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The application of metacommunity theory to the management of riverine ecosystems

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Abstract

River managers strive to use the best available science to sustain biodiversity and ecosystem function. To achieve this goal requires consideration of processes at different scales. Metacommunity theory describes how multiple species from different communities potentially interact with local-scale environmental drivers to influence population dynamics and community structure. However, this body of knowledge has only rarely been used to inform management practices for river ecosystems. In this article, we present a conceptual model outlining how the metacommunity processes of local niche sorting and dispersal can influence the outcomes of management interventions and provide a series of specific recommendations for applying these ideas as well as research needs. In all cases, we identify situations where traditional approaches to riverine management could be enhanced by incorporating an understanding of metacommunity dynamics. A common theme is developing guidelines for assessing the metacommunity context of a site or region, evaluating how that context may affect the desired outcome, and incorporating that understanding into the planning process and methods used. To maximize the effectiveness of management activities, scientists, and resource managers should

update the toolbox of approaches to riverine management to reflect theoretical advances in metacommunity ecology.

1 | INTRODUCTION

The management of streams and rivers for the benefit of aquatic biodiversity and ecosystem service provisioning is grounded in community ecology (Lake et al., 2007). For instance, applications of biomonitoring data in streams are based on known relationships between the taxonomic composition of local biological communities and environmental attributes such as water chemistry, habitat availability, local climate, and geology. These relationships often inform development of numeric water quality criteria intended to protect aquatic life (Davis & Simon, 1995). Similarly, the practice of stream restoration is based on the idea that by improving habitat and other environmental conditions, the flora and fauna will recover toward a desired condition (i.e., "if you build it, they will come"; Hilderbrand et al., 2005; Palmer et al., 1997). Campaigns to eradicate invasive species and diseases such as rock snot (*Didymosphenia geminata*; Spaulding & Elwell, 2007) and trout whirling disease (*Myxobolus cerebralis*; Hedrick et al., 1998) use community ecology to evaluate the effects of these species and prioritize which taxa to remove. Finally, multispecies conservation plans often focus on land acquisition and preservation to protect critical habitats (Knopf et al., 1988). Many of these management approaches have been developed around the principles of niche theory, the idea that a strong association exists between local habitat conditions and community composition through processes that sort species into those that can persist and those that cannot persist under those environmental and biotic conditions. This relationship is often referred to as "local sorting" or "niche selection" (Leibold & Chase, 2018).

In the past decade, there has been explosion of research incorporating niche theory into a broader landscape level framework that also recognizes the effects of connectivity and dispersal on community composition. This metacommunity concept links traditional ideas of local sorting with regional processes of dispersal to better understand community dynamics and ecosystem processes at multiple scales (Leibold et al., 2004). Today, the metacommunity concept is an integral part of our understanding of community ecology, and the framework is widely used in both theoretical and empirical investigations (Logue et al., 2011). However, practical applications of the metacommunity concept have lagged behind theoretical advances (Heino, 2013; Schiesari et al., 2019). Just as the metacommunity concept has improved our understanding of the processes shaping ecological communities, it should also guide how we use community theory in the management of natural ecosystems (Brown et al., 2011; Costello et al., 2012; Van Allen & Rudolf, 2016; Van Looy et al., 2019). Here, we review the basic tenets of this theory as it applies to streams and rivers, summarize where and how the theory can enhance river management, recommend an approach for applying these concepts, and identify a series of research questions that remain to be addressed.

2 | METACOMMUNITY THEORY IN STREAMS AND RIVERS

A major goal of metacommunity theory is to describe how local-scale processes (e.g., species interactions, environmental filtering, and demographic events) and regional processes that affect probabilities of colonization and establishment (e.g., organism dispersal abilities, distance among habitats, and dispersal barriers) interact to influence local community composition. Understanding the relative role of these processes can provide insight into strategies for conservation and management. Early presentations of the metacommunity concept (Leibold et al., 2004) and its recent updates (Leibold & Chase, 2018; Logue et al., 2011) define different paradigms where the spatial variation in local-scale dynamics are produced by spatial variation in the environment, interspecific interactions, dispersal, random demographic processes, or

some combination of these forces. Here, we define the combined effect of all local-scale deterministic processes (e.g., interspecific interactions driving biotic sorting, and environmental sorting) on community composition in a given habitat as that habitat's "local sorting strength." This and other important definitions are organized in Table 1.

A concept central to metacommunity theory is that local scale processes may be constrained by regional scale processes and thus local communities may not simply reflect local processes (Patrick & Swan, 2011; Poff, 1997). The relationship between the relative effects of local sorting and dispersal is expected to be unimodal (Figure 1a). When the number of immigrants colonizing a habitat is very high resulting from source-sink dynamics, local-scale processes such as predation, competition, and abiotic environmental sorting may be less important in explaining local community composition than the identity of the colonizing immigrants (e.g., a mass effects assembly process). Conversely, at very low dispersal, demographic stochasticity is expected to be more important than interspecific interactions (Leibold et al., 2004). Furthermore, at low dispersal, well established inferior competitors may maintain populations in sub-optimal sites due to lack of competition, causing local communities to fail to match environmental conditions and remain in a state of disequilibrium, while also allowing regional coexistence and, thus, higher γ-richness. For example, Patrick and Swan (2011) observed that spatially isolated streams that had experienced major anthropogenic disturbance did not recover original, diverse benthic communities even decades after water quality conditions had improved, presumably due to lack of recolonization. At intermediate levels of dispersal, the local community composition is expected to closely match local conditions. One general hypothesis for streams and rivers is that the importance of local sorting, particularly for passive in-network dispersers, declines with downstream position because connectivity and associated propagule pressure increases, leading to mass effects, while environmental conditions simultaneously become more moderate and exert less selective pressure as stream size increases (Brown & Swan, 2010; Swan & Brown, 2014; Tonkin et al., 2018).

Applied ecologists working in riverine ecosystems are well positioned to incorporate metacommunity theory into management actions because the types of data needed are, in many cases, already being collected. Analyses to quantify the drivers of metacommunity structure and temporal dynamics require spatially explicit species composition and environmental data from multiple communities. For example, one commonly used statistical analysis is variation partitioning, which is used to estimate the degree to which local environmental effects versus regional dispersal-driven effects account for observed patterns of community assembly (Legendre et al., 2005; Legendre & Legendre, 2012). The wealth of large-scale riverine biomonitoring datasets collected by local, state, and federal agencies (Carlisle et al., 2010) is ideal for metacommunity analyses (Hampton et al., 2013). As a result, the literature on metacommunity dynamics of streams and rivers encompasses a disproportionately large proportion of published metacommunity studies (Tornwall et al., 2015). Leveraging available data with these methods allows investigators to draw inferences about the spatial distribution and the importance of dispersal in shaping community assembly across landscapes, opening the door to many management applications.

3 | MANAGEMENT APPLICATIONS

In this section, we highlight opportunities where metacommunity theory can be used by applied ecologists and management professionals seeking to enhance the tools currently available in the field of river management. We focus on the specific areas of biomonitoring, restoration, conservation, and invasive species management, as these encompass the majority of management activities. The concepts we describe are encapsulated in a holistic conceptual diagram (Figure 1). We also provide an analysis of biomonitoring data as a case study for how these ideas may be applied. Where possible, we provide concrete suggestions for applications, and where knowledge gaps persist, we identify future areas of study we believe may be fruitful. These suggestions and research needs are summarized in Table 2. Our recommendations provide an expanded set of management strategies that capture both local and regional influences on metacommunity dynamics.

3.1 | Biomonitoring

In biological assessments, inferences regarding ecological status are based on ecological quality indices that reflect the magnitude of departure of observed communities from those expected to occur under reference (baseline) conditions (Hawkins et al., 2010). The utility of biological assessments depends on how accurately and precisely assemblage composition expected under reference conditions (or the values of derived assemblage-level metrics) can be predicted from a combination of regional (e.g., climate, geology) and local factors (e.g., water chemistry, stream size,), and whether

TABLE 1 Definitions

Category	Term	Definition
Biological organization	Metacommunity	A set of local communities that are linked by dispersal of multiple interacting species
	Community	The individuals of all species that potentially interact within a habitat at the local scale
	Population	All individuals of a single species within a habitat at the local scale
Spatial scale	Local scale	Scale corresponding to a single habitat capable of holding a community
	Regional scale	Scale corresponding to a large area containing multiple local habitats and capable of supporting a metacommunity
	Biogeographic scale	Scale corresponding to area containing multiple regions, where evolutionary processes driving patterns in diversity and composition become easily recognizable
Theory	Niche theory	Conceptual framework organized around defining an organism's role in an ecosystem and the factors that dictate whether an organism will persist in an ecosystem
	Metacommunity theory	Conceptual framework that integrates the concepts within niche theory with additional regional processes including habitat connectivity and organism dispersal ability
Local and spatial processes	Environmental sorting	The process by which environmental conditions within a local scale habitat prevent colonists from establishing local populations
	Biotic sorting	The process by which organisms present within a local scale habitat influence whether colonists establish local populations via interspecific interactions such as competition and predation
	Local sorting	The combined effects of environmental and biotic sorting occurring within a local scale habitat. Also referred to as "niche selection"
	Mass effects	The process by which continual dispersal (immigration) of organisms influences population abundance of species within a local scale habitat. This process may offset local sorting processes, allowing species to persist in habitats where they would otherwise be absent
	Demographic stochasticity	Random variation in the sizes of populations due to the discrete and probabilistic nature of individual births, deaths, and dispersal movements. Important in small populations, where population variation can lead to extinctions that obscure local sorting processes
Metrics of community state	Local control	The state in which a community within a local scale habitat is composed of species that reflect local environmental conditions
	Disequilibrium	The state in which a community within a local scale habitat is composed of species that do not reflect local environmental conditions
	Sorting strength	The relative strength of local sorting in a local scale habitat when compared to other similar habitats
Spatial definitions	Spatial context	Comprehensive understanding of the multi-scale processes and characteristics in a region, including but not limited to, connectivity, network structure, dispersal, spatial patterns in local sorting strength, community composition, and diversity
	Connectivity	Scale dependent measurement of potential for movement by species among local habitats, considering mode of movement, distance to travel, and ease of movement
	Network centrality	Measure of connectivity for a single local habitat, representing how connected a local habitat is to other local habitats within network
	Colonization	Process by which populations become established at sites from which they were previously absent

TABLE 1 (Continued)

Category	Term	Definition
	Dispersal	Movement of individuals from a site (emigration) to another (immigration)
	Regional species pool	The species inhabiting a watershed or nearby watersheds in a region that have the potential to colonize a local habitat
Statistical analysis terms	Multivariate niche volume	The volume in n-dimensional space occupied by the species in a community at the time of sampling. A community with a large volume is inferred to have more wide spread generalist species
	Volume deviation	The difference between the observed multivariate niche volume for a community and that expected for the community based on random community assembly from the regional species pool. Negative values indicate that the community is experiencing environmental filtering, reducing the volume relative to random assembly
	Variation partitioning	Statistical analysis designed to partition explainable variation in a response variable into components (E, S, E-S) that can be attributed to different predictors in isolation or in tandem. E is the proportion of variation explained by the nonspatial environment. S is the proportion of variation explained by spatial variation in the response variable not shared by the measured environmental variables. E-S is the proportion of variation explained by spatially structured (nonrandom) environmental variation
Management terms	Biomonitoring	Performance of surveys of biological communities for the purposes of assessing the health of the surveyed sites and/or the region in which those sites occur
	IBI	Index of Biotic Integrity, an index developed to assess the health of a local scale stream reach from the identity and numbers of the resident species found there
	Reference condition	Criteria used for determining whether a habitat meets the definition of a site in best available condition. May include both environmental and community information. Is derived from data collected at undisturbed, least disturbed, or best available habitat site
	Ecological restoration	The practice of manipulating an ecosystem to achieve management goal such as returning to reference condition, restoring lost ecosystem functions, or enhancing native biodiversity. Differentiated from ecological engineering by an intent to enhance the ecological condition of the system rather than solely benefit human user groups

assemblage composition changes in response to anthropogenic disturbance. Both of these requirements rely on the assumption that local environmental and habitat conditions are the primary factors determining the specific taxa that occur in each waterbody. The tighter the association between local sorting and assemblage composition, the more accurately reference values can be predicted (Figure 1b). Prediction errors are often thought to be caused by failure to include important local environmental predictors, inaccuracies in the modeling method used to make predictions, or the inherent stochastic temporal variability of assemblage composition in natural ecosystems.

By contrast, metacommunity theory predicts that the underlying assumption of strong local sorting is only expected to be true at intermediate levels of dispersal (Figure 1a). Therefore, measurements of dispersal or site connectivity can help clarify both the sources and magnitudes of prediction error. For example, in sufficiently connected sites, strong local sorting is expected to promote high predictability, whereas limited dispersal in poorly connected sites may reduce the precision of predictions. Strong dispersal, including mass effects, may also decrease predictability, but the effect on model precision is likely to be more variable (Ron et al., 2018; Vannette & Fukami, 2017) depending on how closely the composition of the colonizing organisms match the predicted composition of the sink community. These predictions are supported by a small but growing body of evidence. For example, recent analyses show that the precision of multi-taxa distribution models used to predict the taxa expected to occur at a site under natural conditions is higher in

FIGURE 1 Conceptual diagram of the factors driving metacommunity dynamics and impacts on various aspects of stream and river management. (a) Regional scale factors (dotted box, cream text boxes) affect connectivity among habitats, which interacts with dispersal ability of resident organisms to influence the total amount of dispersal among habitats. Dispersal among habitats has a unimodal relationship with local sorting strength, defined as the amount of variation in community composition that local environmental variables can explain. Sorting strength is predicted to have positive relationships with b. biomonitoring precision (inset: electrofishing for aquatic life uses assessment), c. restoration success (inset: examples of restoration projects changing channel morphology), and d. conservation success (inset: individual enjoying ecosystem services provided by a healthy river). In contrast, local sorting is predicted to have a negative relationship with e. habitat invasibility when regional processes are not considered (inset: examples of non-native taxa, rusty crayfish (*Orconectes rusticus*) and western mosquitofish (*Gambusia affinis*). Arrow colors denote the sign of the expected relationship among factors (red = negative, green = positive) with gradient arrow indicating nonlinear relationships. Inset graphs display the functional form of the expected relationships

landscapes where waterbodies are more connected (Hawkins unpublished data). Model precision in more connected landscapes is higher than that in less connected landscapes (Hawkins unpublished data). Consequently, for predictive models developed for a large region, differences among sub-regions in connectivity could result in either type I or type

TABLE 2　Research needs and potential management applications

Category	Research needs	Management actions
Biomonitoring	Develop best practices for using variation partitioning or other similar approaches within watersheds and drainage basins to quantify strength of local sorting.	Account for spatial and metacommunity context in the development of predictive niche models for biological communities. Use predications about the variation in strength of local sorting within different regions in the development of biomonitoring models and Indices of Biotic Integrity (IBI).
	Incorporate spatial predictors, such as network position and mean distance to sources of colonists, in predictive niche models to better account for spatial context and species-specific differences in dispersal strength on site-specific probabilities of species or metric occurrence.	
	Devise separate models or treatments for groups of taxa that share similar dispersal behaviors or syndromes. For example, IBI's may be enhanced if poor dispersers and univoltine species are given greater weight in index scores than strong dispersers and multivoltine species.	Apply enhanced IBI models that incorporate metacommunity principles. In the absence of such models, recognize that biomonitoring indices are sensitive to spatial processes and that scores should be interpreted in light of these potential limitations.
Restoration	Develop monitoring protocols for characterizing the size and spatial distribution of regional species pools and dispersal abilities of focal taxa.	Determine whether there are suitable source populations in the regional species pool before starting a restoration project with goal of community restoration and whether those populations can disperse to the selected site.
	Develop protocols for accurately characterizing the dispersal or connectivity of river reaches. For example, is network centrality alone a good indicator? What additional characteristics of the spatial context should be quantified? Should colonization be directly measured with drift nets or terrestrial traps to capture dispersing adult insects?	Avoid restoration projects in areas where dispersal is too strong or too weak (Swan & Brown, 2017). For example, confluences and mainstems are likely to be a low return zone for restoration efforts due to dispersal surplus (Altermatt & Fronhofer, 2018). Highly disconnected areas of river corridor may fail to respond to restoration because of dispersal limitation.
	Develop or refine statistical approaches for quantifying the relative importance of factors impacting colonization. For example, analysis of trait distributions present among organisms within the community may provide some inference.	Determine whether restrictions to colonization are trait-based or environment-based and develop strategies accordingly. • Are there physical barriers (dams, weirs, etc.) or are species lacking dispersal strength/restricted to aquatic dispersal? • Can barriers be targeted to improve restoration outcomes? • Can stepping-stone restoration projects improve colonization chances? • In the worst-case scenario, will assisted migration efforts help?
	Identify catchment-level stressors that may override local habitat restoration efforts: are local restoration approaches swamped by regional-scale issues, such as catchment water quality. Terrestrial taxa often respond more strongly to local river habitat restoration due to instream water quality issues (Pilotto et al., 2018).	If insufficient knowledge of the regional biota and connectivity is available, first efforts of restoration should focus on sites within regions of moderate impairment to maximize the probability for biological response (Stoll et al., 2016).

(Continues)

TABLE 2 (Continued)

Category	Research needs	Management actions
Conservation	Develop tools and procedures for measuring connectivity and evaluating the relationship between connectivity and the health of native species or communities.	Measure connectivity within and among conservation sites and then strategically increase or decrease connectivity to meet management goals.
	Develop conservation prioritization schemes that managers can use to optimize metacommunity connectivity and maximize resilience.	Prioritize explicit maintenance or restoration of habitat connectivity in more pristine areas where human perturbations are low.
	Develop guidelines for using multi-species connectivity and dispersal analyses, such trait-based joint species distribution models or analyses of surrogate species, to assess connectivity priorities for conservation management plans (Meurant et al., 2018).	For multi-species conservation action plans, consider how optimal levels of connectivity may differ among target species. Maximizing connectivity for the poorest dispersers in a community may subject better dispersers to mass effects conditions, resulting in loss of rare taxa.
Invasive Species	Empirically evaluate theoretical predictions about the relationship between sorting strength, native dispersal pressure, and habitat invasibility. Develop best practices for using variation partitioning and similar methods to identify the spatial configuration of local sorting strength.	Determine the relative probability of invasion success among locations in the river network and help identify areas to prioritize efforts.
	Incorporate dispersal data in models to determine the need/frequency for maintenance eradication visits.	Focus eradication efforts in habitats or locations where local control is strong.
	Develop methods for inferring the relative importance of factors that affect local control and build a system for calculating trade-offs between various habitat management actions.	Perform habitat management to increase the relative strength of local sorting, to create conditions where native communities have a higher probability of resisting invasions. This can be altering local habitat conditions or decreasing connectivity.

II errors of inference when the model is applied to specific locations. Restricting the regional extent of assessment models based on differences in within-region connectivity and considering the degree to which study areas are fragmented may improve model accuracy and precision (Heino, 2013). Furthermore, the use of statistical approaches such as variation partitioning to infer the relative strength of local sorting within watersheds can help identify regions where local sorting is likely to be strong and prediction precision is expected to be high (Table 2, see example in Section 4).

Similar dynamics may also occur at finer spatial scales. Simulations show that biocriteria metrics—often termed "indices of biotic integrity"—can be affected by an interaction between impairment level, dispersal intensity, and the location of a site within a stream network (Siqueira et al., 2014). Strong, local stressors can overwhelm dispersal effects (Xiong et al., 2016), and pervasive stress across a region can decrease dispersal potential from the regional species pool to individual locations (Patrick & Swan, 2011). Similarly, strong dispersal from healthy source populations can improve the appearance of environmentally degraded sites by inflating biocriteria scores that do not reflect local conditions. These observations can inform management strategies and help us interpret biomonitoring data. For example, given that stream connectivity varies according to the network centrality of the site in the network (Altermatt et al., 2013; Brown & Swan, 2010), we might predict that biomonitoring index precision declines as you move to larger streams with higher connectivity (Table 1). However, the balance between local and dispersal-driven assembly processes along the river corridor also depends on characteristics such as the type of organism (Tonkin et al., 2018). For instance, less mobile species may respond more strongly to site-to-site variation in environmental factors (Beisner et al., 2006), whereas organisms with many generations per year, such as multivoltine insects with an adult flying stage, may respond less strongly to the environment because they have more dispersal opportunities per year to spread across a region (Saito et al., 2015). Explicitly including spatial predictor variables that represent dispersal strength (Cid et al., 2020), traits that define the spatial scale of organisms' dispersal ability (Guzman et al., 2019), and accounting for the spatial structure of sampling sites (Grenouillet et al., 2008) may improve empirical models predicting community

composition (Table 2). The degree to which these factors can be effectively quantified in assessments relies on access to data collected from a sufficiently dense sampling network.

3.2 | Restoration

River restoration is costly, and these costs are not often translated into biological gains (Palmer et al., 2010). The effectiveness of river restoration depends on many different factors, including the intensity of restoration actions, the geophysical setting, and the scale of restoration (Palmer et al., 2010). One overarching cause of restoration failures is a lack of attention to ecological theory (Palmer et al., 2010). Many river restoration projects focus on improving local conditions, often with the associated goal of a subsequent improvement in aquatic life. Dispersal dynamics are rarely considered (Swan & Brown, 2017), but dispersal constraints and barriers to recolonization are a frequent cause for a lack of biological response to habitat restoration (Sundermann et al., 2011; Tonkin et al., 2014). Many restoration projects fall into the trap of fixing local habitat conditions and assuming unlimited recolonization potential, an operational tactic referred to as the "Field of Dreams" Hypothesis (Palmer et al., 1997). The role of dispersal limitation and impoverished regional species pools in limiting restoration success has led scientists to consider the reintroduction of whole communities as a mitigation tool following restoration (Jourdan et al., 2019). However, an alternative approach would be prioritizing locations known to have adequate dispersal or to actively increase spatial connectivity among sites that will be restored. In reviewing all of these scenarios, it becomes clear that incorporating metacommunity dynamics into river restoration planning is crucial for ensuring that biological communities responds as desired after restoration.

Experimental evidence suggests that catchment-scale influences can override local-scale restoration measures. For example, using experimental flume systems, Brown et al., 2018 demonstrated that while local habitat had a strong influence on both headwater and mainstem streams, augmented dispersal only affected communities colonized from headwater streams (Brown et al., 2018). A lack of mainstem response to dispersal indicated that those communities were already structured by dispersal-driven dynamics, whereas the headwater response to dispersal indicated that those systems were dispersal-limited and open to new colonists through augmented dispersal (Brown et al., 2018). Similarly, Tornwall et al., 2017 demonstrated that manipulations of local habitat (substrate complexity) had stronger effects on headwater macroinvertebrate communities than on mainstem communities, presumably because dispersal-driven dynamics are more important to the assembly of mainstem communities than to headwater communities (Tornwall et al., 2017). Therefore, considering the spatial setting into which restoration projects are placed (Leps et al., 2016), is an important first step (Table 2).

Restoration in regions with either dispersal surplus or dispersal limitation may have limited success (Stoll et al., 2016), with the best locations for restoration situated in regions of intermediate habitat quality that are under the strongest local control (Figure 1c, Table 2). Restoring stream reaches at well-spaced intervals (i.e., "stepping stones") may also allow dispersal among restored habitats (Gellert et al., 2012; Kail & Hering, 2009). For instance, recent work suggests that restoration may be more ecologically successful in headwaters where a greater concordance between species' habitat needs and local habitat availability is expected. In contrast, dispersal-driven factors are likely to be more influential in more well-connected mainstems (Swan & Brown, 2017). In some cases, connectivity of the proposed restoration site may be increased or decreased to achieve a desirable balance between local and regional control via barrier removal (e.g., weirs and culverts) or engineering construction of hydraulic barriers (e.g., plunges; Figures 1a and 4, Table 2). Previous work has demonstrated that distance to the nearest colonist source, whether along the river network or overland, is a key indicator of potential restoration success for benthic invertebrates (Patrick & Swan, 2011; Tonkin et al., 2014), as is the occupancy rate among habitats in the regional species pool (Tonkin et al., 2014). Thus, assessing whether desired potential colonists are present in a watershed or in nearby watersheds is an important step before starting a restoration project (Table 2). Public monitoring data are often freely available to assess the regional species pool surrounding candidate restoration sites, particularly for fish, prior to physical restoration. If these data are not available, and if restoring biodiversity is a goal, an initial region-wide rapid assessment of streams may be necessary to ensure that potential colonists are present prior to performing the restoration.

3.3 | Conservation

Conservation efforts have historically focused on the habitats of target species of concern with the assumption that actions that benefit these "umbrella" species will benefit other taxa in the habitat. One operational strategy is

conserving local environmental conditions to reflect habitat needs of the target species. This strategy is most likely to be successful where local sorting control is high (Figure 1d). However, in recent years conservation efforts have increasingly focused on multiple species (Moilanen et al., 2005) and understanding the different connectivity needs of different species is a necessary component of effective conservation action (Albert et al., 2017). For habitat conservation plans that cover multiple species, this process entails conserving or restoring dispersal corridors favored by different taxa (Table 2). The classic determinations of "umbrella" species whose habitat needs guarantee local persistence do not necessarily extend to metacommunities, as maintaining persistence of species distributions and temporal dynamics across a metacommunity requires identifying a different or expanded set of traits among surrogate taxa (Meurant et al., 2018). In the Western Riverside Multi-species Habitat Conservation Plan (CA, USA), for example, planned corridor types provide connectivity for imperiled species inhabiting a large range of terrestrial, riparian, and instream communities (WRCRCA, 2003). In this context, metacommunity theory may assist conservation prioritization (Brown et al., 2011), as new approaches (see Section 4) have been developed for determining the extent local sites are connected to regional dynamics at different temporal and/or spatial scales (Ruhi et al., 2017; Tonkin et al., 2014). Translating this information into concrete planning for resilient meta-communities is an area of ongoing management emphasis (Isaac et al., 2018).

In addition to promoting regional stability of focal species (Cavallaro et al., 2015), increasing or decreasing connectivity among communities affects access to food resources, either through blocking subsidies or restricting wide ranging foraging (Cloern, 2007), and alters exposure to competition, predation, or disease (Rahel, 2013). Thus, failure to consider connectivity can lead to failure of conservation efforts. For example, a multi-million-dollar riparian project in the lower Colorado River failed to restore populations of endangered Southwestern Willow Flycatcher (*Empidonax traillii extimus*), a riparian obligate species, because important river processes that promoted floodplain connectivity and aquatic macroinvertebrate food subsidies to the riparian zone were not established (Rubin et al., 2018).

In more pristine areas, managers may focus on maintaining longitudinal connectivity by preventing flow disruptions such as dams, culverts, and excessive water extraction, or by preserving riparian corridors (Poff, 2018). In regions with patches of threatened species, conservation actions that increase connectivity may be the best course of action (Figure 1a). For example, in Japan (Figure 2a), ladders were widely installed on small agricultural dams to increase the regional functional connectivity of threatened salamanders (Taguchi & Natuhara, 2009). In the Santa Ana River, re-wetting portions of the river corridor and restoring historical flow regime in reaches dominated by sewage treatment outflows (Figure 2b) benefits many at-risk species by increasing habitat connectivity (ICFI, 2014).

In some management scenarios, however, it may be desirable for a manager to decrease connectivity, for example, to restore natural disconnections or to prevent the spread of invasive species or disease to conserve native fauna (Strecker & Brittain, 2017). Barriers, such as dams and electric fences, and alterations to flow regimes are increasingly being used strategically to reduce connectivity among communities (Rahel, 2013). After the restoration of flows and native fish populations to Fossil Creek in central Arizona, USA, a fish barrier was constructed by the United States Bureau of Reclamation to exclude invasive species common in nearby Verde Creek (Figure 2c, (Marks et al., 2010). In the Great Lakes, a number of nonphysical barriers including electric fences, bubble curtains, and acoustic deterrents have been installed to limit the dispersal of Asian Carp into bays and canals with high value to commercial fisheries (Noatch & Suski, 2012). In addition to creating artificial barriers, naturally low connectivity created by intermittent flows in xeric regions or natural debris dams in forested catchments can be conserved or restored. These types of periodic natural barriers not only limit the movement of undesirable species or diseases, but they also change local sorting strength within communities and so can be used to manipulate local control to benefit native communities (Table 2).

3.4 | Invasive species management

One of the most pernicious threats to native aquatic biodiversity and ecosystem functioning is invasive species (Thomaz et al., 2015). The threats posed by aquatic invasives are well documented from both a biological and economic perspective (Lovell & Stone, 2005). Yet, management of aquatic invasives is in its infancy both in terms of development as a discipline (N'Guyen et al., 2016), and in approaches to prevention, control, and eradication of invaders (Sepulveda et al., 2014 but see Chen & Olden, 2017). While the problems presented by aquatic invasives are multifaceted and inherently interdisciplinary (Crowely et al., 2017), both theory and preliminary empirical work suggest that a metacommunity approach to understanding invasions may provide insights on prevention and management.

The only explicit metacommunity framework presented to date for aquatic invasives suggests that two factors control invasion success: empty or weakly occupied niches on landscapes and propagule pressure (Howeth &

Leibold, 2010). Two major themes emerge from this framework: (i) invasibility decreases as the relative importance of local sorting strength increases (Figure 1e); (ii) invasibility decreases with increased dispersal of natives.

From the perspective of the local community, high local diversity has traditionally been assumed to be more likely to repel invaders (Elton, 1958; MacArthur & Levins, 1967), an idea that has come to be known as the Biotic Resistance Hypothesis (BRH). The BRH has clear links with the Howeth and Leibold (2010) framework, which suggests that invasion success is low where local sorting is strong. However, tests of the BRH have shown mixed support and high degrees of context dependence (Howeth, 2017; Levine & D'Antonio, 1999; Shurin et al., 2000). That context, in many cases, depends on rate and distance of dispersal (Howeth, 2017; Shurin et al., 2000). While the widespread dispersal of invasives can be damaging (Sinclair et al., 2015), the dispersal of natives can provide resistance to invasion (Howeth, 2017; Shurin et al., 2000).

Stream and river corridors are important invasion pathways, and the structure of river systems is one factor that can dictate rate and extent of spread (Rinaldo et al., 2018). From the perspective of preventing or controlling invasions, dispersal can act both positively and negatively in invasion scenarios, depending on which species are dispersing and how (Sinclair et al., 2015). Dispersal acts positively by increasing invasion resistance in native communities (Howeth, 2017), or by promoting the recovery of native species after invasion (Sinclair et al., 2015). However, dispersal can also act negatively when invasives are rapidly spread (Sinclair et al., 2015). These results suggest that activities like dam removal, which are oft-used restoration strategies, can actually benefit invaders by removing barriers to dispersal. Thus, the use of metacommunity theory in confronting invasions relies on (a) identifying whether the forces driving invasion are local or regional and (b) implementing control measures based on that relative balance (Table 2).

Statistical approaches that assess the degree of local control in ecosystems can be used in conjunction with riverine biomonitoring data to map out areas of high and low invasion risk (Table 2, see example Section 7). A high degree of

FIGURE 2 (a) an endangered Japanese Giant salamander (*Andrias japonicus*) blocked by a dam in the Kiso River drainage in Gifu Province, Japan. Courtesy of Ito Yoshihiro. (b) Restoring flow connectivity to the Santa Ana River has been vital to the survival of the endangered Santa Ana Sucker (*Catostomus santaanae*). (c) Following the restoration of flows and native fish communities in Fossil Creek, AZ, a dam was constructed on the lower creek to prevent the recolonization of invasive fish from the downstream Verde River. Natural materials were included in the design of the fish barrier in order to preserve wilderness characteristic and recreational value

resistance to invasion would be expected where natives are the primary dispersers (Howeth, 2017). Mouillot (2007) suggests that when local sorting is the major driving force in structuring fish metacommunities, habitat restoration, and preservation are the most effective strategies for dealing with invasive species. However, in systems where community dynamics are more dependent on dispersal, focusing on actions that alter landscape-scale connectivity to the benefit of native species is more important (Mouillot 2007).

4 | PUTTING IT TOGETHER: THEORY AND PRACTICE

Looking across these areas of riverine management, several key themes emerge. Regardless of the goal, projects should begin with an assessment of the spatial context of the focal habitats. The first step of this process is defining the boundaries of the region that include the site or sites of interest (e.g., watershed; catchment) and then assembling community data that is spatially distributed across the region. If no such data exists, new spatially balanced surveys can be designed and implemented, however, the importance of stream invertebrates for aquatic ecosystem health assessments usually results in such data already being available from government or nonprofit entities for these taxa. Once assembled, the data are used to assess spatial connectivity such as network density or centrality (Estrada & Bodin, 2008), the presence and distribution of dispersal barriers such as dams and road crossings (Clarkin et al., 2003; Januchowski-Hartley et al., 2013), the dispersal modes and abilities of the target species (Poff et al., 2006; Radinger & Wolter, 2014; Twardochleb et al., 2021) and the size and compositional identity of the regional species pool. Multivariate analyses may be used to assess the relative strength of local and regional processes in driving community assembly (Legendre et al., 2005). Armed with this information, managers can determine how metacommunity context may influence the likelihood of success for different management actions in different locations and use that information to inform decision making (Figure 3). If the metacommunity context is unfavorable for a proposed project—for example, local sorting is relatively weak or spatial connectivity is low, managers can then choose to move the spatial location of the project, change their strategy, identify ways to alter the metacommunity context to maximize success, or understand at the outset that the ecological community may not change or "improve" (Figure 3).

Some of these suggested analyses are conceptually easy to implement, consisting of visually assessing spatially mapped data to evaluate patterns in taxonomic richness, biodiversity, and community composition and locating dispersal barriers. However, quantitative assessment of local sorting strength and dispersal is more statistically complex. In the next sections, we demonstrate how spatially distributed community and environmental data can inform both regional and site-level estimates of the strength of local sorting in streams and discuss basic considerations in the choice of statistical analysis. We showcase two different example analytical frameworks: variation partitioning, a common approach to assessing regional variation in the strength of local sorting (Hawkins, 2012), and a newer framework developed by Blonder et al. (2015) to evaluate the degree of local sorting strength within an individual habitat. These analyses are by no means exhaustive and many advanced methods of analysis exist. However, they do represent an introduction to commonly used techniques and illustrate how signals of metacommunity processes may emerge in commonly collected data.

4.1 | Example of regional scale analysis of sorting strength

To illustrate the utility of quantitative analyses of sorting strength, we apply variance partitioning to continental-scale biomonitoring data collected from streams of the United States. Variation partitioning is used in spatial analysis to separate variation in biological data into parts explained by the nonspatial environment (**E**), the spatial structured environmental variation (**E-S**), and the spatial variation of the target variables that is not shared by the environmental variables (**S**), with the remainder referred to as unexplained variation (Clappe et al., 2018; Gilbert & Bennett, 2010; Legendre, 1993). In metacommunity analysis, portions of variation explained by the environment are often interpreted as being caused by species sorting, but two aspects of the analysis should be considered when interpreting the results. First, portion **S** is often interpreted as representing "pure space" or "spatial processes" but the **S** fraction of variation also includes variation associated with unmeasured, spatially structured environmental gradients (Hawkins, 2012). Second, portion **E-S** can capture spatial correlations between species distributions caused by dispersal limitation and the spatial environmental that are not causally linked, leading researchers to incorrectly infer that all variation in this category is caused by spatially structured environment (Clappe et al., 2018). This can increase proportion of variation
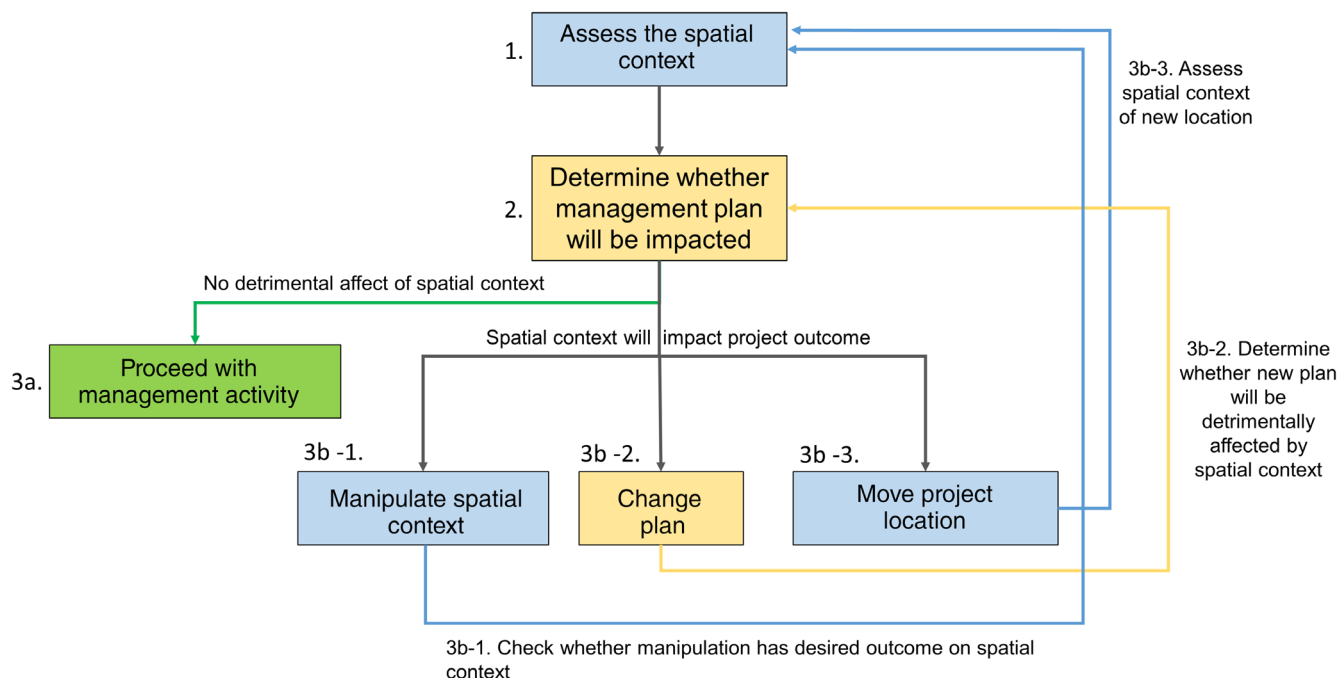
FIGURE 3 Decision tree for incorporating metacommunity theory into management activities. (1) Work begins with surveys or statistical analysis of existing biomonitoring datasets to determine the spatial context of the proposed project. This may include assessing factors like connectivity, dispersal ability of organisms, regional species pools, and the relative importance of local sorting for target communities. (2) Determine whether the current spatial context will prevent management goals from being met. For example, a stream restoration in a site that is under strong regional control (dispersal) from degraded sites is unlikely to result in the assembly of desirable biotic community after the restoration is complete. (3) If there are no problems presented by spatial context, proceed with management plan (3a); however, if there are issues managers can either attempt to change the spatial context (3b-1), change the plan (3b-2), or move the project location (3b-3). In each of these cases (3b-1-3), the managers must then return to step 1 or step 2. For example, if spatial context is manipulated by removing barriers to increase connectivity, postremoval conditions should be assessed to determine how much the manipulation changed connectivity. This is a crucial step before proceeding to 3a because not all manipulations may be successful

explained in **E-S** portion to be on average 25% greater than that actually caused by the spatially structured environment (Gilbert & Bennett, 2010). Despite these issues, variation partitioning remains preferable to other statistical approaches (Gilbert & Bennett, 2010), and recent updates to the method can help with interpretation of the **E-S** fraction of variation (Clappe et al., 2018). For example, Gilbert and Bennett (2010) recommend using the approach but paying close attention to the chosen scale of the analysis to ensure it biologically meaningful and running secondary analyses or experiments to confirm the observed results.

We applied variation partitioning to overlapping regional zones resampled from a continental-scale data set (Patrick & Yuan, 2019). Application of variance partitioning to regional zones allows us to investigate dynamics at spatial scales much smaller than the size of the study area. We analyzed biomonitoring data from the United States Environmental Protection Agency (USEPA) National Rivers and Streams Assessment (NRSA) conducted in 2007–2008 (USEPA, 2016). NRSA employs a spatially balanced sampling design to survey wadeable, perennial streams of the continental United States and is a robust dataset for evaluating large scale patterns in sorting strength. The dataset includes 1269 stream sites with both macroinvertebrate community and associated environmental data (2010). We used the complete suite of environmental variables provided in the NRSA dataset, including habitat and water quality measurements collected in-situ as an example of an analysis with no a priori expectations regarding which environmental variables are most important to consider. We estimated variance components at a spatial scale of 500 km using each sampling location as the center of the region and restricted calculations to regions with >50 sampling events. We randomly selected 50 sampling events per region to our calculations and repeated this 10 times per region and then took the mean value among bootstrapped calculations (Patrick & Yuan, 2019). This approach was used to minimize the effects of variation in sample size among regions and the potential effects of outliers on the calculations. We used the varpart() and pcnm() functions in the vegan library in the statistical program R (R Core Team, 2016) for the variation partitioning

analysis performed on each replicate sub-sample (Oksanen et al., 2014). For visualization we averaged the output values by river basins that were classified as level four according to the United States Geological Survey Hydrologic Unit Code system. For ease of interpretation we focused our interpretation around the E portion of variation (e.g., nonspatial environment) which represents classic species sorting without a spatial component.

## 4.2 | Example of local scale analysis of sorting strength

For the local-scale analysis, we used the same biomonitoring dataset we describe in Section 4.1 but applied a community disequilibrium analysis framework developed by Blonder et al. (2015) to infer the relative strength of local control on stream communities at the site level. In the context of this analysis, a community in disequilibrium is composed of taxa that would not be expected to be present given the suite of environmental conditions observed at the site and our knowledge regarding the typical environmental conditions in which the resident taxa are found. The approach uses the distributional data for species and environmental conditions to develop expected niche distributions for each species in multivariate environmental space. Expected environmental conditions in each location are generated from the observed environmental distributions of each observed species and then the volume of niche space is calculated from distance among species in n-dimensional environmental space (Blonder et al., 2015). Predicted environmental conditions are compared to the observed environmental conditions to determine the degree of match between community and environment. Deviations between the expected and observed environmental conditions and the multivariate volume of niche space occupied by the community can then be used to infer whether the community is being constrained by local environmental conditions or composed of taxa that we would not have expected to observe (Blonder et al., 2015).

For this analysis we focused on a subset of environmental variables (conductivity [µs/cm], turbidity [NTU], pH, dissolved oxygen [mg/L], NO_3^- [mg/L], and NH_4^+ [mg/L]) because they often exhibit strong associations with macroinvertebrate community composition. Within each level III ecoregion (USEPA, 2016), a separate model using all local scale observations (n = 96–250 per region) was developed for taxa—habitat associations. These associations were then used to calculate the volume deviation for each stream community. Values greater than one indicate that the community was representing a larger niche volume than was expected by the observed environmental conditions, suggesting that the site was environmentally permissive, that is, local conditions were not controlling community composition. Statistical distributions of the volume deviation were compared among ecoregions. The relationship between volume deviation and watershed size within and among regions were then assessed to evaluate the previously mentioned hypothesis that strength of local sorting decreases as stream size increases. All analyses were performed using functions in the comclim library (Blonder et al., 2015) in the statistical program R.

4.3 | Interpretation and application

At the regional scale (variation partitioning), we observed significant variation in the estimated degree of environmental sorting (Figure 4a). Sorting strength was more variable in western regions with separation between southern areas (low sorting) and northern areas (high sorting). In eastern regions, sorting strength increased toward the east and north (Figure 4b,c). In contrast, for local scale measurements (community disequilibrium) sorting strength did not follow broad geographic patterns (Figure 4d,e), but did exhibit spatial structuring within regions (Figure 4f). For 36% of the streams in the dataset, processes other than local sorting such as dispersal pressure were inferred to be the dominant forces structuring the local communities (Figure 5a). Within ecoregions, we observed that local sorting strength declined with increasing stream order in five (Northern Appalachians, Northern Plains, Southern Plains, Western Mountains, and Xeric) of the nine ecoregions, comprising approximately 60% of the coterminous United States (Figure 5c).

The results demonstrate that stream communities are not always dominated by local sorting processes and highlight the importance of considering the dependence of these processes on spatial scale. These results also provide some actionable information that could be useful when planning management activities. Fifty-four percent of US wadeable streams were found to be under sufficiently strong local sorting to be considered under "local control," but in 36% of streams, environmental conditions were not the dominant force shaping local communities. In this second group of streams, classic biomonitoring methods may be less informative and approaches that incorporate additional spatial predictors may be useful additions to the management toolbox. Interpretation of this analysis supports the notion that
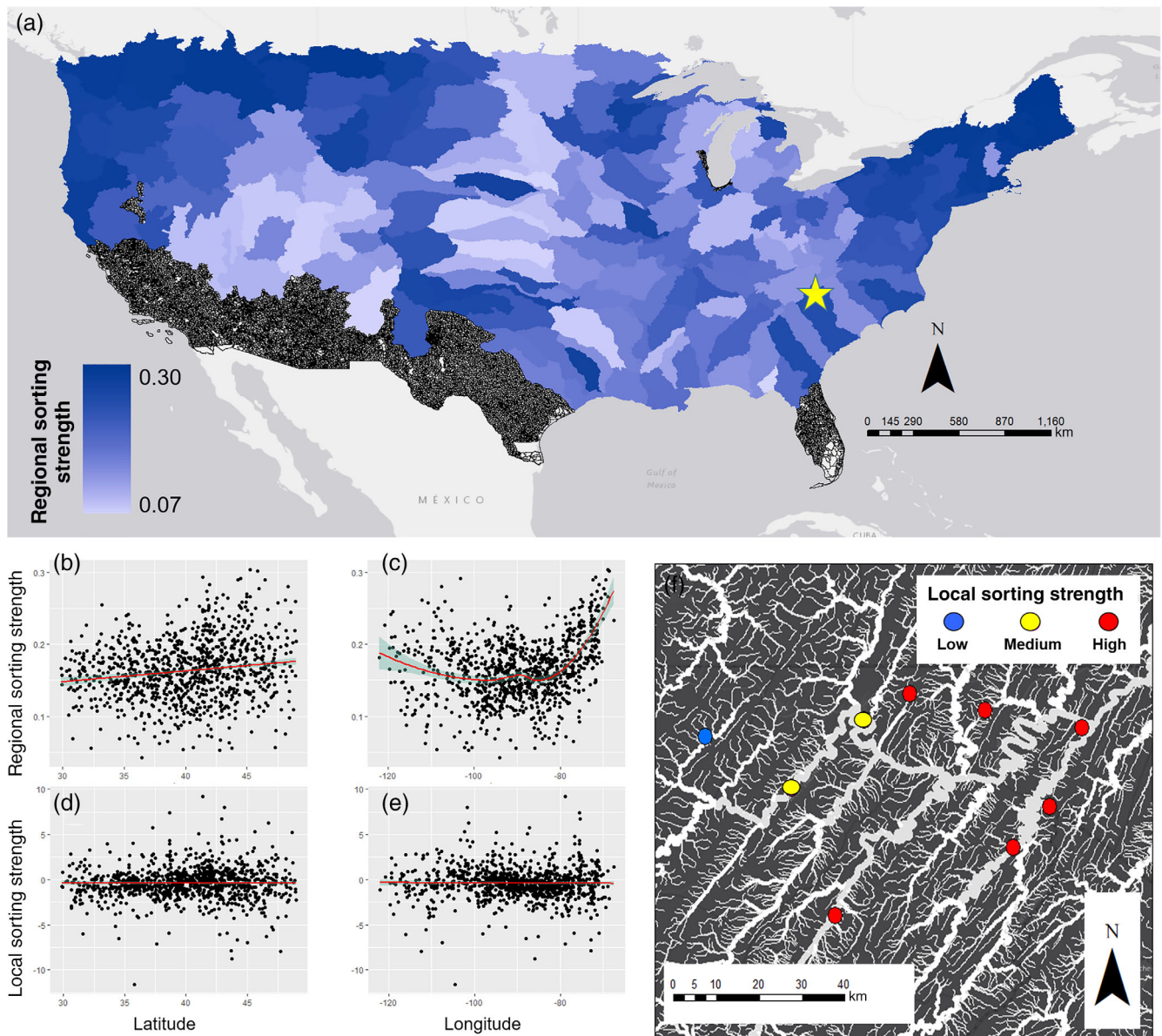
FIGURE 4 Spatial distribution of sorting strength measured at regional (variation portioning) and local (community disequilibrium) scales. (a) Map of regional sorting strength estimated using variation partitioning and mapped at the HUC4 basin scale across the continental United States. Darker blue sites have higher sorting strength. Black areas have no available data. Yellow star is location for panel f. (b–e) Relationships between different estimates of sorting strength and latitude and longitude across the continental United States. Regional scale estimates of sorting strength calculated using variation partitioning increase slightly as you move north (b, $p < .001$, $R^2 = .022$, $df = 2,1220$) and toward the coasts (c, $p < .001$, $R^2 = 0.196$, $df = 2,1220$) with the highest values in the Pacific Northwest and the Atlantic Northeast. Local scale estimates calculated using community disequilibrium methods have no relationship with latitude (d) or longitude (e). (f) Example map of spatial distribution of local sorting strength estimated at the site scale for streams with biomonitoring data in the lower Appalachian Mountains (yellow star in a) of the United States. Sorting strength is ranked as high (red), medium (yellow), or low (blue). In this region, sorting strength is lower in upstream reaches

application of metacommunity theory could be an important enhancement to existing methods, particularly in the south western United States where local control was observed to be weakest. Similarly, based on these analyses it appears that in at least some ecoregions, restoration activities are more likely to be effective in headwater streams than mainstems, agreeing with published case studies (Swan & Brown, 2017).

While these data show some biogeographic patterns in regional measures of sorting strength, we caution that the estimates are likely scale dependent. Although regional estimates show some agreement with local estimates, individual streams may be more influenced by dispersal even within regions where local control is more prevalent. Hence,
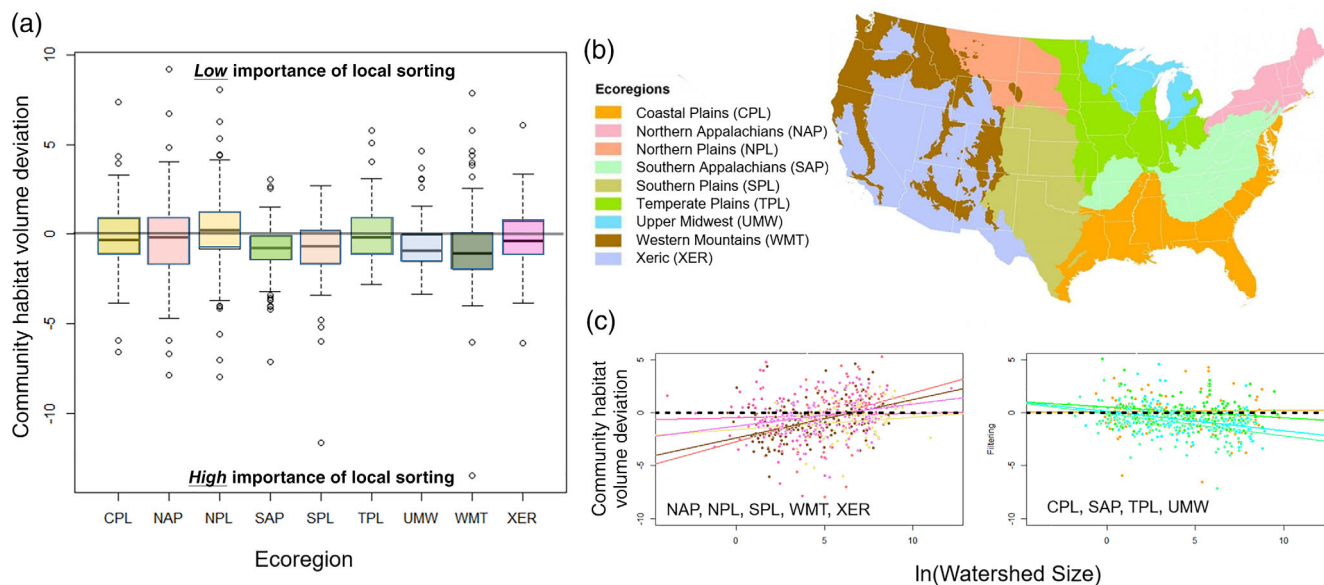
FIGURE 5 Relationships between stream size, ecoregion, and strength of local sorting based on community disequilibrium analysis. (a). Distribution of the deviation from expected community based on species-habitat associations among ecoregions of the United States (CPL, Coastal Plains; NAP, Northern Appalachians; NPL, North Plains; SAP, Southern Appalachians; SPL, Southern Plains; TPL, Temperate Plains; UMW, Upper Midwest; WMT, Western Mountains, XER, Xeric). Values with a magnitude greater than zero indicate that communities are not being structured by local environmental variables. (b). Map of ecoregions of the United States. Ecoregion colors correspond to colors in other panels. (c). Relationship between stream watershed size and community habitat volume deviation within ecoregions (individual lines) of the United States. Left plot shows ecoregions with positive relationships, indicating that, as predicted by theory, sorting strength declines with stream size (NAP, NPL, SPL, WMT, UMW, XER). Right plot shows ecoregions with negative relationships, indicating that sorting strength increases with stream size (CPL, SAP, TPL)

consideration of multi-scale processes is critical when applying these approaches to enhance ecosystem management. Furthermore, characteristics of each system can be unique, and we therefore suggest that practitioners design a study specifically for their region and study question to develop an understanding of the unique spatial context that is relevant for their project and goals.

5 | CONCLUSION

Incorrect inferences regarding ecological condition and the causes of degradation can result in management actions that do not yield the desired outcomes. Explicit incorporation of the metacommunity framework can improve inferences by helping increase our understanding of the causes of community assembly within and among streams, and ultimately enhance many aspects of riverine management including bioassessment, restoration, conservation, and invasive species control. Understanding all the causes of variability in biological reference condition among sites, watersheds, and regions improves our ability to characterize the uncertainty in biological assessments. Understanding the processes that structure communities allows us to determine when, where, and how to implement management interventions for conservation, restoration, and invasive species control, such that the actions have a higher probability of successful outcomes and a greater return on investment. This improved understanding will also allow us to ascertain when project goals for a given system may be unachievable due to logistical and financial constraints.

One of the challenges to better integrate metacommunity theory into river management is developing tools that can effectively operationalize metacommunity theory. We have described some analytical and practical approaches that can be employed immediately, as well as a series of research questions that remain to be answered, showing that much work remains to be done. For example, adjusting scoring tools can help account for differences among waterbodies in the relative importance of regional versus local processes. Similarly, modifications might be made to indices of biotic integrity that incorporate organism dispersal ability into the weighting and scoring formulas. However, we might also need new approaches and analytical tools that better incorporate metacommunity dynamics into river management. The ideas

presented in Table 2 and throughout the manuscript are a first step down that path of expanding our toolbox of approaches, and in reviewing them, there are clear commonalities for how metacommunity theory influences management (Figure 3). In all cases, the first steps are the evaluation of metacommunity processes in the system using available or newly-collected data and using the information gained from those investigations to inform the next steps in the process.

The field of applied metacommunity ecology is still emerging, and many questions remain regarding how to use these ideas to enhance existing management strategies. Operationalizing many of the recommendations in Table 2 will require applied ecologists and ecosystem managers to work together to develop specific approaches and tools for different situations. There must be an open flow of information between practitioners and theoretical ecologists, and as the theory and analysis frameworks continue to develop, so too must the applications. This will be a challenging task and change will not occur overnight. Rather, we foresee a slow and incremental shift occurring in steps. Early partnerships that apply these ideas and demonstrate successful outcomes will act as case studies for others to emulate. Indeed, several of these already exist in terrestrial ecosystems, such as the incorporation of metacommunity theory into the development of Montreal's plan for a network of protected habitats (Albert et al., 2017), but there is room for more innovative trail blazers in freshwater ecosystems. Ultimately, we believe that this effort will increase the effectiveness of riverine ecosystem management and that the lessons learned will have value across a wide variety of other ecosystem types.

CONFLICT OF INTEREST
The authors have declared no conflicts of interest for this article.

AUTHOR CONTRIBUTIONS
Christopher J. Patrick: Conceptualization (lead); formal analysis (lead); project administration (lead); writing – original draft (lead); writing – review and editing (lead). **Kurt Anderson:** Conceptualization (supporting); writing – original draft (supporting); writing – review and editing (supporting). **Bryan Brown:** Conceptualization (supporting); writing – original draft (supporting); writing – review and editing (supporting). **Charles Hawkins:** Conceptualization (supporting); writing – original draft (supporting); writing – review and editing (supporting). **Anya Metcalfe:** Conceptualization (supporting); writing – original draft (supporting); writing – review and editing (supporting). **Pars Saffarinia:** Conceptualization (supporting); writing – original draft (supporting); writing – review and editing (supporting). **Tadeu Siqueira:** Conceptualization (supporting); writing – original draft (supporting); writing – review and editing (supporting). **Christopher Swan:** Conceptualization (supporting); writing – original draft (supporting); writing – review and editing (supporting). **Jonathan Tonkin:** Conceptualization (supporting); writing – original draft (supporting); writing – review and editing (supporting). **Lester Yuan:** Conceptualization (supporting); writing – original draft (supporting); writing – review and editing (supporting).

DATA AVAILABILITY STATEMENT
These data were derived from the following resources available in the public domain: US EPA National Aquatic Resource Surveys, Rivers and Streams 2008-2009, available for download at: https://www.epa.gov/national-aquatic-resource-surveys/data-national-aquatic-resource-surveys.

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