictions from the SDC. In the lake-stream networks we studied, β-diversity was not structured by lake distance alone, but lakes influenced β-diversity in concert with the headwater gradient, potentially by creating spatial barriers for the movement of stream invertebrates, especially in streams modified by larger, deeper lakes (A. J. Brooks et al. 2017; Parisek 2018). Other studies have shown upstream lakes influence dispersal and has been hypothesized to be important in allowing filter feeding communities near lake outlets to maintain their dominance (Richardson and Mackay 1991). Indeed, Simuliidae (Diptera) and filter feeding caddisfly species, which occur in high densities near lakes, have been observed flying upstream and subsequently ovipositing at lake outlets and on the edges of lakes (and reservoirs) close to outflows (Carlsson et al. 1977; Roger S. Wotton 1979). Downstream drift from lakes of early instars to lake outlets maybe the primary mechanism by which filter feeders persist at high densities in lake outlets and lake subsides of food resources allows these species to maintain high densities.

Niche Selection

Niche selection was an important process structuring local diversity. Local diversity was highest in environmentally favorable sites, typically found downstream from the headwaters and downstream from upstream lakes. The mechanisms the RCC and SDC posit structure diversity were only partially supported in our study. The RCC and SDC predicts local diversity to be highest as a result of niche selection, where maximum diel temperature variability and maximum stream metabolism occurs (Vannote et al. 1980; J. V. Ward and Stanford 1983). Although we did not directly quantify diel temperature variability and stream metabolism in our study, numerous studies show that diel temperature variability is lowest near lake outlets, as lakes buffer downstream temperatures, and increases moving downstream of lakes, consistent with the increase in diversity predicted by the SDC (J. V. Ward and Stanford 1983; Baker et al. 2016). Across the longitudinal range of streams, diel temperature variability has also been shown to increase moving downstream from the headwaters (Vannote et al. 1980; J. Ward 1994), but this relationship varies among stream ecosystem types and temporally (Fullerton et al. 2015; Steel, Sowder, and Peterson 2016).

The SDC and RCC predicted relationship between maximum stream metabolism and local diversity was not fully supported with our study. Maximum stream metabolism is hypothesized to increase moving downstream from the headwaters and because of lake influences, stream metabolism is also highest near lakes and decreases downstream of lakes (J. V. Ward and Stanford 1983; R. S. Wotton 1988; Mejia et al. 2018; Kaylor et al. 2019). High densities of filter feeding insects dominate habitats closest to lake outflows, where lakes provide allochthonous pulses of high-quality nutrients (Sheldon and Oswood 1977; Morin and Peters 1988). Moving downstream from lakes, as the lake influence decays and resource production is generated more autochthonously, stream organisms with different feeding strategies start to replace filter feeders. In this study, we show that filter feeders are not necessarily replaced by stream taxa moving downstream from lakes, but that densities of filter feeders decrease in relative abundance moving downstream (Appendix B: Fig. B.2). This change in compositional evenness, rather than simply increased richness, largely drove our observed diversity patterns. Why high stream metabolism near lake outlets leads to community dominance by filter feeders rather than high overall species diversity remains an open question (Cardinale, Nelson, and Palmer 2000; Jonathan M. Chase and Leibold 2002), although higher productivity could lead to a decrease in local diversity as predicted by unimodal productivity-diversity relationships (Tilman and Pacala 1993; Waide et al. 1999; Mittelbach et al. 2001). Also, the form and delivery of primary production, which may vary across and within networks, could allow some functional feeding groups to take advantage of high resource availability. Indeed, these patterns very well may apply across other ecosystems that are connected by spatial resource flows (i.e., metaecosystems; Massol et al. 2011).

Niche selection did account for a large proportion of β-diversity in our study, indicating environmental control over species turnover patterns. Indeed, strong environmental variation exists in lake-stream networks moving from the headwaters downstream, as well as from lake outlets downstream. Higher β-diversity in headwaters has been attributed to a multitude of factors including environmental filtering due to the harsh environmental conditions in support of the MHH (Brown and Swan 2010; Finn et al. 2011). When the environment structures communities, species sort into their preferred habitats based on classic ideas from niche theory and are thus primarily driven by local environmental factors (Jonathan M. Chase and Leibold 2003). This may be due to headwater sites acting as refugia from biotic interactions (i.e., predation, competition) and/or because headwater sites have high environmental variation even at small spatial scales (Clarke et al. 2008; Finn et al. 2011). Corroborating our findings, studies of headwater macroinvertebrate communities have found strong evidence for environmental control over community composition in headwaters (Brown and Swan 2010).

Ecological Drift

Unique to lake-stream networks, community size shows a negative relationship with local diversity, contrary to our predictions (Fig. 2.2d). Typically, communities with smaller size are more prone to ecological drift which drives lower local diversity patterns with smaller community size (Vellend 2016). However, in our case study, local diversity was highest in communities with small sizes and decreased with increasing community density (individuals/m^2). This effect appears to be driven by the spatial food resources provided by lakes, which creates a dominant filter feeding community with large community size and low local diversity. Moving downstream from lakes, community size decreased while local diversity increased, potentially because of the unimodal productivity-diversity relationship (see *Discussion: Niche Selection*). Dominance of prolific filter feeding taxa may prevent less competitive taxa from establishing in these areas. Although empirical studies of ecological drift are rare due to the difficulty in accurately measuring its effects, studies have found similar effects where species richness declines with smaller community size (Gilbert and Levine 2017) or habitat area (Vellend 2004). Further, we used community size as a proxy for ecological drift in line with TEC theory, however, community size may be a response to community diversity rather than community size determining biodiversity. Community size may not be an appropriate proxy for ecological drift and better metrics for community drift, null modeling, and experimental work are needed to build upon our findings and framework (Gilbert and Levine 2017; Siqueira et al. 2020).

In our system, β-diversity decreased with increasing community size and small community sizes were typically found closer to the headwaters and downstream of lakes. In other systems, ecological drift has been shown to strongly structure communities through community size effects on β-diversity (Orrock and Watling 2010), sometimes solely through drift with no effect of spatial or environmental structuring (Siqueira et al. 2020). Because we saw stronger signals of dispersal and niche selection structuring β-diversity, these processes may have overridden the influence of ecological drift. The MHH in its original formulation ignores the influence of ecological drift in driving β-diversity, where other studies have suggested small community size in headwater reaches and further downstream of lakes may play a stronger role in structuring smaller communities (Siqueira et al. 2020).

Conclusions and Future Research Directions

Our investigation revealed how applying the TEC framework can unravel the ecological processes structuring communities. Importantly, we show how combining system specific frameworks and generalizable ecological frameworks can reveal a mechanistic understanding of biodiversity patterns. Even in cases where we found support for predicted biodiversity patterns, the mechanistic reasons were not entirely supported, which was highlighted by the TEC analyses. We demonstrated in our case study that local species diversity is concentrated in downstream reaches of river networks and downstream reaches from lakes and this pattern was driven by niche selection, where local diversity was highest in environmentally favorable sites. Local diversity was also highest in sites with small community sizes, countering predicted effects of ecological drift. Further, β-diversity is higher in headwaters and decreased moving downstream, and this pattern is primarily maintained by niche selection and dispersal.

Critically, the TEC framework used in this case study ignores the process of speciation and an important aspect of niche selection, species interactions. We did not account for speciation in our case study, as our study was situated within a single regional species pool. However, recent research has suggested that speciation can influence community biodiversity even at small spatial scales, especially when local diversity is limited by the number of available species that can thrive under particular environmental conditions (Vellend 2016; Spasojevic et al. 2018; Patrick and Brown 2018; Catano et al. 2021). Future research comparing assembly processes among disjunct mountain ranges or ecosystem types will help elucidate the role of speciation on biodiversity. Efforts to incorporate species interactions into community assembly frameworks is ongoing and will provide a more complete understanding to the TEC and metacommunity ecology (Ovaskainen et al. 2017; Leibold et al. 2020). Further, understanding how specific sites and species are differentially structured by core ecological processes is a pressing need for community ecology moving forward (Leibold et al. 2020).

Alpine headwaters are important reservoirs for biodiversity and management efforts should be focused on these habitats, especially in light of climate driven hydrological changes to high elevation aquatic ecosystems (Hotaling et al. 2017). Despite calls from researchers to integrate research programs in lake-stream networks more holistically (Jones 2010; Baker et al. 2016), few studies have explicitly done so. Further research and integration across lentic and lotic perspectives is needed to understand biodiversity and ecosystem function within these systems to better manage them. In addition, comparisons of biodiversity patterns in lake-stream networks with those in stream networks without lakes could provide further insights into the effects of lakes on stream ecosystems. Lake-stream networks provide an excellent system and framework for managers to track ongoing changes to freshwater ecosystems, through their unique hierarchical spatial structure.

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Figure and Tables

Table 2.1: The four conceptual frameworks of stream ecology and theory of ecological communities in relation to the four core processes of community assembly and the scale of biodiversity responses each framework predicts. X indicates that a conceptual framework substantially considers a particular process or scale.

	Process				Scale		
Conceptual Framework	Dispersal	Speciation	Selection	Drift	Alpha	Beta	Gamma
River Continuum Concept (RCC)			X		X		
Mighty Headwaters Hypothesis (MHH)	X		X			X	
Serial Discontinuity Concept (SDC)	X		X		X	X	
Theory of Ecological Communities (TEC)	X	X	X	X	X	X	X

Table 2.2: Results from GLMMs between the random effects of network (1 | Net), log transformed river distance below upstream lakes (Lake.dist), river distance from headwaters (Head.dist), and the interaction between the two spatial metrics for two species diversity metrics (Shannon diversity and LCBD). Models are listed in order by delta AIC for each species diversity metric. Also included are the effective degrees of freedom (df) and the and the Akiake weights.

Species Diversity	Stream Ecology Framework	Model	ΔAIC	*df*	weight
Shannon Diversity	RCC*SDC	~Head.dist*Lake.dist+(1| Net)	0	6	0.907
	SDC	~Lake.dist+(1| Net)	4.6	4	0.0909
	RCC	~Head.dist+(1| Net)	12.6	4	0.0017
	Null	~1+(1| Net)	15.1	3	<0.001
LCBD	MHH*SDC	~Head.dist*Lake.dist+(1| Net)	0	6	0.9979
	MHH	~Head.dist+(1| Net)	12.3	4	0.0021
	SDC	~Lake.dist+(1| Net)	32.4	4	<0.001
	Null	~1+(1| Net)	36.7	3	<0.001

Table 2.3: Results from GLMMs between Shannon diversity and local contribution to β-diversity (LCBD) as a function of the random effects of network (1 | Net), spatial connectivity (Spatial), environmental favorability (Env), community size (Com.Size), and all pairwise interactions. Models are listed in order by delta AIC for each species diversity metric. Also included are the effective degrees of freedom (df) and the Akiake weights.

Species Diversity	TEC Processes	Model	ΔAIC	*df*	weight
Shannon Diversity	Selection*Drift	~Env*Com.Size+ (1| Net)	0	6	1
	Dispersal*Drift	~Spatial*Com.Size+ (1| Net)	14.3	6	<0.001
	Drift	~Com.Size+ (1| Net)	18.7	4	<0.001
	Dispersal	~Spatial+ (1| Net)	22.4	4	<0.001
	Dispersal*Selection	~Spatial*Env+ (1|Net)	25.2	6	<0.001
	Null	~1+ (1| Net)	25.4	3	<0.001
	Selection	~Env+ (1| Net)	27	4	<0.001
LCBD	Dispersal*Selection	~Spatial*Env+ (1| Net)	0	6	0.975
	Selection*Drift	~Env*Com.Size+ (1| Net)	9.3	6	0.009
	Dispersal*Drift	~Spatial*Com.Size+ (1| Net)	9.6	6	0.008
	Selection	~Env+ (1| Net)	10.5	4	0.005
	Dispersal	~Spatial+ (1| Net)	11.9	4	0.003
	Drift	~Com.Size+ (1| Net)	15.3	4	<0.001
	Null	~ 1+ (1| Net)	18.8	3	<0.001

Table 2.4: Summary of results from the Stream Ecology Frameworks Analysis and the Applied TEC Analysis. We show for each framework and process whether predictions were supported for patterns of biodiversity and why.

Conceptual Framework and TEC Processes	Shannon Diversity	β-diversity (LCBD)
River Continuum Concept	Partial support, diversity increases moving downstream from the headwaters, but not close to upstream lakes.	NA
Mighty Headwaters Hypothesis	NA	Yes, diversity decreases moving downstream from the headwaters, but not close to upstream lakes.
Serial Discontinuity Concept	Yes, diversity increases moving downstream from lakes and also moving downstream from the headwaters	No support for hump shaped pattern. Diversity increases moving downstream from lakes, but only in headwaters.
Drift	No, diversity decreases with community size alone. Diversity increases in environmentally harsh sites with large community sizes. Local diversity also increases in environmentally favorable sites with small community sizes.	Partial support, diversity decreases with community size, but only in environmentally harsh and spatially isolated sites.
Dispersal	Partial support, diversity increases with spatial connectivity, but only in sites with small community sizes.	Yes, diversity decreases with spatial connectivity, but only in environmentally harsh sites.
Selection	Partial support, diversity increases with environmental favorability, but in spatially connected sites with small community sizes.	Yes, diversity decreases with environmental favorability, but only in spatially isolated sites.

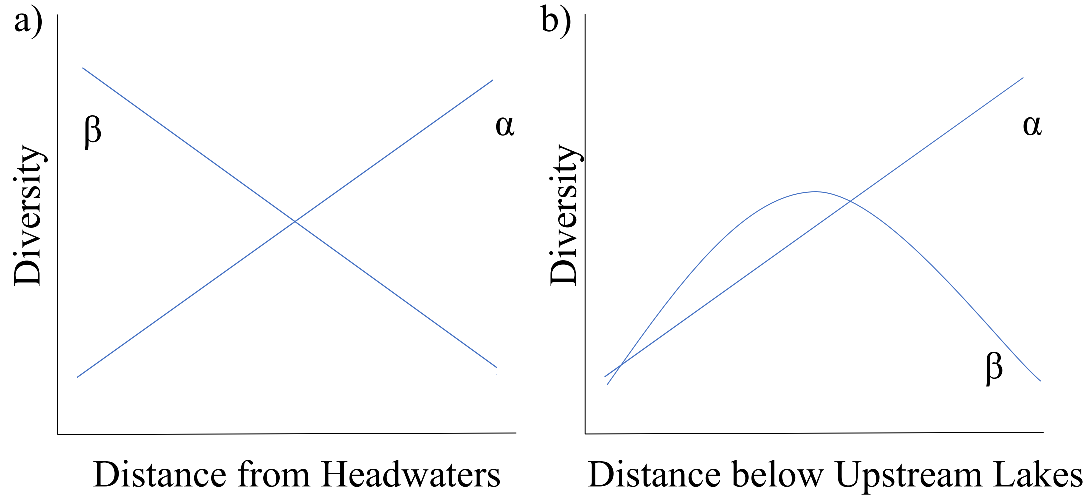

Figure 2.1: Hypothesized relationships for patterns of α and β diversity as a function of a) distance from the headwaters and b) distance below upstream lakes. a) The α-diversity pattern is predicted by the RCC and the β-diversity pattern is predicted by the MHH. b) The α-diversity pattern is predicted by the SDC and the β diversity pattern is a new prediction in this paper. Most of these relationships are presented linearly for simplicity, but the true nature of these relationships may vary among stream types.

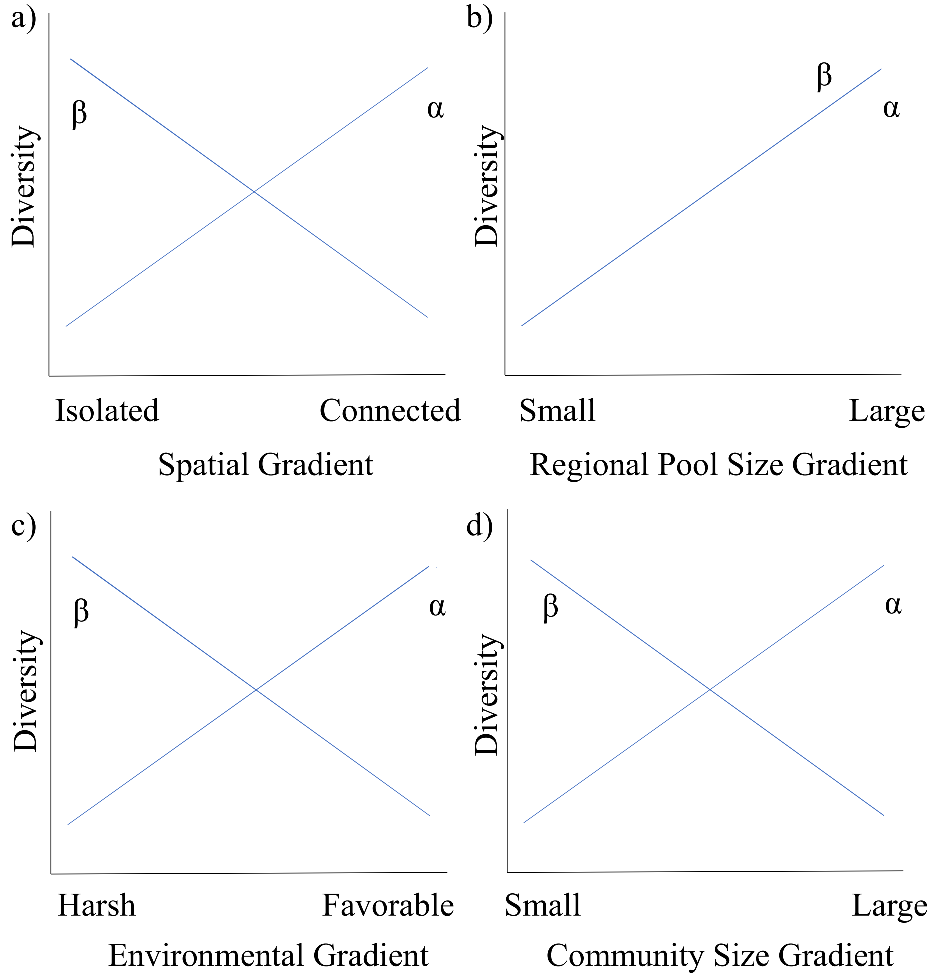

Figure 2.2: Conceptual framework incorporating ecological process from the theory of ecological communities (Vellend 2010; 2016). This framework highlights hypothesized relationships for patterns of α and β diversity along a) spatial, b) regional pool size, c) environmental, and d) community size gradients. This allows direct test of understanding the relative importance of ecological processes structuring communities. a) Species diversity patterns along spatial gradients of connectivity test hypotheses about the importance of dispersal. b) Species diversity patterns changing along regional pool size gradients to test hypotheses about speciation. c) Species diversity patterns changing along environmental gradients test hypotheses about niche selection. d) The effects of community size on influencing patterns of diversity would indicate the influence of ecological drift.

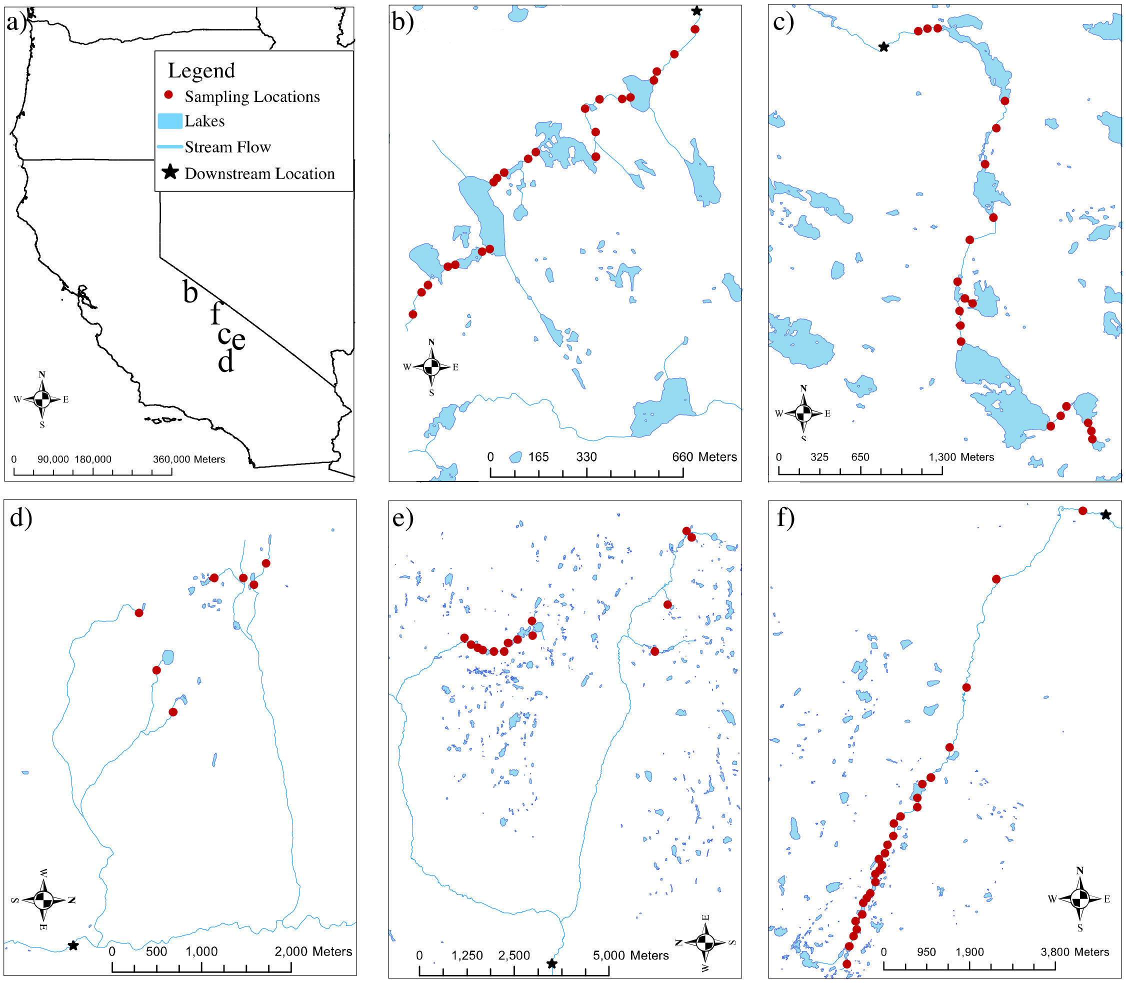

Figure 2.3: Distribution of field sampling sites in the Sierra Nevada, CA (a). Five lake-stream networks (b) Cascade Lake Network, (c) Evolution Lake Network, d) Kern Lake Network, (e) Bubbs Lake Network, and (f) Rock Creek Network were sampled across a spatial gradient from the headwaters moving downstream and a spatial gradient from lake outlets moving downstream.

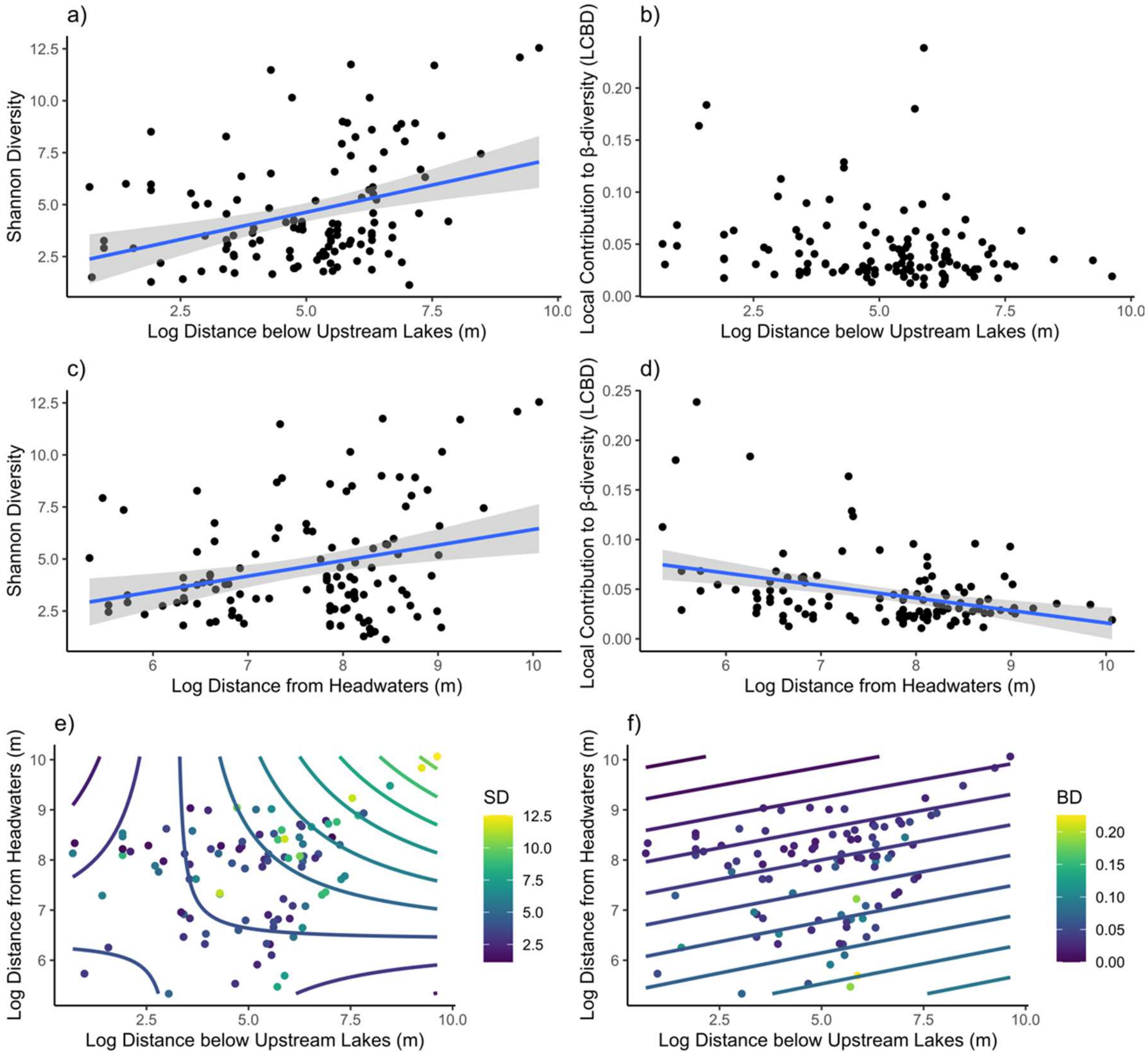

Figure 2.4: Shannon diversity (a, c, and e) and local contribution to β-diversity (b, d, and f) of stream macroinvertebrate communities as a function of log transformed distance below upstream lakes (a and b) or distance from headwaters (c and d) across five lake-stream networks. Interaction contour plots of Shannon diversity (SD; f) and local contribution to β-diversity (BD; f) of stream macroinvertebrate communities as a function of the interaction between log transformed distance below upstream lakes and distance from headwaters. Significant relationships are shown with plotted regression lines or contour lines. Full results from GLMMs are found in Table 2.2.

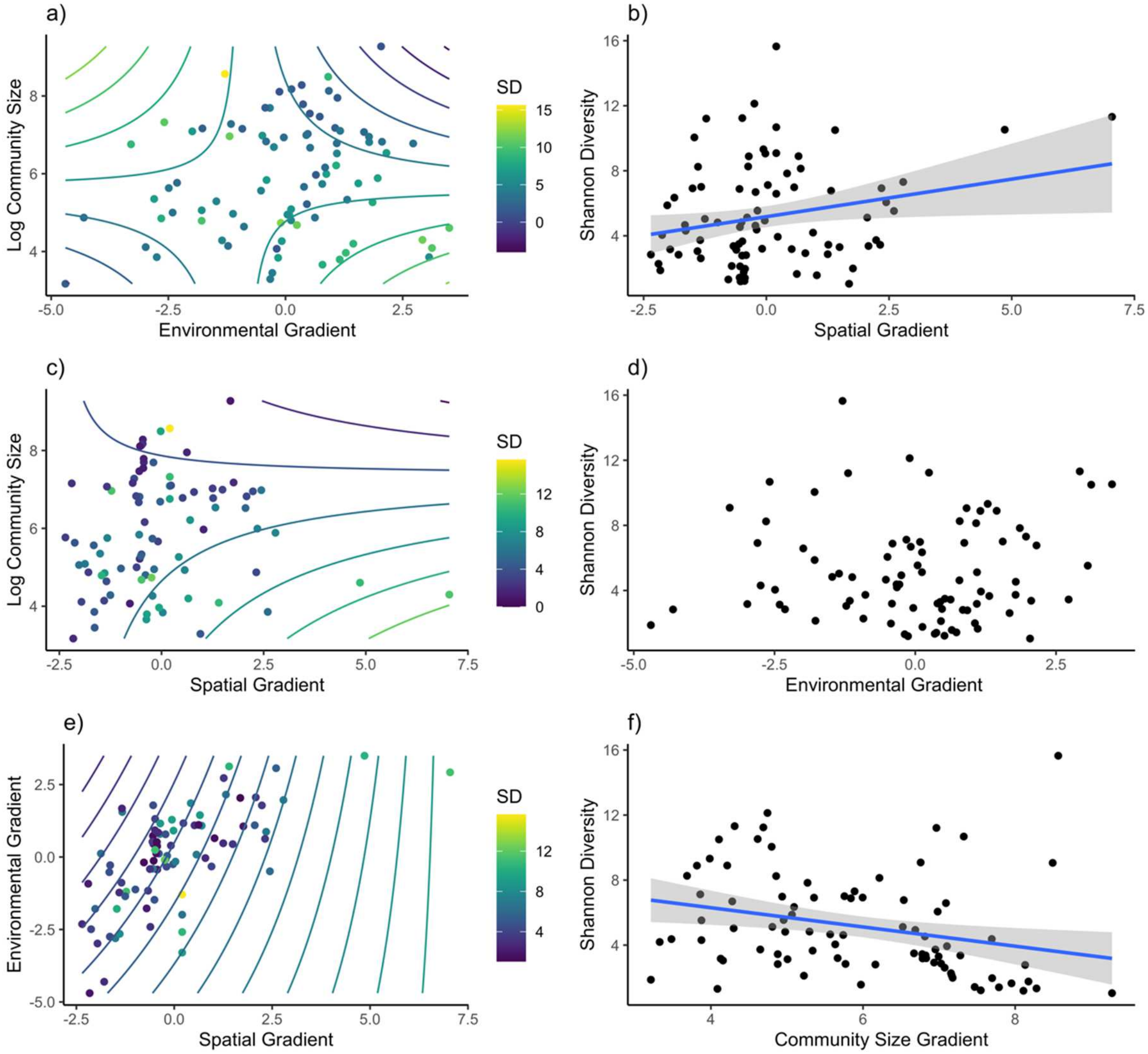

Figure 2.5: Shannon diversity (SD) of stream macroinvertebrate communities as a function of the spatial gradient (b), environmental gradient (d), community size gradient (e), and all pairwise interactions (a, c, and e) among these gradients. Significant relationships are shown with plotted regression lines or contour lines. Full results from GLMMs are found in Table 2.3.

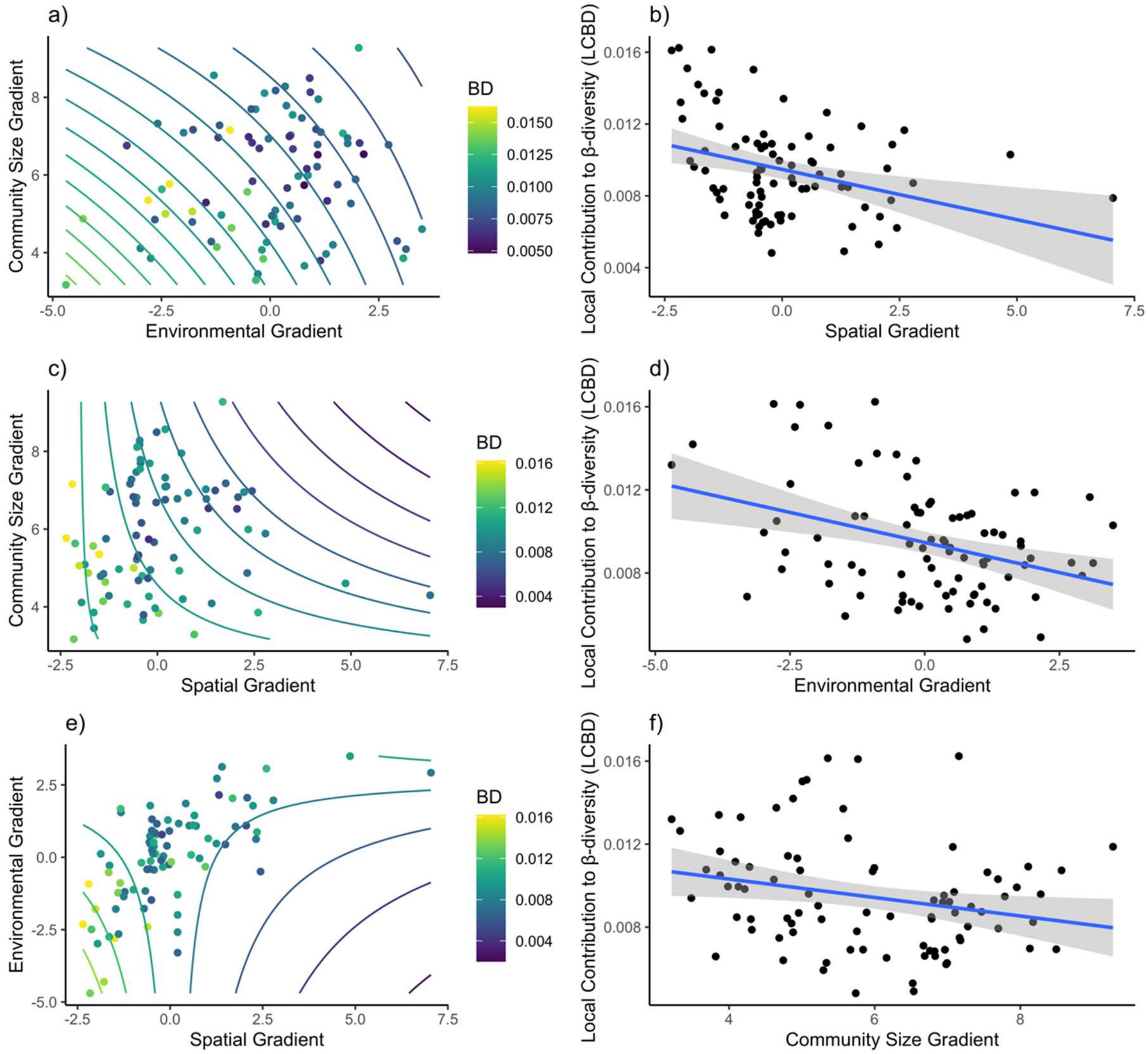

Figure 2.6: Local contribution to β-diversity (BD) of stream macroinvertebrate communities as a function of the spatial gradient (b), environmental gradient (d), community size gradient (e), and all pairwise interactions (a, c, and e) among these gradients. Significant relationships are shown with plotted regression lines or contour lines. Full results from GLMMs are found in Table 2.3.

Chapter 3: The Influence of Non-Native Fish on Stream Macroinvertebrate and Lake Zooplankton Communities Along an Elevational Gradient

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Abstract

The introduction and extirpation of predators can have large impacts on food web structure and ecosystem function. Predators can alter community sizes, thereby increasing the risk of local extinctions, and/or selectively feed on specific body sized organisms, acting as an ecological filter. Species diversity and turnover along environmental gradients in space or time have the potential to buffer or magnify the impact of trophic interactions on ecosystem functioning. In this study, we explored the individual species and community effects of non-native fish predators on lake zooplankton and stream macroinvertebrate communities in the Sierra Nevada, CA. Local diversity, beta diversity, and community structure in zooplankton and macroinvertebrate communities were resilient to non-native fish, which were more structured along elevational gradients and marginally differed among fish and fishless sites. Observed changes in diversity in the presence of fish and along elevational gradients was attributed to species turnover in lakes and in streams was equally related to nestedness and turnover. These findings suggest fish and elevational gradients are acting as ecological filters in lakes, while fish and elevational gradients in streams both alter community size and exclude certain species. We found that fish significantly reduced densities of larger-bodied species in lakes, and in streams subsets of large-bodied taxa were negatively influenced but this pattern was more idiosyncratic. Further, as larger-bodied species densities were lower in the presence of non-native fish, we found that community weighted mean of biomass decreased in the presence of fish in both lakes and streams. Although species turnover and nestedness largely maintained aspects of community diversity and structure over

elevational gradients and in the presence of non-native fish, such changes in larger-bodied taxa and community biomass have important implications in the transfer of energy throughout the food web and to connected riparian and aquatic ecosystems that are dependent on the flow of biomass and nutrients.

Introduction

Humans have introduced and extirpated top predators throughout human history and across the globe (Estes et al. 2011). Change among top predators can have large impacts on food web structure and ecosystem processes, although the magnitude of predator effects (i.e., trophic cascade strength) varies among and within ecosystems (Shurin et al. 2002, Symons and Shurin 2016). The direct effects of predators on local communities can manifest in two non-mutually exclusive ways. Predators can (i) influence ecological drift (changes in species relative abundances that are random with respect to species identities) by altering community size (e.g., density) and thereby increasing the likelihood of extinction, or (ii) by feeding selectively, predators can act as an ecological filter which increases the influence of more deterministic processes (Vellend 2016). Disentangling the mechanisms by which predators structure communities can provide important insights on the management of non-native predator species and communities where predators are locally or regionally extinct (Stier et al. 2016, Ceballos et al. 2017).

In the Sierra Nevada, CA, USA, many historically fishless alpine lakes have been stocked with non-native trout to create recreational fisheries (Bahls 1992). Currently, Sierra Nevada lakes fall into two categories: fishless (i.e., either fish removed or never stocked), or containing self-sustaining populations of non-native fish (Knapp et al. 2001). The effects of non-native fish on Sierra Nevada aquatic communities have been well documented, where non-native trout negatively impact amphibian and native trout species, as well as large-bodied zooplankton and macroinvertebrate species (Knapp et al. 2005, Herbst et al. 2009). These top-down effects results in increased algal and periphyton biomass and changes in microbial communities (Herbst et al. 2009, Symons and Shurin 2016). These previous studies on the effects of fish predation on food web structure in Sierra Nevada aquatic ecosystems have been limited to local perspectives (Stoddard 1987, Knapp et al. 2001, Jones et al. 2020, Knapp et al. 2005, Herbst et al. 2009; but see Symons and Shurin 2016), despite evidence that predators can alter the importance of ecological processes and food web structure across spatial scales (Leibold and Chase 2018).

Species turnover along environmental gradients in space or time has the potential to alter the impacts of environmental change such as non-native fish introductions on ecosystem functioning. Species turnover along environmental gradients is also an indicator of the strength of different forms of selection in driving species composition and maintaining diversity at the regional scale (Anderson et al. 2011). For instance, turnover in zooplankton species composition among Sierra Nevada lakes maintains community biomass in the face of fish introductions at high elevations but not at low elevations (Symons and Shurin 2016). Further, partitioning abundance-based beta-diversity into components of balanced variation (i.e., turnover) and abundance gradients (i.e., nestedness of species assemblages) can further disentangle how communities are organized along gradients through species replacement or species loss (Baselga 2017). Species turnover implies spatial replacement of some species by others due to environmental sorting along elevational gradients among other factors (Qian et al. 2005, Heino and Tolonen 2017). In contrast, nestedness occurs when species in a community are subsets of the regional pool at sites with higher species richness (Ulrich and Gotelli 2007), reflecting a non-random process of species loss as a consequence of factors promoting disaggregation of assemblages, such as predation (Gaston and Blackburn 2000). Interactive effects of multiple environmental gradients (i.e., elevation and fish) on community composition indicate potential interactions among drivers of community organization.

In this study, we explored how predators affect prey communities across ecosystem types (i.e., lakes and streams) and across spatial scales. Fish inhabit and have been widely introduced in lake and stream ecosystems throughout the Sierra Nevada, but different characteristics of these habitat types and organismal groups could cause community responses to differ. We specifically explored the effects of non-native trout predators across an elevational gradient on lake zooplankton and stream macroinvertebrate communities in the Sierra Nevada, CA. We evaluated community responses to non-native trout by examining community diversity and structure, where variaition in diversity and structure among fish and fishless sites would indicate fish effects on the number of species and their abundances. Next, we explored the dual hypotheses of fish influence on communities by partitioning the components of abundance-based dissimilarity into turnover and nestedness, where predators act as an ecological filter excluding certain taxa (i.e., turnover), and/or that fish reduce community size (i.e., nestedness). We also evaluated individual species effects, by examining relative change in species density among fish and fishless sites as a function of species body mass, where a decrease in relative density would indicate a negative effect of fish on larger bodied species. Lastly, we also evaluated community weighted mean (CWM) of species body mass in fish and fishless sites, where higher CWM would indicate a larger community biomass.

Methods

Study Area. The study area was located in the Sierra Nevada of eastern California (USA) and encompasses portions of Inyo National Forest, Yosemite National Park, and Sequoia-Kings Canyon National Park. Over the ice-free months (June-September), lakes and streams were sampled for a range of abiotic and biotic parameters. This field system and the data collected naturally provide spatial and environmental gradients to explore patterns of community structure and diversity (Knapp et al. 2001, 2005, Herbst et al. 2009, Green et al. 2022a).

Sampling Locations and Field Methods. Fish are typically found at lower and mid-elevation stream and lake sites, as some high alpine sites cannot support fish presence without restocking. We controlled for elevation as a confounding factor of fish presence by filtering datasets to elevation bands for streams (elevation > 3200 m) and for lakes, we filtered elevation bands (elevation 1800-3500 m), lake depth (maximum depth > 3 m), and lake area (surface area > 0.5 ha) (Fig. S1; Table S1). Full details of field methods can be found in the data publications (Knapp et al. 2020, Green et al. 2022b).

The stream macroinvertebrate dataset was collected in the summer of 2011, 2018, and 2019 across five distinct catchments in the Sierra Nevada ranging in elevation from 3200m to 3544m. In total 62 stream sites were sampled. At each sampling location, eight to 12 macroinvertebrate samples at each site were collected using a D-frame kick net (250μm mesh, 30cm opening, 0.09m^2 sample area) in riffle habitats, depending on the density of macroinvertebrate samples collected. We took samples by placing the net on the streambed, then turning and brushing all substrate by hand in the sampling area (30cm x 30cm) immediately above the net, with dislodged invertebrates being carried by currents into the net. All macroinvertebrate samples were preserved in 75% ethanol within 48 hours of sampling. Samples were sorted, identified, and counted in the laboratory. Taxa were morphologically identified to the finest taxonomic level possible, usually to genus level for insects (excluding Chironomidae) and order or class for non-insects (Merritt et al. 2019). The replicate samples taken at each site were pooled together and divided by the number of replicates and the area sampled to determine the density of invertebrate communities. Fish presence was determined from visual encounter surveys and verified from previous records.

For lakes, field surveys were conducted from 1995-1997 across lakes ranging across an elevation from 1800m to 3500m for a total of 602 lakes. Zooplankton were collected at each sampling site from a float tube by taking vertical tows from the lake bottom to the surface using a conical sampling net (29.5cm diameter, mesh size 64μm).

One to five replicate samples were taken until sufficient numbers of zooplankton were collected and were stored in 5% sugar formalin. Species identities were determined in the laboratory usually to the species level for crustaceans and rotifers, except for *Cyclopoda* which were identified to family, and the rotifers *Kellicottia*, *Keratella*, and *Polyarthra*, which were identified to genus (Pennak 1989). The density of each taxon (number of individuals/L) was calculated using a net efficiency of 50% (Walters and Vincent 1973). Fish presence was determined using a combination of visual encounter surveys in shallower lakes and gillnets for larger, deeper lakes (Knapp et al. 2001).

Body Size. To calculate zooplankton species body mass, up to 100 individuals of each taxon for each zooplankton samples body size (µm) were measured using a computer-based image analysis system (Knapp et al. 2001). For macroinvertebrate species, the body length (mm) of at least 15 individuals for each taxon were measured under a compound microscope and the average body length measurement was calculated for each taxon across sites. We then used published length–weight regressions to estimate body mass for zooplankton (Dumont et al. 1975, McCauley 1984) and macroinvertebrate (Benke et al. 1999) species.

Statistical Analysis. Non-Metric Multidimensional Dimensional Scaling (NMDS) was used to visualize the influence of elevation and fish presence on zooplankton and macroinvertebrate community structure using the “vegan” package (Oksanen et al. 2019). We applied a Hellinger transformation and the dissimilarity of the species transformed matrix was calculated using the Bray-Curtis dissimilarity method in the “vegdist” function. The effects of elevation and fish presence were evaluated using PERMANOVA through the “adonis” function with the Bray-Curtis dissimilarity as the response variable. We performed the multivariate homogeneity of variances of group dispersions analysis to calculate the effects of fish presence on group dispersion using the “betadisper” function (Oksanen et al. 2019). ANOVA was performed to test whether these group dispersions differed among fish and fishless communities.

To understand the effects of environmental gradients and fish on community diversity, we used Shannon diversity to quantify α-diversity and local contribution to beta diversity (LCBD) to quantify β-diversity for the zooplankton and macroinvertebrate datasets. We quantified Shannon diversity for each site using the exponential of the diversity function in the “vegan” package (Oksanen et al. 2019). LCBD was calculated using the “beta.div” function in the “adespatial” package (Dray et al. 2020), where LCBD quantifies the relative contribution of local sites to the total metacommunity diversity, and whether individual sites have a high contribution to overall β-diversity (Legendre and Cáceres 2013). We calculated the total beta diversity across all communities (BD_{Total}), which was estimated as the variance of the Hellinger-transformed community data matrix, and was later decomposed into the relative contributions of individual sites, called LCBD (Legendre and Cáceres 2013). We fit generalized linear models (GLMs) with Gaussian error distributions for Shannon diversity using the “stats” package to understand the role of elevation and fish on local diversity. For LCBD, we used beta error distributions using the “betareg” package, which can handle data measured on a continuous scale and restricted to the interval 0-1 (Brooks et al. 2017). We ran all models with species diversity metrics (Shannon diversity and LCBD) of lakes or streams as the response variable and predictors included a null model, two single factor models with either elevation or fish presence, and an interaction model with both predictors.

To understand how fish and elevation drive changes in community variability, we partitioned the components of abundance-based dissimilarity ($ß_{bray}$) to explore how diversity is maintained in the presence of fish and along elevational gradients. Components of abundance-based dissimilarity include balanced variation ($ß_{bal}$), where individuals of some species in one site are substituted by the same number of individuals of different species in another site (i.e., turnover) and abundance gradients ($ß_{gre}$), where some individuals are lost from one site to the other (i.e., nestedness). The sum of both components is known as abundance-based dissimilarity ($ß_{bray}= ß_{gre}+ ß_{bal}$) (Baselga 2013, 2017). We used the “beta.pair.abund” function in the “betapart” package using the Bray-Curtis dissimilarity method to calculate the components of abundance based dissimilarity (Baselga 2013, 2017). We ran beta regression models to determine differences among the balanced variation and abundance gradient components for lakes and streams separately. We also used beta regression models to determine differences in lake and stream total abundance-based dissimilarity ($ß_{bray}$).

To understand the influence of fish predation on species density, we modeled the relative change in each species density as a function of body mass, where species average densities were calculated across sites in the presence and absence of fish. We determined species relative change in density by dividing average density in the presence of fish by the average of species density in the absence of fish. Only species that occurred in both fish and fishless sites were included in this analysis. Species density and species body mass were log +1 transformed prior to analyses to meet assumptions of normality and homogeneity of variances and modeled using Gaussian error distributions. We fit GLMs to understand the role fish on individual species relative change in density. We ran models with relative change in density as the response variable and for predictors we used species body mass and a null model. For species that were absent from fish or fishless sites, we used GLMs to assess how body mass varied among species who were absent from fish or fishless sites and compared those models to a null model.

We tested the effect of fish and environmental gradients on zooplankton and macroinvertebrate body size using the community weighted mean (CWM). This approach evaluates the relationship between species abundance and the variability in body sizes among taxa. CWM was calculated using the "dbfd" function in the "FD" package for each site (Laliberté and Legendre 2010). We used GLMs with Gaussian error distributions to model CWM of zooplankton or macroinvertebrates as the response variable and predictors included a null model, two single factor models with either elevation or fish presence, and an interaction model with both predictors.

For all GLMs, we implemented an information-theoretic approach for model selection and inference (Burnham and Anderson 2002). Using a model selection approach, we assessed delta AIC of all GLMs to determine best fit models via the "AICtab" function in the "bbmle" package (Bolker 2020). R-squared values for GLMs were determined by using the "r2" function in the "performance" package. For all analyses, we verified that response variables met all appropriate assumptions of distributions prior to analyses. We used the “check_collinearity” function in the “performance” package to detect for multicollinearity by calculating variance inflation factors (VIF) of models, all of which were less than 1.01, where values of 1 indicate no correlation and values above 5 indicate high degrees of correlation (Lüdecke et al. 2021). All analyses and data visualizations were carried out using R version 4.0.2 (R Development Core Team 2022).

Results

Community structure in both lakes and streams were determined by elevation (Fig. 1; Table 1; Lake: p-value < 0.05, $R^2=0.11$; Stream: p-value < 0.05, $R^2=0.07$). Fish presence/absence also had a significant effect on lake zooplankton and stream macroinvertebrate communities, although this explained a smaller proportion of variation in community structure (Fig. 1; Table 1; Lake: p-value < 0.05, $R^2=0.04$; Stream: p-value <0.05, $R^2=0.05$). We also found a difference in the community dispersion of lake zooplankton communities by fish, but not in stream macroinvertebrate communities (Fig. 1; Table S2; Lake: p-value < 0.001; Stream: p-value > 0.05).

The regional (γ) diversity of zooplankton in Sierra Nevada lakes from this study was 28 taxa. In lakes, Shannon diversity of lake zooplankton was best explained by elevation, where local diversity increased moving down in elevation (Fig. 2b; Table 2; $w_{elevation} = 0.8$, $R^2 = 0.28$). The model of fish and elevation was also well supported in explaining local diversity, although fish and fishless lakes did not differ in local diversity

(Fig. 2a; Table 2; $w_{elevation*fish} = 0.2$, $R^2 = 0.28$). Local contribution to beta-diversity (LCBD) was best explained by the interaction model of fish and elevation, where LCBD increased with elevation and was slightly higher in lakes with fish present than fish absent (Fig. 2c-d; Table 2; $w_{elevation*fish} = 0.95$, $R^2 = 0.12$).

The regional diversity of stream macroinvertebrates from this study was 100 taxa. In streams, Shannon diversity of stream macroinvertebrates was best explained by the model including the interactive effects of elevation and fish, where local diversity was slightly higher in fishless than fish sites and local diversity increased moving down in elevation (Fig. 2e-f; Table 2; $w_{elevation*fish} = 0.99$, $R^2 = 0.26$). LCBD was best explained by the individual elevation model, where LCBD increased moving up in elevation (Fig. 2h; Table 2; $w_{elevation} = 0.73$, $R^2 = 0.13$). There was also support for the model including the interactive effects of elevation and fish in explaining LCBD, where LCBD was marginally higher in fishless than fish sites (Fig. 2g-h; Table 2; $w_{elevation*fish} = 0.23$, $R^2 = 0.16$).

Zooplankton communities were structured more by balanced variation in species abundances (i.e., turnover in species composition and replacement), as opposed to the abundance gradients (i.e., nestedness) (Fig. 3a; Table 3; $w_{beta\ componenet} = 1$, $R^2 = 0.28$). Macroinvertebrate communities were also more structured by balanced variation than abundance gradients, although the differences were not as pronounced as they were for lake zooplankton (Fig. 3b; Table 3; $w_{beta\ componenet} = 1$, $R^2 = 0.01$). In lakes, average ß diversity related to balanced variation in species abundances was higher ($ß_{bal} = 0.45$) than ß diversity related to abundance gradients ($ß_{gra} = 0.13$). In streams, average ß diversity related to balanced variation in species abundances was also higher ($ß_{bal}$= 0.4) than ß diversity related to abundance gradients ($ß_{gra}$= 0.37). Overall, average ß diversity was higher in lake zooplankton communities ($ß_{bray}$= 0.81) compared to stream macroinvertebrate communities ($ß_{gra}$= 0.78), although this did not explain much of the variation in total ß diversity (Fig. 3; Table 3; $w_{ecosystem}$= 1, R^2 = 0.03).

In lakes, the relative change in zooplankton species density from fishless to fish sites was negatively related to zooplankton body size (Fig. 4a; Table 4). *Polyarthra vulgaris* and *Synchaeta sp.* were notably absent from sites with fish present and *Alona sp.*, *Alonella excisa*, *Ascomorpha sp.*, *Polyphemus pediculus*, and *Trichotria sp.* were found exclusively in sites with fish present (Fig. S2; Table S4). In streams, no relationship emerged among the relative change in macroinvertebrate species density from fishless to fish sites as a function of body size (Fig. 4b; Table 4). The large number of macroinvertebrate species absent from fish or fishless sites may have obscured this relationship; we identified 41 species that were found exclusively in fish present sites, while only 8 species were found exclusively in fish absent sites (Fig. S2; Table S4). For these species that did occur exclusively with or without fish, we found that body mass did not differ among these two groups (Fig. S3; Table S3).

In lakes, community weighted mean (CWM) of body mass was best explained by the interactive model of elevation and fish (Fig. 5a; Fig. S4a; Table 5; $w_{elevation*fish}$ = 1, R^2 = 0.34). CWM of zooplankton body mass was higher in fishless than fish sites and increased moving down in elevation. For stream macroinvertebrates, CWM of body mass was best explained by fish, where fishless sites had higher CWM of body mass than sites with fish present (Fig. 5b; Table 5; $w_{fish} = 0.87$, $R^2 = 0.27$). CWM was also well explained by the interactive model of elevation and fish, where CWM generally decreased moving down in elevation (Fig. 5b; Fig. S4b; Table 5; $w_{elevation*fish} = 0.13$, $R^2 = 0.27$), although the individual model of elevation on stream CWM was not supported in model selection.

Discussion

Our study indicates that overall community structure and diversity were largely resilient to the presence of non-native fish, but finer aspects of community structure such as species composition and community biomass were strongly influenced by fish presence. Community diversity (Shannon diversity and LCBD) marginally differed among fish and fishless sites and were principally structured along elevational gradients. Partitioning the components of beta diversity revealed differences among lake and stream ecosystems in the maintenance of species diversity. Fish and elevational gradients act as both ecological filters excluding subsets of species and reducing species density in streams. While in lakes, fish and elevational gradients act solely as ecological filters. At the species level, fish negatively influenced large-bodied taxa in lakes and had strong effects on specific large-bodied macroinvertebrate taxa, but this pattern in streams was more idiosyncratic. We saw the strongest effects of fish on CWM of body mass, which was much higher in fishless than sites with fish, indicating that fish have strong effects on community biomass across aquatic ecosystems. This fish effect has potentially important downstream effects throughout the food web and implications in ecosystem function. Although this turnover in community composition largely maintains diversity and structure, the species primarily turning over from fish present to fish absent sites appear to be smaller bodied species, driving the changes we observed in CWM of body mass.

In lakes, local diversity did not differ among fishless and fish lakes, however beta-diversity (LCBD) was higher in fish than fishless lakes. In streams, Shannon diversity and LCBD were slightly higher in fishless than fish sites. These results confirm findings by Herbst et al. (2009) which also found fish in high elevation streams have small effects on community structure and diversity. These marginal effects of fish on community diversity indicate that environmental control of diversity outweighs the influence of fish on stream and lake communities. Alternatively, the reduction of native macroinvertebrate predators by trout (i.e., *Doroneuria spp.*) might result in reduced predation for some macroinvertebrate species and a release from invertebrate predation on prey taxa (Lancaster 1990). Species diversity patterns along elevational gradients largely matched those predicted by theory, where local diversity decreased moving downstream and beta-diversity increased moving upstream (Vannote et al. 1980, Finn et al. 2011, Doretto et al. 2020, Green et al. 2022a). In addition, turnover of taxa negatively influenced by fish may indicate that these communities are fairly resilient in the face of fish presence.

However, our analysis revealed community biomass decreased in the presence of fish in both lakes and streams, being substantial in streams. This pattern has also been reported in other studies of zooplankton (Symons and Shurin 2016, Detmer et al. 2017, Jones et al. 2020) and macroinvertebrates (Flecker and Townsend 1994). Differences in CWM among lakes and stream might reflect fundamental difference between the open water habitat where zooplankton live and the greater habitat heterogeneity in stream benthic environments. Changes in community biomass have important implications for the transfer of energy throughout the food web and to connected riparian and aquatic ecosystems that are dependent on the flow of biomass and nutrients (Massol et al. 2011, Piovia-Scott et al. 2016).

Partitioning β-diversity into its components revealed that lake and stream communities were more structured by balanced variation in species abundances (i.e., turnover via substitution) than abundance gradients (i.e., subsets), although there was variation among ecosystems. Communities maintained diversity along elevational gradients and in the presence of fish due to turnover of species in lakes and turnover and nestedenss in streams. These results suggest that in lakes non-native fish are largely excluding species from local communities acting as an ecological filter, rather than changes in abundances that would result from fish reducing community size. This effect on beta diversity of high turnover versus low nestedness was more pronounced for lake zooplankton communities than stream macroinvertebrates. Macroinvertebrate community variation was more structured by turnover than nestedness, but only marginally. This suggests in streams that fish both act as an ecological filter excluding species and by reducing community size and changes in species abundances. These results might reflect fundamental differences in the two clades, as noted earlier the large differences in the regional diversity and the smaller number of stream sites sampled.

We observed strong effects of fish on individual taxa in both lakes and streams, where in lakes zooplankton change in relative density was negatively related to zooplankton body size. Therefore, fish are preferentially feeding on large-bodied zooplankton in lakes, such as *H. shoshone* and *D. melanica*, which other studies have also reported are negatively influenced by non-native fish (Knapp et al. 2001, Symons and Shurin 2016, Jones et al. 2020, Symons et al. 2021). In streams, we observed substantial variation in individual taxa response to fish presence and this relative change in density was not related to macroinvertebrate body size. Densities of several common taxa notably declined in the presence of fish including *Doroneuria*, *Ameletus*, *Paraleptophlebia, Dixa*, which have also been seen observed in other Sierra Nevada streams (Herbst et al. 2009). Despite some large changes in individual taxa as a function of fish presence, the density of many common species were not substantially different, corroborating results from previous studies (Flecker and Townsend 1994, Herbst et al. 2009). In streams, there were many taxa absent from either fishless or fish present sites in our macroinvertebrate dataset (Table S4). This most likely reflects differences in the sample size of the two datasets and the overall regional diversity of the two clades used in this analysis. In our analysis of lakes, we analyzed 602 lakes and for streams we analyzed 62 sites. As for regional diversity, regional diversity of zooplankton species throughout the Sierra Nevada is 39 species and regional diversity of stream macroinvertebrates is 516 taxa (Knapp unpublished; Herbst unpublished). Thus, future studies of the influence of fish on stream macroinvertebrate diversity should focus on synthesizing larger datasets of streams to assess whether species are truly excluded from sites as a function of fish.

As we focused on average body size for taxa, site specific changes in body size might have better explained variance in species density and CWM we observed. Indeed, other studies have found evidence that zooplankton body size increases with elevation, but only in lakes with fish (Symons and Shurin 2016). In our study, we found that community biomass was higher in fishless than fish present lakes and streams, regardless of elevation. Contrary to our study, turnover in zooplankton species composition among Sierra Nevada lakes maintains community biomass in the face of fish introduction at high elevation but not at low elevation (Symons and Shurin 2016). This could reflect differences in the number of lakes surveyed or the elevational gradients between the two studies.

High elevation aquatic ecosystems are important reservoirs for biodiversity and are currently under the influence of multiple environmental stressors, such as the introduction of non-native species and climate driven hydrological and environmental changes to aquatic ecosystems (Hotaling et al. 2017). Although we found community structure and diversity are largely maintained in the presence of non-native fish, the large differences in community biomass and the influence of individual large-bodied taxa warrant further investigation. Future studies should focus efforts on better understanding the ecosystem influences of this fish-induced biomass effect on lakes, streams, and the transport of this biomass to connected riparian and aquatic food webs (Sarnelle and Knapp 2005, Piovia-Scott et al. 2016). A better understanding of the ecosystem influences of fish should help guide land management of high elevation aquatic ecosystems in the face of these multiple disturbances.

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Figures and Tables

Table 3.1: PERMANOVA results of lake zooplankton and stream macroinvertebrates communities using the adonis function and “bray” method in the vegan package.

Ecosystem	Factor	*df*	Sum of Squares	F model	p value	R^2
Lake	Fish	1	2.7	10.272	0.01	0.03
	Elevation	1	9.569	36.408	0.01	0.11
	Residual	294	77.271			0.86
	Total	296	89.54			1
Stream	Fish	1	0.5368	3.5246	0.01	0.05
	Elevation	1	0.7342	4.821	0.01	0.06
	Residual	66	10.0513			0.89
	Total	68	11.3222			1

Table 3.2: GLMs of zooplankton and macroinvertebrate community diversity response to fish presence, elevation, and the interaction between the two variables. Community diversity metrics include Shannon Diversity and Local Contribution to Beta Diversity (LCBD). Models are ranked by ΔAIC separately for each diversity metric and dataset. Each model is presented with AIC, the degrees of freedom, Akaike weights w_i, and the fraction of null deviance (R^2) explained.

Ecosystem	Diversity	Model	ΔAIC	*df*	w_i	R^2
Lakes	Shannon Diversity	~Elevation	0	3	0.8	0.28
		~Fish*Elevation	2.8	5	0.2	0.28
		~1	95.3	2	<0.001	0.00
		~Fish	95.6	3	<0.001	0.01
	LCBD	~Fish*Elevation	0	5	0.946	0.12
		~Elevation	5.7	3	0.054	0.09
		~Fish	19.2	3	<0.001	0.04
		~1	29.1	2	<0.001	0.00
Streams	Shannon Diversity	~Fish*Elevation	0	5	0.987	0.26
		~Elevation	9.6	3	0.0079	0.08
		~Fish	11.3	3	0.0035	0.06
		~1	12.9	2	0.0015	0.00
	LCBD	~Elevation	0	3	0.733	0.13
		~Fish*Elevation	2.3	5	0.229	0.16
		~1	6.6	2	0.027	0.00
		~Fish	8.4	3	0.011	0.00

Table 3.3: Results from GLMs of lake zooplankton and stream macroinvertebrate community dissimilarity as a function of two beta diversity components, nestedness ($ß_{gre}$) and turnover ($ß_{bal}$). Lake and Stream total beta diversity ($ß_{bray}$) across ecosystems as a function of ecosystem type. Models are ranked by ΔAIC separately for each dataset and analysis. Each model is presented with AIC, the degrees of freedom, Akaike weights w_i, and the fraction of null deviance (R^2) explained.

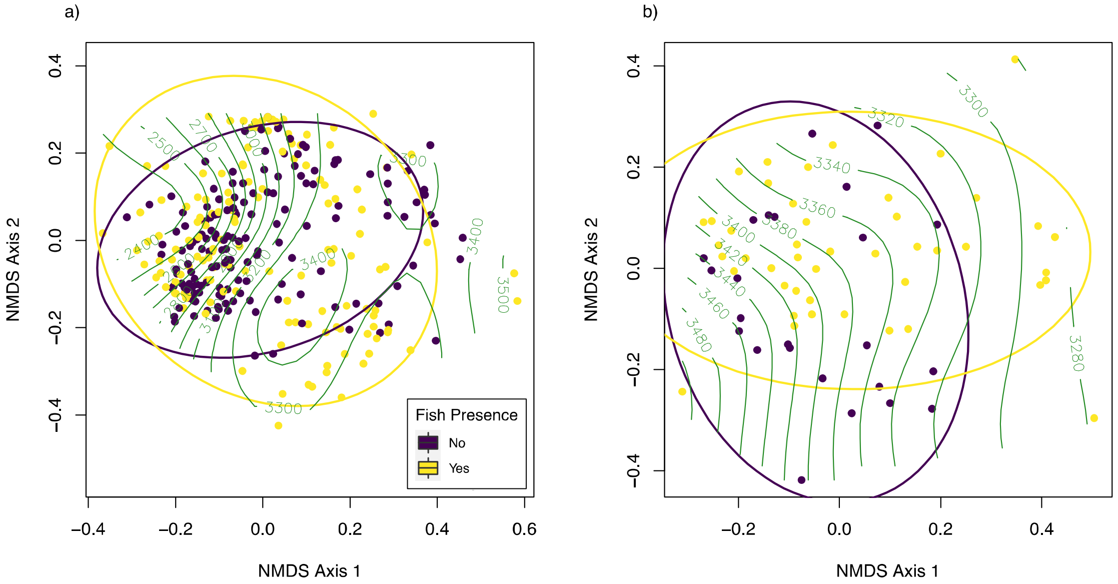
Ecosystem	Model	ΔAIC	*df*	w_i	R^2
Lake $ß_{gre}$+ $ß_{bal}$	~Beta diversity component	0	3	1	0.28
	~1	28033.1	2	<0.001	0
Stream $ß_{gre}$+ $ß_{bal}$	~Beta diversity component	0	3	1	0.01
	~1	24.5	2	<0.001	0
Lake and Stream $ß_{bray}$	~ Ecosystem	0	3	1	0.03
	~1	119.3	2	<0.001	0

Table 3.4: GLMs of the effect of fish on relative changes in species density for lake zooplankton and stream macroinvertebrate communities. Models are ranked by ΔAIC separately for each diversity metric and dataset. Each model is presented with AIC, the degrees of freedom, Akaike weights w_i, and the fraction of null deviance (R^2) explained.

Ecosystem	Model	ΔAIC	*df*	w_i	R^2
Lake	~Body Mass	0	3	0.936	0.13
	~1	5.4	2	0.064	0
Stream	~1	0	2	0.71	0
	~Body Mass	1.8	3	0.29	0.003

Table 3.5: GLMs of zooplankton and macroinvertebrate community weighted mean (CWM) of body mass response to fish presence, elevation, and the interaction between the two variables. Models are ranked by ΔAIC separately for each dataset. Each model is presented with AIC, the degrees of freedom, Akaike weights w_i, and the fraction of null deviance (R^2) explained.

Ecosystem	Model	ΔAIC	*df*	w_i	R^2
Lake CWM	~Fish*Elevation	0	5	1	0.34
	~Elevation	33.7	3	<0.001	0.25
	~Fish	94.5	3	<0.001	0.08
	~1	117.8	2	<0.001	0.00
Stream CWM	~Fish	0	3	0.87	0.27
	~Fish*Elevation	3.9	5	0.13	0.27
	~1	19.3	2	<0.001	0.00
	~Elevation	21.2	3	<0.001	0.00



communities from Sierra Nevada, CA using NMDS (zooplankton stress = 0.17; macroinvertebrate stress = 0.15). Contour calculated using the "ordisurf" function from the "vegan" package describe elevation (m). The convex hulls describe fish and fishless sites using the "ordihull" function.

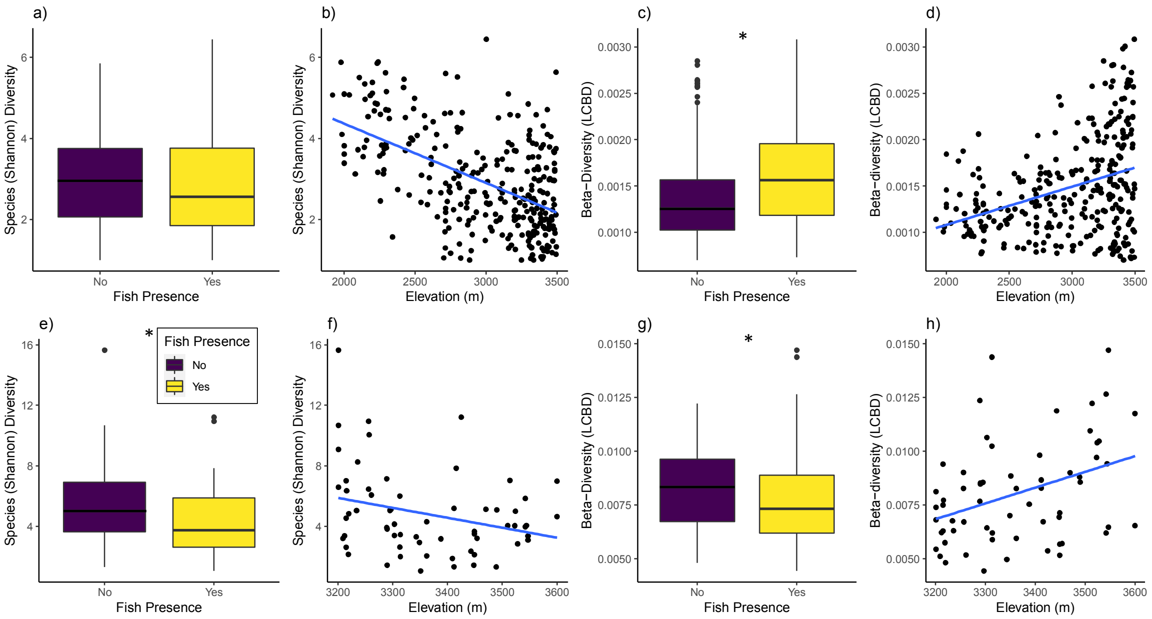


Figure 3.2: Zooplankton (a-d) and macroinvertebrate (e-h) community diversity response as a function of fish presence (a, c, e, g) and along elevational gradients (b, d, f, h). Community diversity metrics include Shannon Diversity (a, b, e, f) and Local Contribution to Beta Diversity (LCBD; c, d, g, h). Asterisks in boxplots and best fit lines in scatterplots denote significant models.

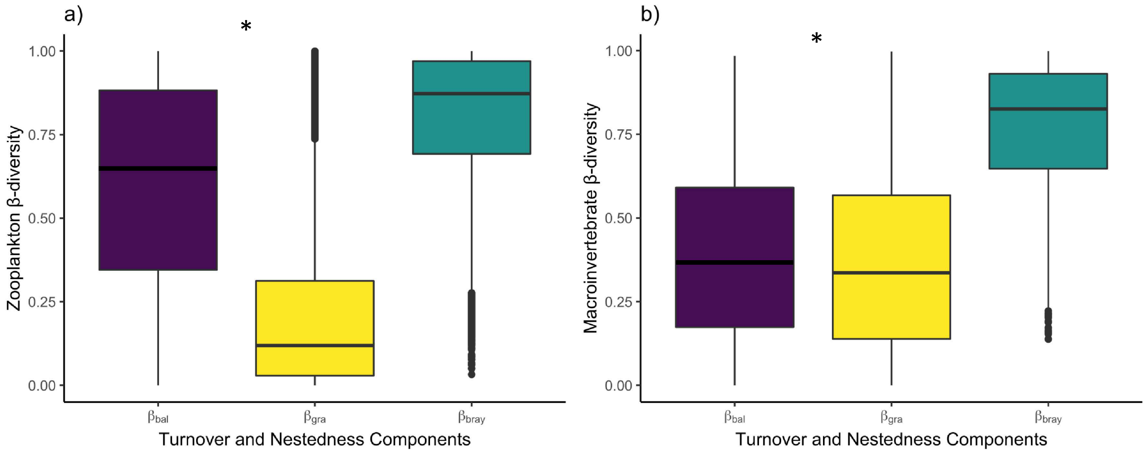


Figure 3.3: Zooplankton (a) and macroinvertebrate (b) community dissimilarity as a function of the turnover and nestedness components of beta diversity: balanced variation in abundance ($ß_{bal}$), abundance gradients ($ß_{gre}$), and total beta diversity ($ß_{bray}$). Asterisks in boxplots denote significant models.

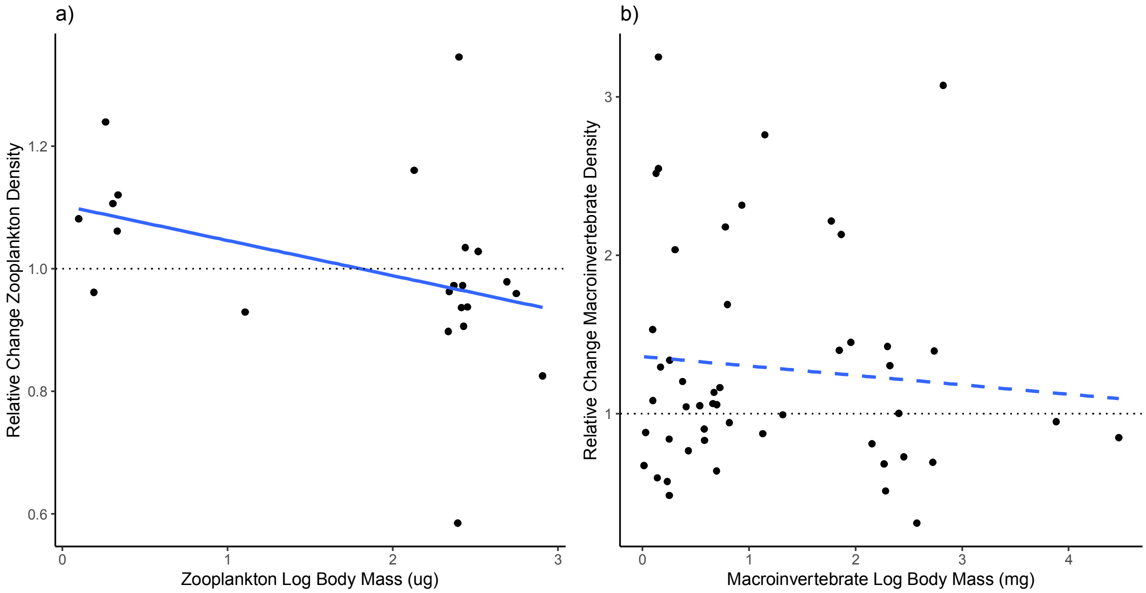


Figure 3.4: Zooplankton (a) and macroinvertebrate (b) relative change in species density from fishless to fish sites as a function of log transformed body mass. Only species that occur in both fish and fishless sites are included in this figure and analysis. Solid blue line indicates a significant relationship and dashed blue line indicates an insignificant relationship. The horizontal dashed line represents no change in species density among fish and fishless sites.

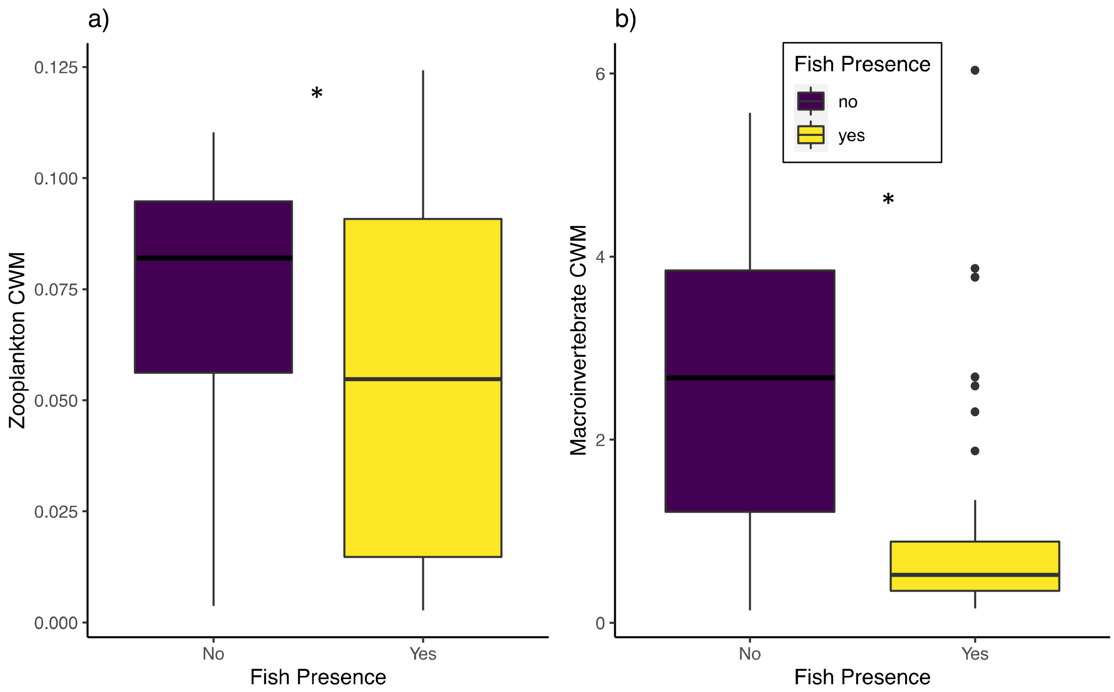


Figure 3.5: CWM of zooplankton (a) and macroinvertebrate (b) community biomass as a function of fish presence. Asterisks in boxplots denote significant models.

Conclusions

Species persistence and diversity are strongly regulated by spatial and trophic factors in ecological communities. Identifying the relative importance of these factors is a fundamental goal in community ecology and a practical problem for conservation ecology, ecosystem restoration, and the management of invasive species (Chase et al. 2020, de Silva et al. 2021, Patrick et al. 2021). Yet our theoretical understanding of spatial and trophic effects on communities surpasses our empirical understanding.

In this dissertation, I investigated how spatial factors and trophic interactions influence the persistence of species and patterns of biodiversity with laboratory microcosm studies, field observational studies in pristine environments, and through data synthesis. The studies outlined here contribute to a growing body of research that spatial and environmental heterogeneity promote species persistence and biodiversity, but top-down or bottom-up effects can alter species and community responses. Synthesis of trophic metacommunity ecology (Holt 2002, Beger et al. 2010, Gravel et al. 2011, Pillai et al. 2011, Guzman et al. 2019) is critical, because species on different trophic levels often respond to space differently (Leibold and Chase 2018). Spatial structure and the loss or fragmentation of habitat affect species on higher trophic levels more strongly (Pillai et al 2011; Barter and Gross 2016; Liao et al 2017; Ryser et al. 2019). The loss or introduction of top predators can have significant and unexpected consequences on food web stability due to their disproportionately large top-down effects on lower trophic levels (Woodward et al. 2012).

The chapters of my dissertation share the common theme of seeking to understand how spatial factors and trophic interactions influence the persistence of species and patterns of biodiversity. In chapter one, I demonstrated in a synthesis of spatial predator-prey protists microcosm experiments that spatial factors are robust in predicting dynamics across spatial systems varying in size and connectivity and that the strength of responses vary with top-down (i.e., predation) or bottom-up (i.e., productivity) effects. In Chapter two, I showed that stream ecology frameworks partially predicted macroinvertebrate diversity, but not entirely for the reasons theory predicted. By framing our analysis using The Theory of Ecological Communities framework, we were able to disentangle the mechanisms structuring biodiversity patterns and provided an analytical framework toward generalization of biodiversity research across ecosystems. Finally, in chapter three, I showed that although individual zooplankton and macroinvertebrate taxa in Sierra Nevada lakes are negatively influenced by non-native fish, community diversity and structure is not strongly altered by fish, as species turnover maintained diversity in the face of environmental change. However, the species replacing taxa negatively influenced by fish were much smaller and in higher abundances, suggesting that differences in fish and fishless community biomass may influence the transfer of energy throughout the food web and to connected riparian and aquatic ecosystems that are dependent on the flow of biomass and nutrients.

Understanding how spatial structure and trophic interactions influence the persistence and diversity of ecological communities is a pivotal goal of both fundamental and applied ecology (Leibold and Chase 2018, Chase et al. 2020, da Silva et al. 2021, Patrick et al. 2021). This dissertation demonstrates that maintaining connectivity, large habitat areas and, importantly, variation in connectivity and habitat sizes, appears particularly necessary given that species on different trophic levels maintain persistence by utilizing habitats differently. Further, the studies in alpine Sierra Nevada, CA aquatic ecosystems highlights these areas are important reservoirs for biodiversity and management efforts should be focused on these habitats, especially in light of climate driven hydrological changes to high elevation aquatic ecosystems (Hotaling et al. 2017). Moving forward, incorporating both the spatial network structure of habitats and trophic interactions will help progress fundamental ecological theory and guide better management of ecological communities.

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Appendix A

Supplementary Material for Chapter 1: Productivity and Trophic Interactions Alter Spatial Benefits of Metacommunity Persistence Across Network Sizes and Structures

Supplementary Tables.

Table A.1: Results from generalized linear models analyzing the effects of productivity (prod.), predator identity (predator), log metacommunity size (meta.size), log nearest neighbor connectivity (connectivity), and all additive combinations among those variables on local time to prey and predator extinction. Models are listed in order by delta AIC for each species separately. Also included are the effective degrees of freedom (*df*) and the fraction of null deviance (R^2) explained by the model.

Response	Model	ΔAIC	*df*	w_i	R^2
Time to Prey Extinction	~ prod.+meta.size+connectivity+predator	0	6	1.00	0.59
	~ prod.+meta.size+connectivity	44.5	5	<0.001	0.58
	~ prod.+meta.size+predator	89.6	5	<0.001	0.57
	~ prod.+meta.size	191.7	4	<0.001	0.55
	~ prod.+connectivity	301.9	4	<0.001	0.54
	~ prod.+connectivity+predator	303.9	5	<0.001	0.54
	~ meta.size+connectivity+predator	971	4	<0.001	0.43
	~ meta.size+connectivity	1051.1	3	<0.001	0.41
	~ meta.size+predator	1065.7	3	<0.001	0.41
	~ meta.size	1107.7	2	<0.001	0.40
	~ connectivity+predator	1472.2	3	<0.001	0.34
	~ connectivity	1857.2	2	<0.001	0.28
	~ prod.+predator	2481.8	4	<0.001	0.18
	~ prod.	2489.4	3	<0.001	0.18
	~ predator	3408.8	2	<0.001	0.02
	~1	3554.7	1	<0.001	0.00
Time to Predator Extinction	~ prod.+meta.size+connectivity+predator	0	6	1.00	0.26
	~ prod.+connectivity+predator	30.5	5	<0.001	0.26
	~ prod.+meta.size+predator	112.7	5	<0.001	0.24
	~ prod.+predator	164.1	4	<0.001	0.23
	~ prod.+meta.size+connectivity	636.6	5	<0.001	0.15
	~ prod.+meta.size	638.7	4	<0.001	0.15
	~ prod.+connectivity	657	4	<0.001	0.15

	~ prod.	783.4	3	<0.001	0.13
	~ meta.size+connectivity+predator	1032	4	<0.001	0.09
	~ connectivity+predator	1120.2	3	<0.001	0.07
	~ meta.size+connectivity	1181.3	3	<0.001	0.06
	~ connectivity	1192.2	2	<0.001	0.06
	~ meta.size+predator	1442.5	3	<0.001	0.02
	~ meta.size	1442.9	2	<0.001	0.02
	~ predator	1525.9	2	<0.001	0.00
	~1	1544.8	1	<0.001	0.00

Table A.2: Results from generalized linear models analyzing the effect of productivity (prod.), predator identity (predator), log metacommunity size (meta.size), log nearest neighbor connectivity (connectivity), and all additive combinations among those variables on predator and prey occupancy at both the local bottle and regional metacommunity scale. Models are listed in order by delta AIC for each species separately. Also included are the effective degrees of freedom (*df*), Akaike weights (w_i), and the fraction of null deviance (R^2) explained by the model.

Response	Model	ΔAIC	*df*	w_i	R^2
Local Prey Occupancy	~ prod.+meta.size+connectivity+predator	0	6	1.00	0.41
	~ prod.+connectivity+predator	40.9	5	<0.001	0.37
	~ prod.+predator	47.8	4	<0.001	0.36
	~ prod.+meta.size+predator	48.8	5	<0.001	0.37
	~ prod.+meta.size+connectivity	66.4	5	<0.001	0.35
	~ prod.+connectivity	74.4	4	<0.001	0.34
	~ prod.	81	3	<0.001	0.33
	~ prod.+meta.size	82.7	4	<0.001	0.33
	~ meta.size+connectivity+predator	246.9	4	<0.001	0.17
	~ meta.size+connectivity	350.9	3	<0.001	0.07
	~ meta.size+predator	389.8	3	<0.001	0.03
	~ connectivity+predator	401.5	3	<0.001	0.02
	~ meta.size	405.2	2	<0.001	0.01
	~ connectivity	409.6	2	<0.001	0.01
	~ predator	411.5	2	<0.001	0.01
	~1	416.7	1	<0.001	0.00
Local Predator Occupancy	~ prod.+meta.size+connectivity+predator	0	6	1.00	0.61
	~ prod.+connectivity+predator	32.1	5	<0.001	0.60
	~ prod.+meta.size+predator	113.9	5	<0.001	0.58
	~ prod.+predator	168.6	4	<0.001	0.56
	~ prod.+meta.size+connectivity	822.6	5	<0.001	0.37
	~ prod.+connectivity	827	4	<0.001	0.37
	~ prod.+meta.size	833.1	4	<0.001	0.37
	~ prod.	953	3	<0.001	0.33
	~ meta.size+connectivity+predator	1307.4	4	<0.001	0.23
	~ meta.size+connectivity	1430.6	3	<0.001	0.19
	~ connectivity+predator	1618.7	3	<0.001	0.14
	~ connectivity	1623.7	2	<0.001	0.13
	~ meta.size+predator	2025.4	3	<0.001	0.02

	~ meta.size	2036.5	2	<0.001	0.01
	~ predator	2072.7	2	<0.001	0.00
	~1	2076.1	1	<0.001	0.00
Regional Prey Occupancy	~ prod.+meta.size+connectivity+predator	0.00	6	1.00	0.48
	~ prod.+connectivity+predator	232.70	5	<0.001	0.43
	~ prod.+meta.size+connectivity	232.90	5	<0.001	0.43
	~ prod.+meta.size+predator	266.40	5	<0.001	0.43
	~ prod.+predator	267.80	4	<0.001	0.43
	~ prod.+connectivity	378.50	4	<0.001	0.41
	~ prod.	407.50	3	<0.001	0.40
	~ prod.+meta.size	408.30	4	<0.001	0.40
	~ meta.size+connectivity+predator	1393.20	4	<0.001	0.22
	~ meta.size+connectivity	2058.30	3	<0.001	0.09
	~ meta.size+predator	2269.00	3	<0.001	0.05
	~ meta.size	2434.00	2	<0.001	0.02
	~ connectivity+predator	2456.10	3	<0.001	0.02
	~ predator	2497.00	2	<0.001	0.01
	~ connectivity	2529.10	2	<0.001	0.01
	~1	2556.80	1	<0.001	0.00
Regional Predator Occupancy	~ prod.+meta.size+connectivity+predator	0.00	6	1.00	0.71
	~ prod.+connectivity+predator	94.40	5	<0.001	0.70
	~ prod.+meta.size+predator	520.50	5	<0.001	0.64
	~ prod.+predator	871.80	4	<0.001	0.59
	~ prod.+meta.size+connectivity	1602.10	5	<0.001	0.48
	~ prod.+connectivity	1661.70	4	<0.001	0.47
	~ prod.+meta.size	1695.50	4	<0.001	0.47
	~ prod.	2349.40	3	<0.001	0.37
	~ meta.size+connectivity+predator	2601.20	4	<0.001	0.34
	~ meta.size+connectivity	3291.30	3	<0.001	0.24
	~ connectivity+predator	3899.20	3	<0.001	0.15
	~ connectivity	3920.30	2	<0.001	0.15
	~ meta.size	4943.70	2	<0.001	0.00
	~ meta.size+predator	4944.60	3	<0.001	0.00
	~1	4972.10	1	<0.001	0.00
	~ predator	4973.40	2	<0.001	0.00

Table A.3: Results from generalized linear models analyzing the effect of productivity (prod.), predator identity (predator), log metacommunity size (meta.size), log nearest neighbor connectivity (connectivity), and all additive combinations among those variables on predator and prey extinction and colonization dynamics. Models are listed in order by delta AIC for each species separately. Also included are the effective degrees of freedom (*df*), Akaike weights (w_i), and the fraction of null deviance (R^2) explained by the model.

Response	Model	ΔAIC	*df*	w_i	R^2
Prey Colonization	~ prod.+connectivity+predator	0	5	0.64	0.33
	~ prod.+meta.size+connectivity+predator	1.1	6	0.36	0.33
	~ prod.+connectivity	13.9	4	<0.001	0.31
	~ prod.+meta.size+connectivity	15.8	5	<0.001	0.31
	~ prod.+meta.size+predator	65	5	<0.001	0.25
	~ meta.size+connectivity+predator	79.2	4	<0.001	0.23
	~ meta.size+connectivity	81.6	3	<0.001	0.23
	~ meta.size+predator	94.3	3	<0.001	0.21
	~ connectivity	102.4	2	<0.001	0.20
	~ prod.+meta.size	104.2	4	<0.001	0.20
	~ connectivity+predator	104.4	3	<0.001	0.20
	~ meta.size	121.2	2	<0.001	0.18
	~ prod.+predator	159.1	4	<0.001	0.14
	~ prod.	176.6	3	<0.001	0.11
	~ predator	245.1	2	<0.001	0.03
	~1	264.7	1	<0.001	0.00
Predator Colonization	~ prod.+meta.size+connectivity+predator	0	6	1.00	0.44
	~ prod.+connectivity+predator	21.8	5	<0.001	0.42
	~ prod.+meta.size+predator	100.1	5	<0.001	0.38
	~ prod.+predator	120.2	4	<0.001	0.37
	~ prod.+meta.size+connectivity	311.7	5	<0.001	0.26
	~ prod.+connectivity	322.4	4	<0.001	0.25
	~ prod.+meta.size	325.1	4	<0.001	0.25
	~ meta.size+connectivity+predator	405.5	4	<0.001	0.20
	~ prod.	409.3	3	<0.001	0.20
	~ connectivity+predator	539.7	3	<0.001	0.12
	~ meta.size+connectivity	597.9	3	<0.001	0.09
	~ connectivity	608.7	2	<0.001	0.08
	~ meta.size+predator	689.4	3	<0.001	0.03

	~ predator	698.6	2	<0.001	0.03
	~ meta.size	744.4	2	<0.001	0.00
	~1	745.3	1	<0.001	0.00
Prey Extinction	~ prod.+meta.size+connectivity+predator	0	6	0.92	0.44
	~ prod.+connectivity+predator	4.8	5	0.08	0.44
	~ prod.+connectivity	14.7	4	<0.001	0.43
	~ prod.+meta.size+connectivity	15.3	5	<0.001	0.43
	~ prod.+meta.size	186.7	4	<0.001	0.31
	~ prod.+meta.size+predator	188.5	5	<0.001	0.31
	~ meta.size+connectivity+predator	249.7	4	<0.001	0.26
	~ meta.size+connectivity	284.9	3	<0.001	0.24
	~ connectivity+predator	301.7	3	<0.001	0.22
	~ connectivity	302.5	2	<0.001	0.22
	~ prod.+predator	361.5	4	<0.001	0.18
	~ prod.	370.2	3	<0.001	0.18
	~ meta.size+predator	522	3	<0.001	0.07
	~ meta.size	571.4	2	<0.001	0.03
	~ predator	604.4	2	<0.001	0.01
	~1	616.2	1	<0.001	0.00
Predator Extinction	~ prod.+meta.size+connectivity+predator	0	6	0.80	0.51
	~ prod.+connectivity+predator	3.5	5	0.14	0.50
	~ prod.+meta.size+predator	4.9	5	0.07	0.50
	~ prod.+predator	63.3	4	<0.001	0.42
	~ prod.+meta.size+connectivity	130.4	5	<0.001	0.32
	~ prod.+meta.size	132.8	4	<0.001	0.32
	~ prod.+connectivity	202.3	4	<0.001	0.22
	~ meta.size+connectivity+predator	214	4	<0.001	0.20
	~ meta.size+connectivity	214.2	3	<0.001	0.20
	~ meta.size	221.4	2	<0.001	0.19
	~ meta.size+predator	222.8	3	<0.001	0.19
	~ connectivity+predator	229.1	3	<0.001	0.18
	~ prod.	258	3	<0.001	0.14
	~ connectivity	265	2	<0.001	0.13
	~ predator	346.2	2	<0.001	0.01
	~1	351.7	1	<0.001	0.00

Table A.4: Results from GLMs analyzing the effect of predator and prey observed occupancy on predicted occupancy at the regional and local scale, as well as the effects of observed occupancy on colonization and extinction probability at the local scale. Results are presented for the entire duration of the experiment. Each model was compared to a null model. Models are ranked by ΔAIC separately for each scale and response variable. Each model is presented with AIC, the degrees of freedom, Akaike weights (w_i), and the fraction of null deviance (R^2) explained.

Scale	Response	model	ΔAIC	*df*	w_i	R^2
Network	Prey observed occupancy	~prey predicted occupancy	0	3	1	0.80
		~1	76.9	2	<0.001	0
	Predator observed occupancy	~predator predicted occupancy	0	3	1	0.85
		~1	101.9	2	<0.001	0
Local	Prey observed occupancy	~prey predicted occupancy	0	3	1	0.85
		~1	420.1	2	<0.001	0
	Predator observed occupancy	~predator predicted occupancy	0	3	1	0.93
		~1	684.7	2	<0.001	0
	Prey colonization probability	~prey observed occupancy	0	3	1	0.51
		~1	153.4	2	<0.001	0
	Predator colonization probability	~predator observed occupancy	0	3	1	0.84
		~1	390.8	2	<0.001	0
	Prey extinction probability	~prey observed occupancy	0	3	1	0.47
		~1	140.5	2	<0.001	0
	Predator extinction probability	~predator observed occupancy	0	3	1	0.68
		~1	233.6	2	<0.001	0

Supplementary Figures.

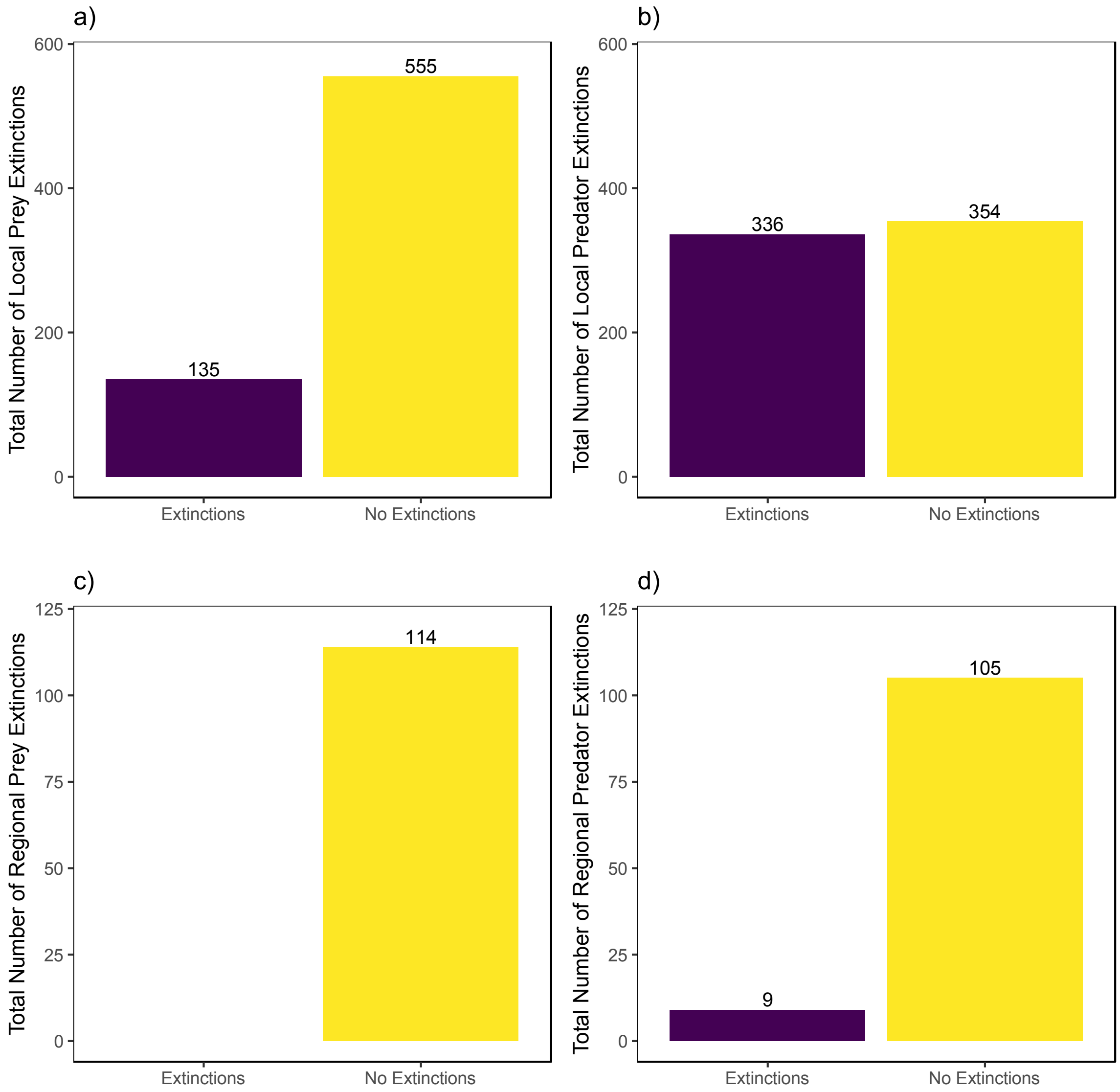

Figure A.1: Total number of local (a, b) and regional (c, d) extinctions for prey (a, c) and predators (b, d), where extinction was defined by species experiencing 0 density at any time point throughout the experiment.

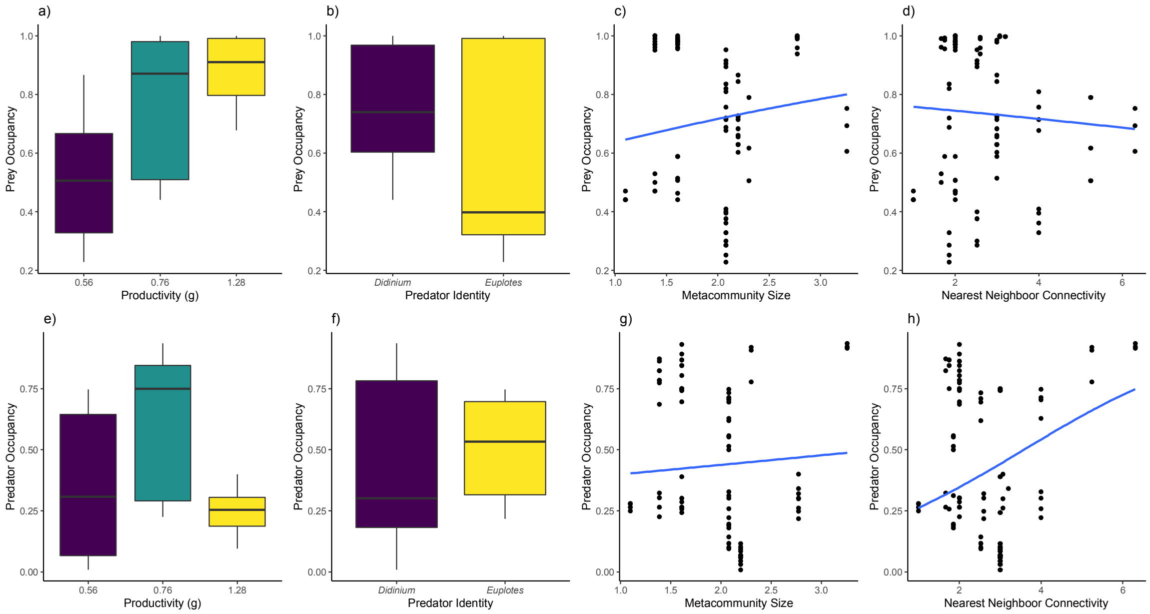

Figure A.2: Regional occupancy dynamics of prey (a-d) and predator (e-h) species as a function of productivity (a, e), predator identity (b, f), metacommunity size (c, g), and connectivity (d, h). Best fit lines are shown as GLMs for individual predictor variables.

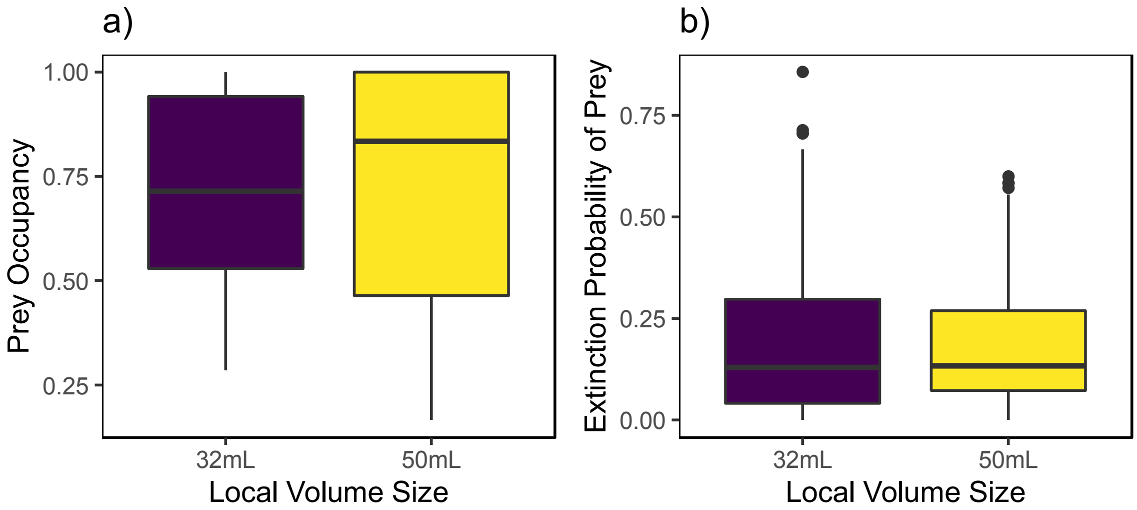

Figure A.3: Local prey occupancy (a) and extinction probability of prey (b) as a function of local volume used in microcosm experiments. Results from anova analyses were non-significant and indicate that variation in volume used in experimental microcosms did not influence outcomes in this synthesis.

Appendix B

Supplementary Material for Chapter 2: Rethinking biodiversity patterns and processes in stream ecosystems

Supplementary Tables.

Table B.1: Summary Spatial PCAs used in TEC analyses where the variables log transformed river distance below upstream lakes (Lake.dist), log transformed river distance from headwaters (Head.dist), upstream lake area (Up.Lake.area), and elevation were used to create the spatial gradient.

Network	Spatial Variable	PC1
Cascade	Head.dist	-0.58
	Lake.dist	-0.45
	Up.Lake.area	-0.34
	Elevation	0.58
Evo	Head.dist	-0.66
	Lake.dist	-0.33
	Up.Lake.area	-0.08
	Elevation	0.68
Bubbs	Head.dist	0.66
	Lake.dist	0.43
	Up.Lake.area	-0.25
	Elevation	-0.57
Rock	Head.dist	-0.57
	Lake.dist	-0.53
	Up.Lake.area	0.26
	Elevation	0.57

Table B.2: Summary output from the Spatial PCA used to create a spatial gradient from isolated to connected sites.

Network	Component	PC1
Cascade	Standard deviation	1.63
	Proportion of Variance	0.66
	Cumulative Proportion	0.66
Evo	Standard deviation	1.46
	Proportion of Variance	0.53
	Cumulative Proportion	0.53
Bubbs	Standard deviation	1.35
	Proportion of Variance	0.45
	Cumulative Proportion	0.45
Rock	Standard deviation	1.73
	Proportion of Variance	0.75
	Cumulative Proportion	0.75

Table B.3: Summary Environmental PCA used in the TEC analyses where the variables Temperature (Temp), Benthic Chlorophyll (Chlorophyll), Conductivity, Dissolved Oxygen (DO), pH, Discharge, and the landscape variable shrub percentage were used to create the environmental gradient.

Network	Environmental Variable	PC1
Cascade	Temp	0.31
	Chlorophyll	0.45
	Conductivity	-0.33
	DO	0.51
	pH	-0.41
	Discharge	-0.32
	Shrub	0.25
Evo	Temp	0.66
	Chlorophyll	0.18
	Conductivity	-0.26
	DO	-0.27
	pH	0.49
	Discharge	0.38
	Shrub	-0.09
Bubbs	Temp	0.47
	Chlorophyll	-0.24
	Conductivity	-0.15
	DO	0.52
	pH	0.46
	Discharge	-0.33
	Shrub	-0.32
Rock	Temp	0.37
	Chlorophyll	0.14
	Conductivity	0.41
	DO	-0.53
	pH	-0.26
	Discharge	0.47
	Shrub	0.33

Table B.4: Summary output from the Environmental PCA used to create and environmental gradient of environmentally harsh to environmentally favorable sites.

Network	Components	PC1
Cascade	Standard deviation	1.66
	Proportion of Variance	0.40
	Cumulative Proportion	0.40
Evo	Standard deviation	1.44
	Proportion of Variance	0.30
	Cumulative Proportion	0.30
Bubbs	Standard deviation	1.79
	Proportion of Variance	0.46
	Cumulative Proportion	0.46
Rock	Standard deviation	1.74
	Proportion of Variance	0.43
	Cumulative Proportion	0.43

Supplementary Figures.

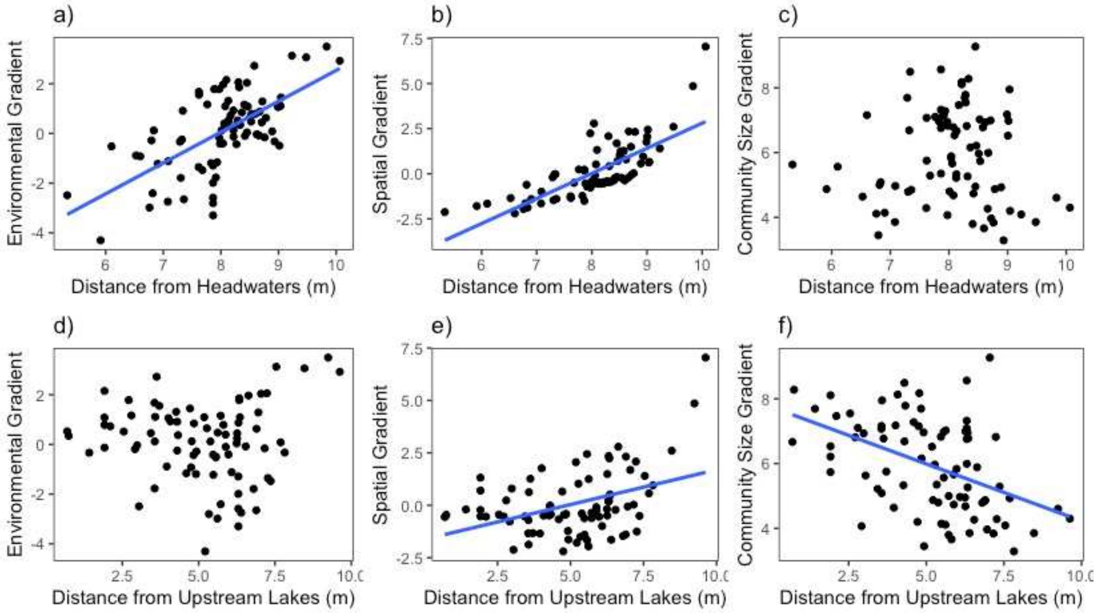

Figure B.1: Relationships between the two spatial gradients used in the Stream Ecology Analyses and the three gradients used in the TEC analyses.

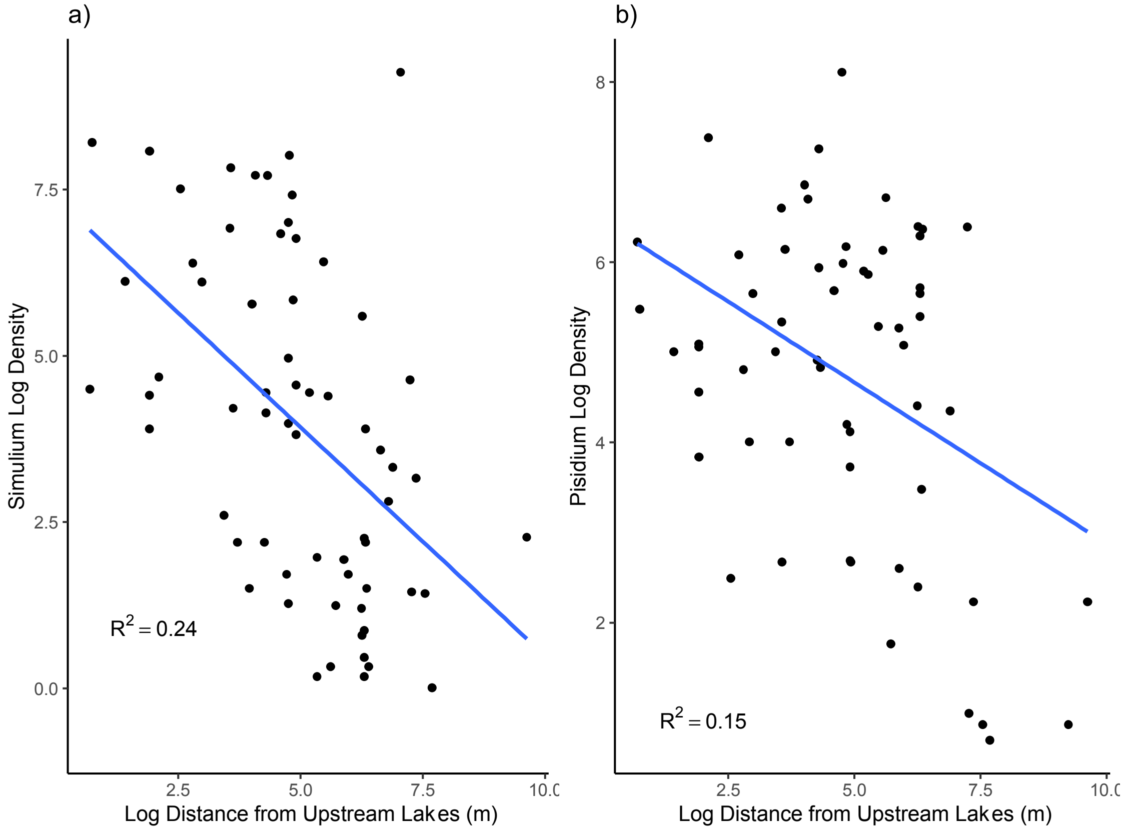

Figure B.2: Density of a) *Simulium* and b) *Pisidium*, two common filter feeding species as a function of log distance from upstream lakes. We ran a simple linear model of log *Simulium* density or log *Pisidium* density as a function of log distance from upstream lakes to validate the models and obtain R^2 values.

Appendix C

Supplementary Material for Chapter 3: The influence of non-native fish on stream macroinvertebrate and lake zooplankton communities along elevational gradients

Supplementary Methods.

Fish presence in the Sierra Nevada, CA is influenced by elevation and fish occupancy generally decreases with elevation (Knapp et al. 2001). In order to determine whether elevation and fish occupancy was a confounding factor, we ran an ANOVA on fish presence/absence as a function of elevation. We determined the significance of this relationship using p-values and for both lake and stream datasets, and we did not find a significant effect of elevation on fish presence (Figure C.1; Table C.1).

Supplementary Tables.

Table C.1: Results from ANOVAS on the differences in fish and fishless sites as a function of elevation. This table corresponds with Figure C.1.

Ecosystem	Factor	Estimate	Std.Error	t value	P-value
Lake	(Intercept)	3127.24	21.03	148.737	<2e-16
	Fish	46.62	29.21	1.596	0.111
Stream	(Intercept)	3379	26.1	129.474	<2e-16
	Fish	-24.3	32.49	-0.748	0.457

Table C.2: Multivariate homogeneity of group dispersions test from lake zooplankton and stream macroinvertebrates as a function of fish.

Ecosystem	Factor	*df*	Sum of Squares	Mean of Squares	F value	P-value
Lake	Fish	1	0.2895	0.289516	14.952	0.0001357
	Residuals	295	5.7122	0.019364		
Stream	Fish	1	0.00362	0.0036164	0.4272	0.5156
	Residuals	67	0.56716	0.0084651		

Table C.3: GLMs of zooplankton and macroinvertebrate species body mass as a function of fish. This analysis included species missing from either fishless or fish present sites. Models are ranked by ΔAIC separately for each species and dataset. Each model is presented with AIC, the degrees of freedom, Akaike weights w_i, and the fraction of null deviance (R^2) explained.

Ecosystem	Model	ΔAIC	*df*	w_i	R^2
Lake	~1	0	2	0.73	0
	~Fish	2	3	0.27	0
Stream	~1	0	2	0.73	0
	~Fish	2	3	0.27	0

Table C.4: Lake zooplankton and stream macroinvertebrate species absent from either fishless or fish present sites.

Ecosystem	Taxa	Site Absent From
Lake	*Alona sp.*	Fishless
	Alonella excisa	Fishless
	Ascomorpha sp.	Fishless
	Polyphemus pediculus	Fishless
	Trichotria sp.	Fishless
	Polyarthra vulgaris	Fish
	Synchaeta sp.	Fish
Stream	*Aedes*	Fishless
	Alloperla	Fishless
	Allotrichoma	Fishless
	Blephariceridae	Fishless
	Brachycentrus	Fishless
	Callibaetis	Fishless
	Calliperla	Fishless
	Centroptilum	Fishless
	Cheumatopsyche	Fishless
	Claassenia	Fishless
	Cleptelmis	Fishless
	Deuterophlebia	Fishless
	Ephemerella	Fishless
	Glutops	Fishless
	Hesperoperla	Fishless
	Hexatoma	Fishless
	Hirudinea	Fishless
	Hydra	Fishless
	Hydropsyche	Fishless
	Lepidostoma	Fishless
	Limnophila	Fishless
	Malenka	Fishless
	Megarcys	Fishless
	Monophilus	Fishless
	Narpus	Fishless
	Nemertea	Fishless

	Ochrotrichia	Fishless
	Oreodytes	Fishless
	Orohermes	Fishless
	Pedicia	Fishless
	Perlinodes	Fishless
	Planorbidae	Fishless
	Polycentropus	Fishless
	Rhithrogena	Fishless
	Rhizelmis	Fishless
	Sanfilippodytes	Fishless
	Siphlonurus	Fishless
	Skwala	Fishless
	Stictotarsus	Fishless
	Tipula	Fishless
	Wiedeman	Fishless
	Arctopsyche	Fish
	Chyranda	Fish
	Culiseta	Fish
	Lednia	Fish
	Limonia	Fish
	Nixe	Fish
	Sciara	Fish
	Soyedina	Fish

Supplementary Figures.

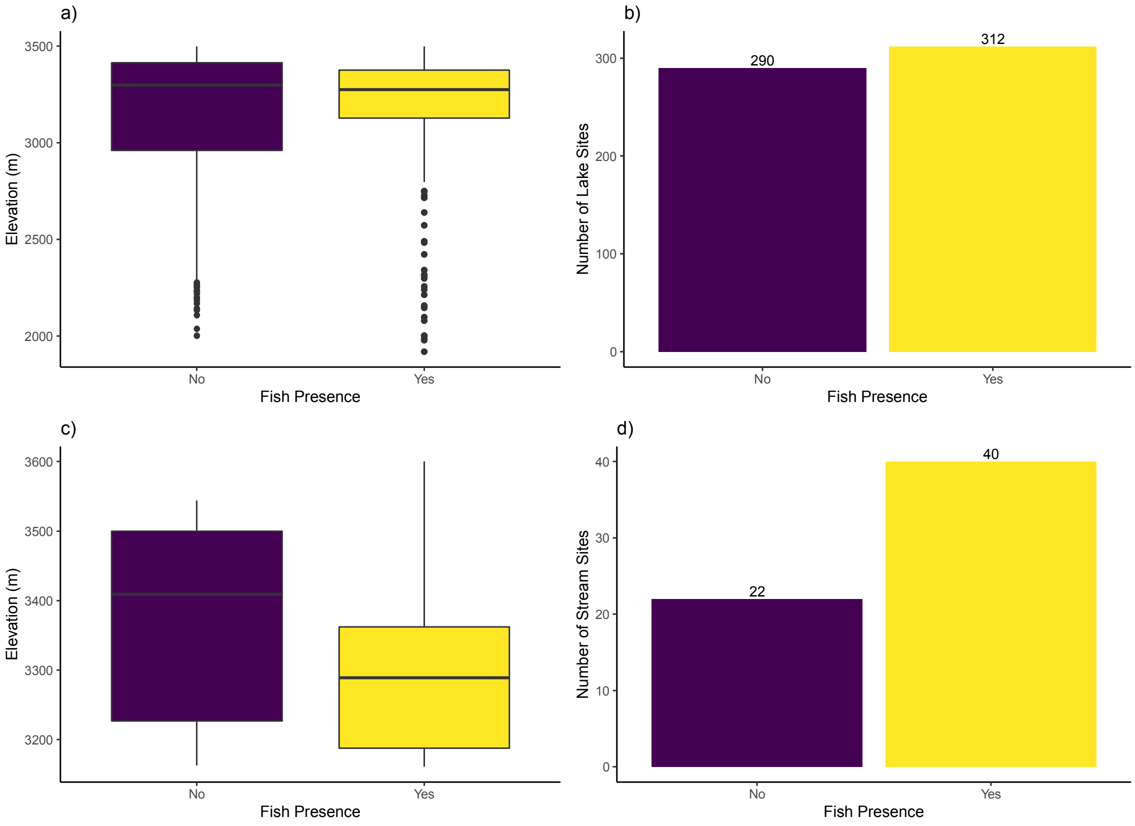

Figure C.1: Relationship between fish presence and elevation for two datasets on Sierra Nevada, CA lakes (a) and streams (c) and the total number of fish and fishless lake (b) and stream sites (d).

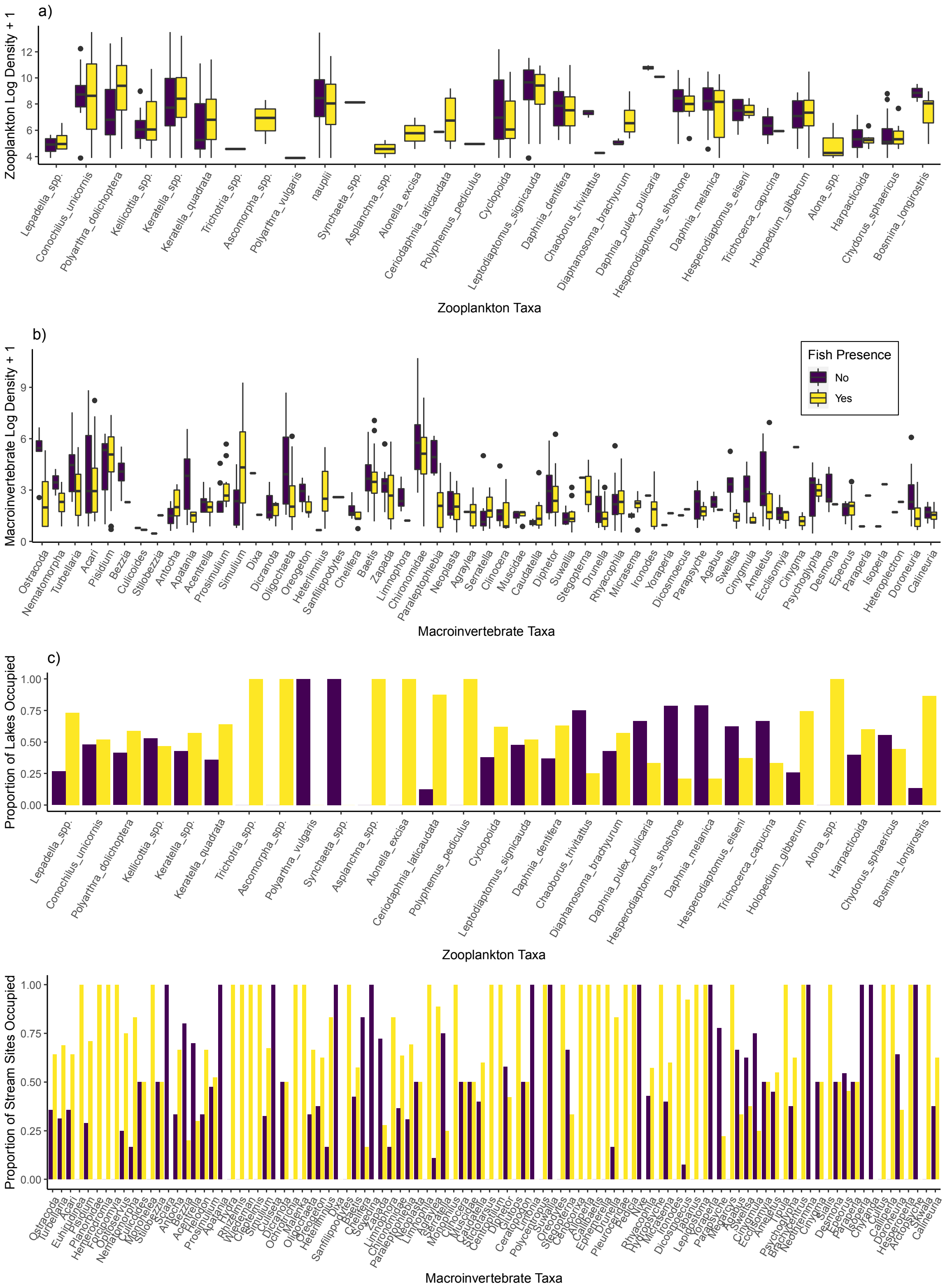
a)
Zooplankton Log Density + 1
4
6
8
10
12
Lepadella_spp.
Conochilus_unicornis
Polyarthra_dolichoptera
Kellicottia_spp.
Keratella_spp.
Keratella_quadrata
Trichotria_spp.
Ascomorpha_spp.
Polyarthra_vulgaris
nauplii
Synchaeta_spp.
Asplanchna_spp.
Alonella_excisa
Ceriodaphnia_laticaudata
Polyphemus_pediculus
Cyclopoida
Leptodiaptomus_signicauda
Daphnia_dentifera
Chaoborus_trivittatus
Diaphanosoma_brachyurum
Daphnia_pulex_pulicaria
Hesperodiaptomus_shoshone
Daphnia_melanica
Hesperodiaptomus_eiseni
Trichocerca_capucina
Holopedium_gibberum
Alona_spp.
Harpacticoida
Chydorus_sphaericus
Bosmina_longirostris
Zooplankton Taxa
b)
Macroinvertebrate Log Density + 1
0
3
6
9
Fish Presence
No
Yes
Ostracoda
Nematomorpha
Turbellaria
Acari
Pisidium
Bezzia
Culicoides
Stilobezzia
Antocha
Apatania
Acentrella
Prosimulium
Simulium
Dixa
Dicranota
Oligochaeta
Oreogeton
Heterlimnius
Sanfilippodytes
Chelifera
Baetis
Zapada
Limnophora
Chironomidae
Paraleptophlebia
Neoplasta
Agraylea
Serratella
Clinocera
Muscidae
Caudatella
Diphetor
Suwallia
Stegopterna
Drunella
Rhyacophila
Micrasema
Ironodes
Yoraperla
Dicosmoecus
Parapsyche
Agabus
Sweltsa
Cinygmula
Ameletus
Ecclisomyia
Cinygma
Psychoglypha
Desmona
Epeorus
Paraperla
Isoperla
Heteroplectron
Doroneuria
Calineuria
Macroinvertebrate Taxa
c)
Proportion of Lakes Occupied
0.00
0.25
0.50
0.75
1.00
Lepadella_spp.
Conochilus_unicornis
Polyarthra_dolichoptera
Kellicottia_spp.
Keratella_spp.
Keratella_quadrata
Trichotria_spp.
Ascomorpha_spp.
Polyarthra_vulgaris
Synchaeta_spp.
Asplanchna_spp.
Alonella_excisa
Ceriodaphnia_laticaudata
Polyphemus_pediculus
Cyclopoida
Leptodiaptomus_signicauda
Daphnia_dentifera
Chaoborus_trivittatus
Diaphanosoma_brachyurum
Daphnia_pulex_pulicaria
Hesperodiaptomus_shoshone
Daphnia_melanica
Hesperodiaptomus_eiseni
Trichocerca_capucina
Holopedium_gibberum
Alona_spp.
Harpacticoida
Chydorus_sphaericus
Bosmina_longirostris
Zooplankton Taxa
Proportion of Stream Sites Occupied
0.00
0.25
0.50
0.75
1.00
Macroinvertebrate Taxa

Figure C.2: Zooplankton (a, c) and macroinvertebrate (b, d) species density (a, b) and proportion of occurrence as a function of fish presence. The order of each x-axis is based on average body size, from smallest to largest species.

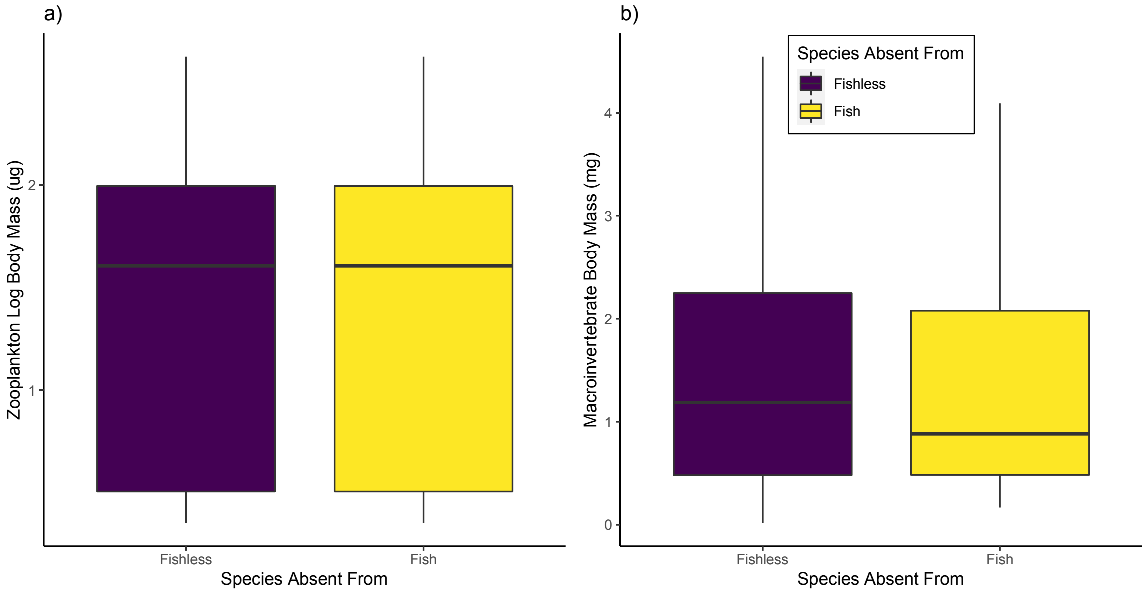

Figure C.3: Zooplankton (a) and macroinvertebrate (b) species body mass as a function of whether species were absent from fish or fishless sites. This analysis only included species that were missing from either fish or fishless sites.

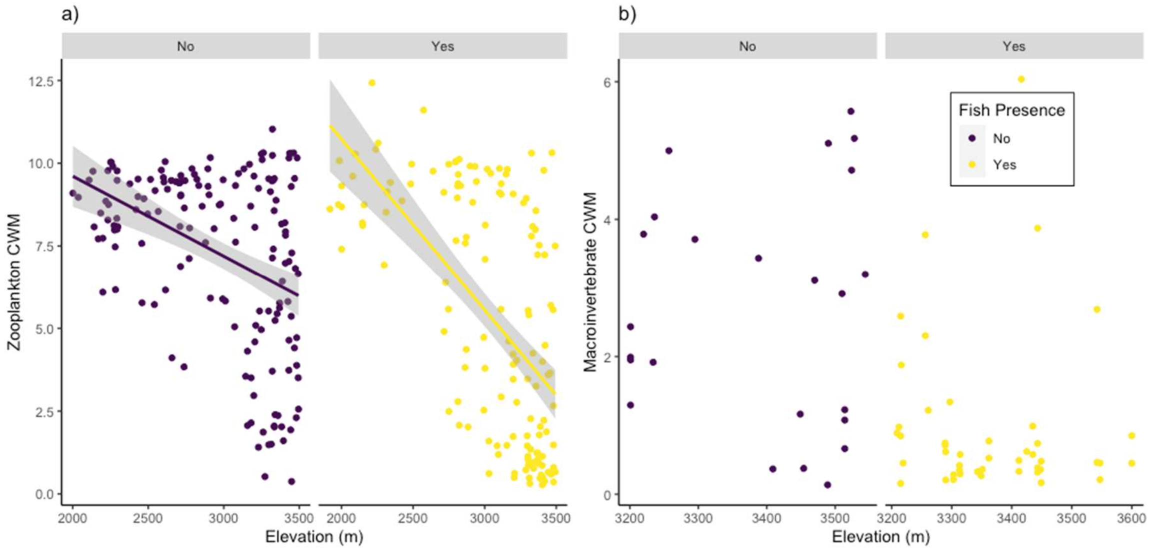

Figure C.4: CWM of zooplankton (a) and macroinvertebrate (b) community biomass along an elevational gradient. Significant relationships are shown with plotted regression lines.