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ARTICLE

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, California, USA to test established stream ecology frameworks and compared them with 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 that 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 the 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.

KEYWORDS
community assembly, diversity, macroinvertebrate, spatial, stream ecology, theory of ecological communities

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) (Leibold et al., 2020; Leibold & Chase, 2018; Vellend, 2010, 2016). 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 for linking patterns in biodiversity with processes (Leibold et al., 2020; Siqueira 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 & 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 & 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 (Dias et al., 2014; Oberdorff et al., 2019; Tedesco et al., 2012; Townsend, 1989). 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 & 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 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 long-standing conceptual frameworks in stream biodiversity is the river continuum concept (RCC; Doretto et al., 2020). The RCC describes a linear view of streams, in which 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., first-fourth 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 (Figure 1a; Finn et al., 2011). Despite the majority of studies finding positive relationships between local diversity and downstream distance, many studies have found the opposite or no patterns at all, calling into question the generality of the RCC (please refer to 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 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 (please also refer to Brown & Swan,

TABLE 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

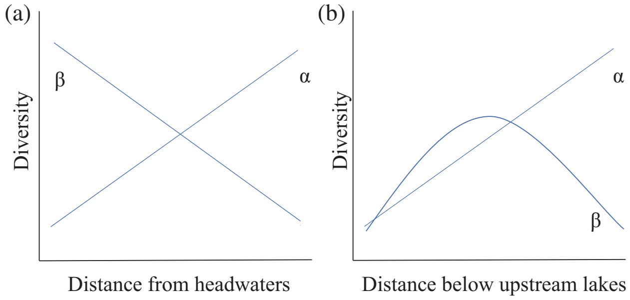

FIGURE 1 Hypothesized relationships for patterns of α- and β-diversities as a function of (a) distance from the headwaters and (b) distance below upstream lakes. (a) The α-diversity pattern is predicted by the river continuum concept (RCC) and the β-diversity pattern is predicted by the mighty headwaters hypothesis (MHH). (b) The α-diversity pattern is predicted by the serial discontinuity concept (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

2010; Carrara et al., 2012; Schmera et al., 2018; Figure 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), hump-shaped patterns of β-diversity (Wang et al., 2020), and no pattern (Harrington et al., 2016; Tonkin et al., 2016). The MHH posits that dispersal and niche selection influence β-diversity (Table 1; Finn et al., 2011) and there is empirical support that dispersal and niche selection (Brown & 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 with 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 (Figure 1b; Ward & Stanford, 1983). The few empirical tests of the SDC lend support to the concept (Ellis & Jones, 2013; Ellis & Jones, 2016; Guzy et al., 2018; Mwedzi et al., 2016; Voelz & Ward, 1991), 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 & Mackay, 1991). These communities are replaced by more typical stream communities increasingly downstream (Robinson & Wayne 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 (Figure 1b). The SDC focuses on how dispersal and niche selection drive local community diversity and now, through this paper, community variability (Table 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 with 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). Furthermore, 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; Herbst et al., 2019; von Schiller et al., 2017). Therefore, 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 TEC 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 toward 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 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, California (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 & Wilson, 1967; Vellend, 2016), although this relationship has also been shown theoretically (Mouquet & 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 & Harms, 2009). Compositional dissimilarity is predicted to decrease with increasing dispersal due to mixing (Figure 2a; Hubbell, 2001; Mouquet & 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 (Figure 2b; Chase, 2003; Cornell, 1985; Cornell & Harrison, 2014; Kraft et al., 2011; Srivastava, 1999). Importantly, local-scale processes (competition, niche partitioning) can also create opportunities for speciation over longer time scales (Mittelbach & Schemske, 2015).

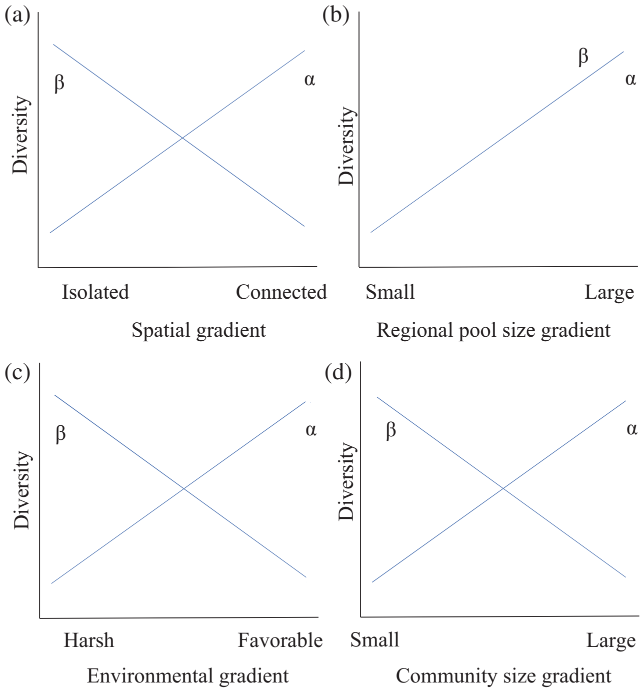

FIGURE 2 Conceptual framework incorporating ecological processes from the theory of ecological communities (Vellend, 2010, 2016). This framework highlights hypothesized relationships for patterns of α- and β-diversities along (a) spatial, (b) regional pool size, (c) environmental, and (d) community size gradients. This allows direct testing of understanding the relative importance of the 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

Environmental gradients have a long history in ecology to explain local control of community structure, from this point forwards referred to as niche selection. In stream ecosystems, environmental gradients should include relevant environmental variables to which stream biota respond, 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 (Figure 2c; Chase & Leibold, 2003; Chase & Myers, 2011).

Last, 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 & Watling, 2010). If ecological drift is important, local diversity should increase and community dissimilarity should decrease with increasing community size (Figure 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 therefore random birth and death events are more likely to alter community composition (Orrock & 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 1) using landscape biodiversity patterns from macroinvertebrate stream communities across a series of high-elevation lake–stream networks in Sierra Nevada, California. 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 (Baker et al., 2016; Jones, 2010). 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 (Nelson et al., 2009; Sadro et al., 2012; Soranno, 1999). 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 & Mackay, 1991). Landscape biodiversity patterns in lake–stream networks are poorly understood due to the 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, California. We first tested the predictions from stream ecology theories, (e.g., RCC, MHH, and SDC) in lake–stream networks and then integrated 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 (Figure 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 (Figure 2).

METHODS

Study area

The study area was located in the Sierra Nevada of eastern California (USA) and encompasses portions of Inyo National Forest and Sequoia and Kings Canyon National Parks. 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 (Figure 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 ($n = 11$–36) and the downstream lake gradient varied ($n = 1$–9). This field system and the data collected naturally provide spatial gradients relevant to test stream ecology theories. In addition, these data are 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

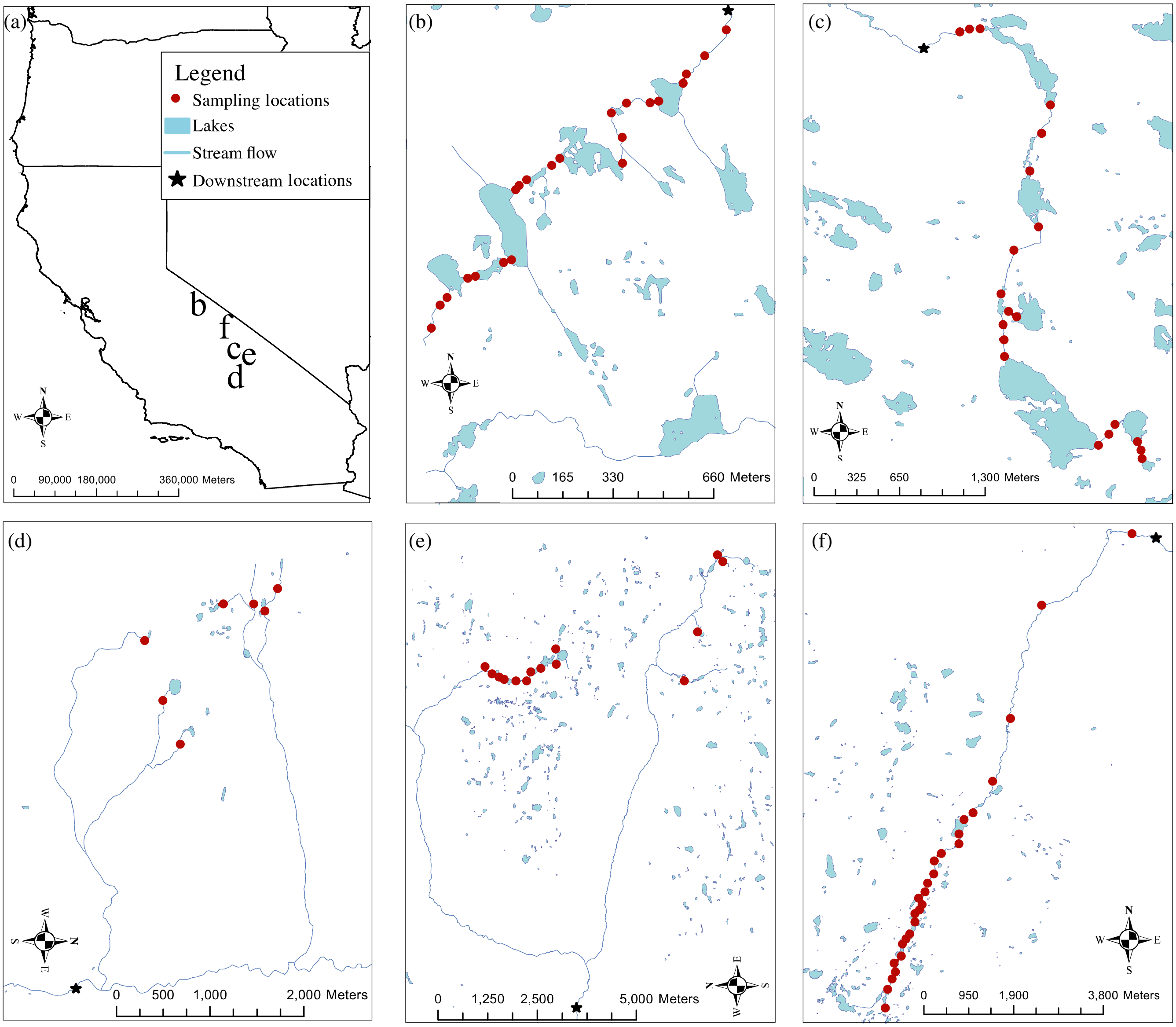

FIGURE 3 Distribution of field sampling sites in the Sierra Nevada, California (a). Five lake–stream networks: (b) Cascade Lake Network, (c) Evolution Lake Network, (d) Kern Lake Network, (e) Bubbs Lake Network, and (f) Rock Creek Network, were sampled across a spatial gradient from the headwaters moving downstream and a spatial gradient from lake outlets moving downstream

depth × current velocity × 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 were 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 s (Herbst & Cooper, 2010). Chlorophyll measurements were taken using a handheld fluorometer (Turner Designs Aquafluor), which measured raw fluorescence units. Florescence 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.

In total, 8–12 macroinvertebrate samples at each site were collected using a D-frame kick net (250 μm mesh, 30 cm opening, 0.09 m^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 (30 cm × 30 cm) immediately above the net, with dislodged invertebrates being carried by currents into the net. All macroinvertebrate samples were preserved in 75% ethanol within 48 h 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 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.

Spatial data

Stream distance measurements were taken using the R package *riverdist*, which utilizes data from the USGS National Hydrological Dataset Flowline 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 (US Geological Survey, 2016). In cases in which 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 five 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 β-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 & De Cáceres, 2013). We calculated the total β-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 & De 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 (Figure 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 (Figure 1).

We fit GLMMs using the *glmmTMB* package with Gaussian error distributions for local diversity and β error distributions for LCBD to identify spatial drivers of local and β-diversity (M. E. Brooks, Kristensen, 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 assumed that these spatial metrics are proxies for environmental and/or spatial processes. We used a model selection approach by assessing ΔAIC 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 (Figure 2). We removed sites from this analysis where environmental data were 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 (section "*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, Wolfenden, et al., 2017; Kurthen et al., 2020; Parisek, 2018). 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 S1: Tables S1, S2).

To estimate the effect of niche selection, we used an environmental gradient ranging from environmentally favorable to environmentally harsh sites. We ran a 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 S1: Tables S3 and S4).

To estimate the effect of ecological drift on communities, we used community size as a proxy for the effect of ecological drift (Orrock & Watling, 2010; Siqueira et al., 2020; Vellend, 2016). 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 of interpreting three-way interaction models. We used a model selection approach in the same manner as previously described (section "*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 β-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 last, 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; Figure 4e; Table 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; Figure 4a; Table 2) and little to no support with the effect of headwater distance alone (weight = 0.0017, ΔAIC = 12.6; Figure 4c; Table 2).

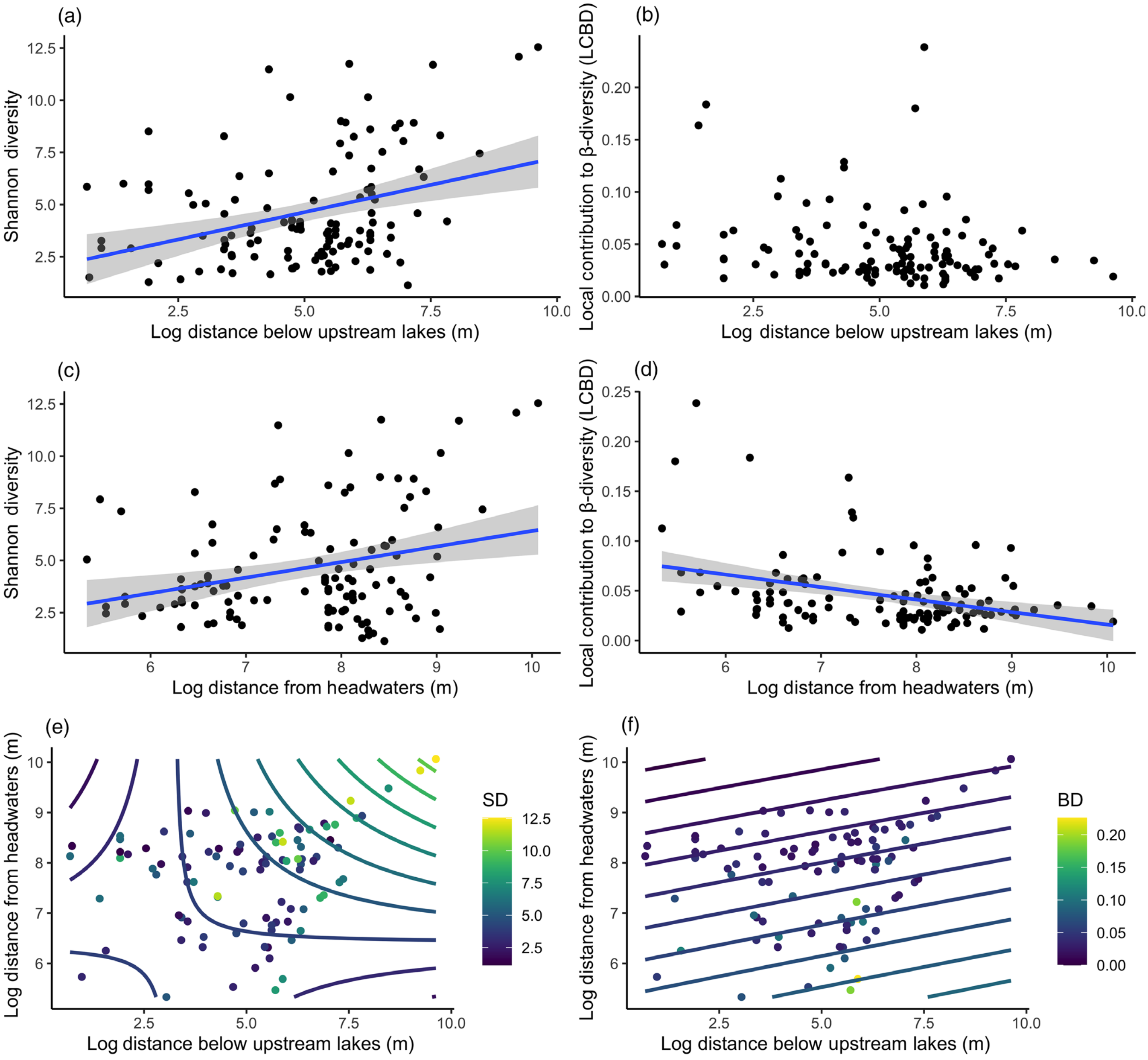

FIGURE 4 Shannon diversity (a, c, e) and local contribution to β-diversity (b, d, f) of stream macroinvertebrate communities as a function of log-transformed distance below upstream lakes (a, b) or distance from headwaters (c, d) across five lake–stream networks. Interaction contour plots of Shannon diversity (SD; e) 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 generalized linear mixed models (GLMMs) are found in Table 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 β-diversity decreased (weight = 0.99, ΔAIC = 0; Figure 4f; Table 2). Model selection provided less support that β-diversity was highest in headwaters and declined moving downstream (weight = 0.0021, ΔAIC = 12.3; Figure 4d; Table 2).

Biodiversity patterns and processes from applied TEC framework

Model selection determined that local diversity was structured interactively along the environmental and

TABLE 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 ΔAIC for each species diversity metric. Also included are the effective degrees of freedom (df) and the Akaike weights

Species diversity and 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

Abbreviations: LCBD, local contribution to β-diversity; MHH, mighty headwaters hypothesis; RCC, river continuum concept; SDC, serial discontinuity concept.

community size gradients (weight = 1, ΔAIC = 0; Figure 5a; Table 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; Figure 5a; Table 3). All other models of local diversity had low degrees of support (weight ≤ 0.001; Figure 5; Table 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; Figure 6e; Table 3). All other models of β-diversity had low degrees of support (weight ≤ 0.01; Figure 6; Table 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 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 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 that 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 S1: Figure S1). 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

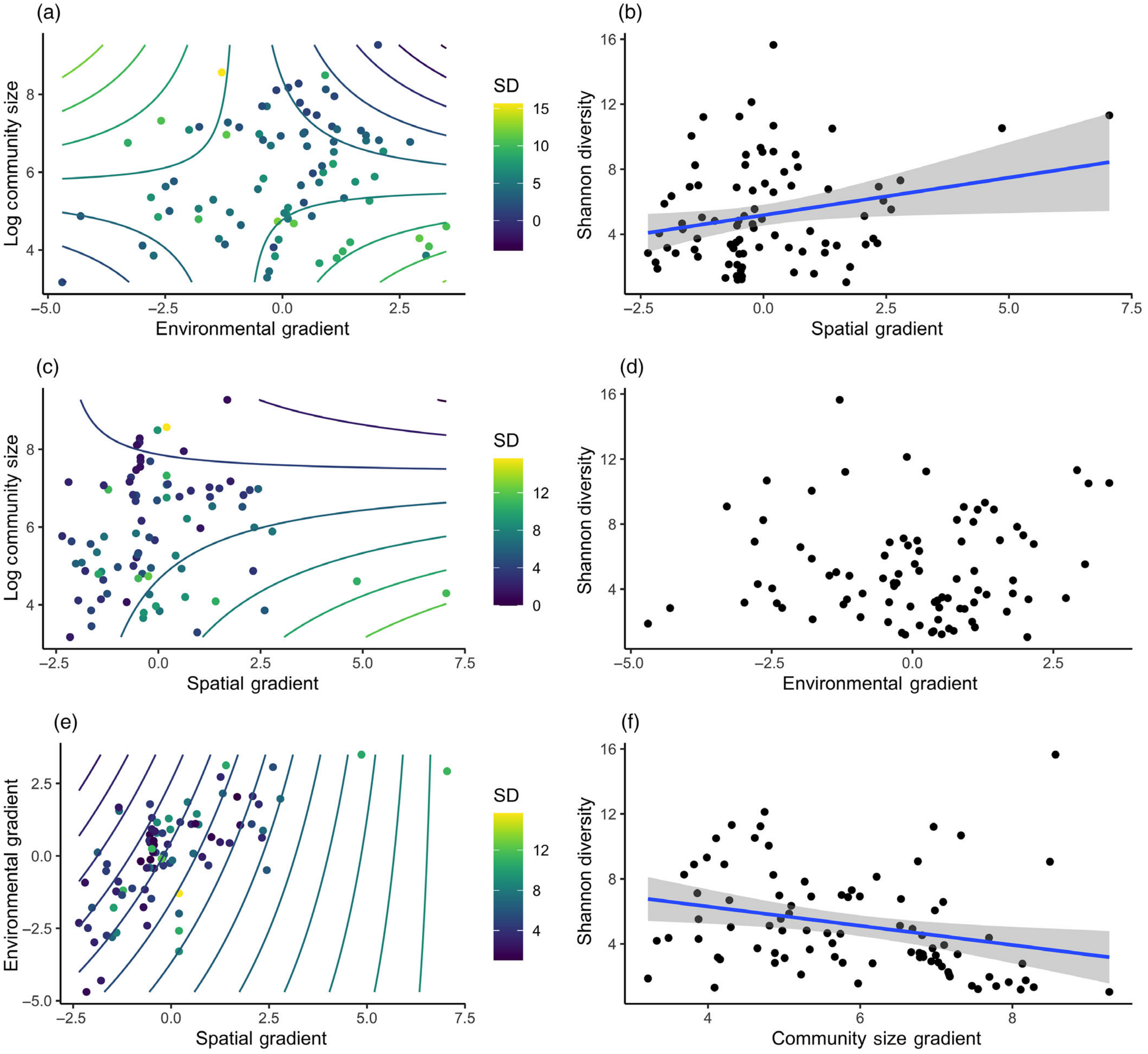

FIGURE 5 Shannon diversity (SD) of stream macroinvertebrate communities as a function of the spatial gradient (b), environmental gradient (d), community size gradient (f), and all pairwise interactions (a, c, e) among these gradients. Significant relationships are shown with plotted regression lines or contour lines. Full results from generalized linear mixed models (GLMMs) are found in Table 3

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. Therefore, our results highlight the challenge of using individual stream ecology frameworks as none was 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 increase with increasing spatial connectivity (Figure 2a), dispersal was not the primary process structuring local diversity in our study. The pattern of local diversity increasing with dispersal is widely supported (Cadotte, 2006; Kalmar & Currie, 2006; MacArthur &

TABLE 3 Results from generalized linear mixed models 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 ΔAIC for each species diversity metric. Also included are the effective degrees of freedom (df) and the Akaike weights

Species diversity and theory of ecological communities 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

Wilson, 1967), although there are studies that show a hump-shaped relationships (Cadotte, 2006; Mouquet & Loreau, 2003) and in which dispersal had no effect (Shurin, 2000; Warren, 1996). 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 (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. Furthermore, 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 (Brown & Swan, 2010; Clarke et al., 2008). In addition, incorporating further metrics such as overland distance metrics and dispersal traits may provide more support in explaining the influence of dispersal (Brown & Swan, 2010; Tonkin et al., 2018). Last, local species richness in areas of low diversity may not be limited by dispersal, but by processes occurring at smaller scales such as niche selection and ecological drift.

At larger spatial scales, dispersal influenced β-diversity, whereas β-diversity was highest in spatially isolated areas and decreased with increasing spatial connectivity. This supports the MHH and associated mechanisms in which 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 & 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, Wolfenden, et al., 2017; Parisek, 2018). Other studies have shown that upstream lakes influence dispersal and this has been hypothesized to be important in allowing filter-feeding communities near lake outlets to maintain their dominance (Richardson & Mackay, 1991). Indeed, Simuliidae

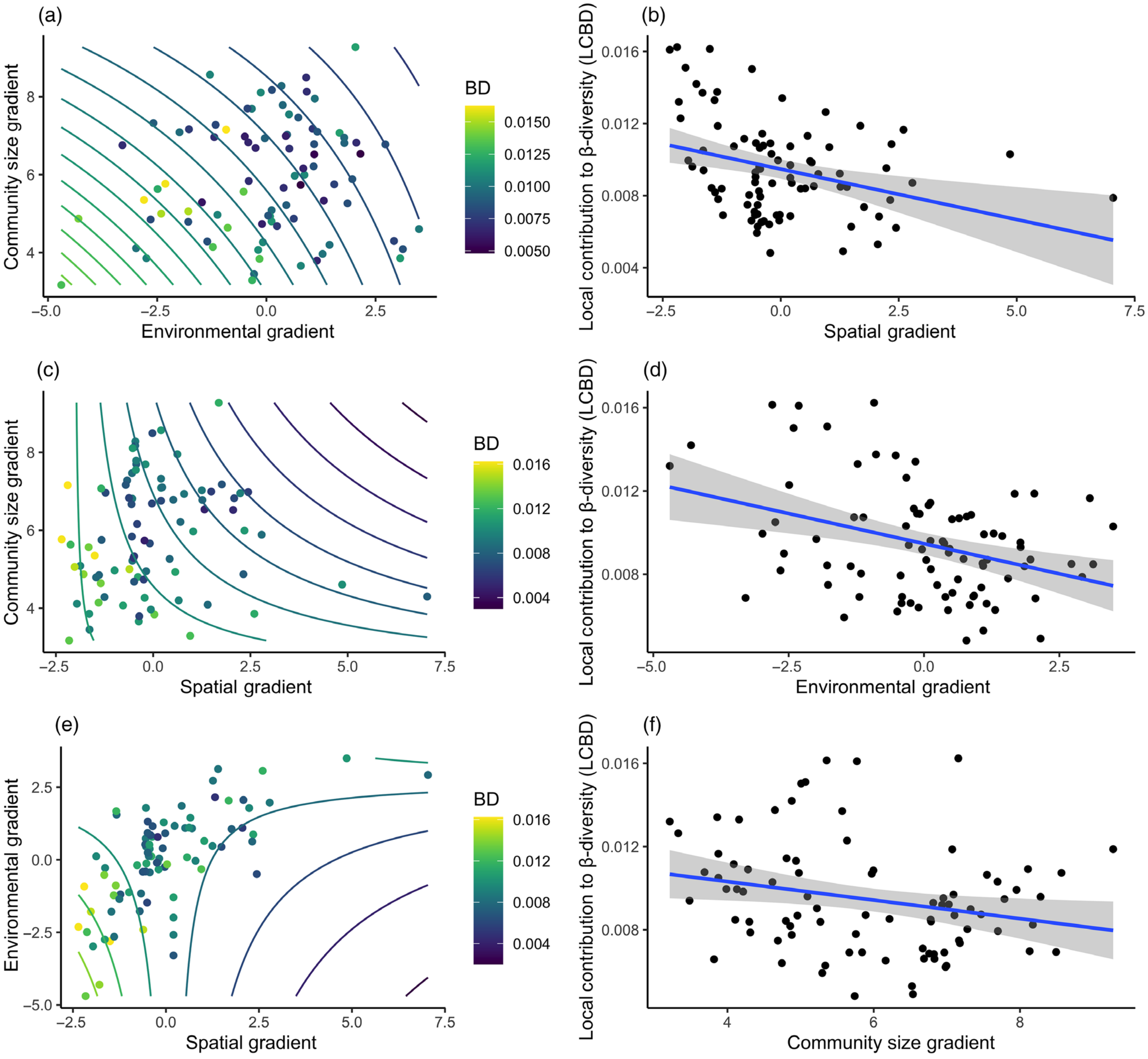

FIGURE 6 Local contribution to β-diversity (BD) of stream macroinvertebrate communities as a function of the spatial gradient (b), environmental gradient (d), community size gradient (f), and all pairwise interactions (a, c, e) among these gradients. Significant relationships are shown with plotted regression lines or contour lines. Full results from generalized linear mixed models (GLMMs) are found in Table 3

(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 may be the primary mechanism by which filter feeders persist at high densities in lake outlets; lake subsides of food resources allow 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 in which the RCC and SDC posit structure diversity were only partially supported in our study. The RCC and SDC predict local diversity to be highest as a result of niche selection, in which maximum

TABLE 4 Summary of results from the stream ecology frameworks analysis and the applied theory of ecological communities (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

diel temperature variability and maximum stream metabolism occurs (Vannote et al., 1980; Ward & Stanford, 1983). Although we did not directly quantify diel temperature variability and stream metabolism in our study, numerous studies have shown 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 (Baker et al., 2016; Ward & Stanford, 1983). Across the longitudinal range of streams, diel temperature variability has also been shown to increase moving downstream from the headwaters (Vannote et al., 1980; Ward, 1994), but this relationship varies among stream ecosystem types and temporally (Fullerton et al., 2015; Steel et al., 2016).

The SDC and RCC predicted that relationships between maximum stream metabolism and local diversity were 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 (Kaylor et al., 2019; Mejia et al., 2018; Ward & Stanford, 1983; Wotton, 1988). High densities of filter-feeding insects dominate habitats closest to lake outflows, where lakes provide allochthonous pulses of high-quality nutrients (Morin & Peters, 1988; Sheldon & Oswood, 1977). 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 S1: Figure S2). 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 et al., 2000; Chase & Leibold, 2002), although higher productivity could lead to a decrease in local diversity, as predicted by unimodal productivity–diversity relationships (Mittelbach et al., 2001; Tilman & Pacala, 1993; Waide et al., 1999). 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 may very well 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 & 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 therefore primarily driven by local environmental factors (Chase & 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 & Swan, 2010).

Ecological drift

Unique to lake–stream networks, community size shows a negative relationship with local diversity, contrary to our predictions (Figure 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 (please refer to section "*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 in which species richness declines with smaller community size (Gilbert & Levine, 2017) or habitat area (Vellend, 2004). Furthermore, 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 & 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 & 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, whereas other studies have suggested that 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 in which 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 the predicted effects of ecological drift. Furthermore, 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 (Catano et al., 2021; Patrick & Brown, 2018; Spasojevic et al., 2018; Vellend, 2016). Future research comparing assembly processes among disjunct mountain ranges or ecosystem types will help to elucidate the role of speciation on biodiversity. Efforts to incorporate species interactions into community assembly frameworks are ongoing and will provide a more complete understanding to the TEC and metacommunity ecology (Leibold et al., 2020; Ovaskainen et al., 2017). Furthermore, 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 (Baker et al., 2016; Jones, 2010), 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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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data (Green et al., 2022) are available from Dryad at https://doi.org/10.5061/dryad.2fqz612qw.

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