How Does the Landscape Affect Metacommunity Structure? A Quantitative Review for Lentic Environments

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Abstract

Purpose of Review We conducted a literature review to understand how landscape patterns affect ecological processes in metacommunities in lentic environments. Our aim was to identify trends in these studies considering taxa, aquatic systems, landscape metrics, and response variables. We also recorded whether studies were presenting the exclusive effect of landscape on metacommunities (i.e., the effect of landscape independent from other environmental variables). Finally, we provide some guidelines for future studies.

Recent Findings We identified a consistent increase in the number of studies from 2006 to 2018. Insects and amphibians were the most studied organisms and ponds (ponds and pools) were the systems most studied. Patch-level metrics and landscape-level metrics were similarly reported. Beta diversity was more common than alpha diversity as a response variable, especially for those employing taxonomic data. Finally, most studies reported the effect of landscape separated from other variables, although the metrics used and their effects on metacommunities varied.

Summary Our understanding of how landscape affects the structure of metacommunities in lentic systems is still limited, because of the low number of studies, the approaches used to assess the contribution of landscape, and the variety of landscape metrics used in these studies. We recommend that future studies aiming to understand the role of landscape on metacommunities should avoid summarizing local and landscape variables or different landscape metrics into a single variable, but carefully choose the best landscape metric to match the hypothesis being tested.

Keywords Beta diversity · Dispersal · Landscape patterns · Patch size · Ponds · Spatial ecology

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Introduction

Although previously defined as a set of local ecological communities connected by the dispersal of species [1, 2], the metacommunity concept emerged as a driving concept in ecology in the mid-2000s [3, 4]. Since then, studies that employed the metacommunity framework have traditionally focused on the relative importance of spatial and environmental processes to the variation in species composition among local communities [5, 6], and especially on the role that the local environment and dispersal play in structuring metacommunities [7–9]. Dispersal across the landscape depends on several factors, such as matrix permeability, species dispersal ability, and degree of habitat fragmentation [10, 11]. Understanding how these landscape patterns affect biodiversity is a primary focus of landscape ecology. Thus, there is an overlap between the metacommunity theoretical framework, and the concepts applied in landscape ecology. For example,

Ryberg and Fitzgerald [12•] found that landscape composition and configuration (i.e., quality of focal habitat, number, and size of surrounding focal habitat) determined the metacommunity structure of lizards across multiple scales. Furthermore, they argued that a lack of explicit recognition of landscape heterogeneity can hamper our understanding of how landscape–dispersal interactions shape metacommunity structure. Therefore, there is a clear need to better integrate the concepts and practices of both metacommunity and landscape ecology to improve our understanding of how communities are structured in space.

Metacommunity and landscape ecology have many theoretical roots in common, including the theory of island biogeography [13] and metapopulation [1, 14–16]. For example, both provide a spatial perspective to community ecology and emphasize the role of spatial scale, connectivity (via dispersal), and spatial variation in environmental conditions and resources [16, 17]. As desirable as it would be, these two subdisciplines do not yet share a common language or theoretical framework. Somehow, during the development of its theoretical underpinnings, the metacommunity framework diverged from landscape ecology and adopted different terms to refer to the same process. This divergence becomes clear when we take the importance of flow of individuals (i.e., dispersal) among different habitat types to structure communities: a landscape ecologist would call it spillover effect [18], while a metacommunity ecologist would call it mass effect (or species sorting, depending on the relative strength of dispersal and distinctiveness of patches) [19]. Yet, these two concepts basically describe the same process [20], so the divergence between the two subdisciplines is more a case of tradition than a profoundly different theoretical concept.

Despite this common historical root and overlapping concepts, few studies have actually tried to connect the concepts and approaches of metacommunity and landscape ecology. For example, Biswas and Wagner [21] proposed that landscape contrast (i.e., the average difference in habitat quality between adjacent patches) should be used to represent landscape variation in metacommunity ecology. They developed a connection among levels of landscape contrasts and the four initial metacommunity archetypes (i.e., species sorting, mass effects, patch dynamics, and neutral model). These theoretical ideas were operationalized by Ryberg and Fitzgerald [12•] who used landscape metrics to estimate landscape contrast and explain metacommunity structure of lizards. They found that both the diversity and number and size of habitats in the surrounding landscape matrix best explained the metacommunity pattern, consistent with mass effects model as interpreted by landscape contrast.

Landscape resistance is another approach commonly used to explain metacommunity patterns [22, 23]. Landscape resistance estimates distances among local communities by weighting landscape characteristics based on species habitat preferences. Then, it can be measured by the least-cost path species would use as dispersal route or by a range of cumulative costs of landscape resistance between sites, usually based on land use, human construction, and topography [24]. For example, Cañedo-Argüelles et al. [22] used landscape resistance to understand distance-decay relationships and showed that the distribution of aquatic invertebrates with intermediate dispersal capacity was better explained by two landscape resistance measures (calculated using perennial watercourse and topographic distances). Similarly, in boreal streams, Kärnä et al. [23] showed that landscape resistance correlates better with biological dissimilarities of stream insects than overland or watercourse distances between sites.

Given that metacommunity and landscape ecology have common theoretical roots and goals, but distinct methods, our objective was to understand the role of landscape structure on metacommunities in lentic environments. Through a systematic review of the literature, we identified the most evaluated (1) taxa, (2) aquatic systems, (3) response variables, and (4) landscape metrics. Furthermore, we identified studies that reported the effect of landscape on alpha and beta diversity separated from other variables (i.e., the effect of landscape independent from other environmental variables).

Methods

We conducted a literature search using the ISI Web of Knowledge in December 2018 using the following terms: landscape* AND metacommunit* AND (pond* OR pool* OR lake* OR wetland). Studies were restricted to those (1) conducted partially or entirely in lentic aquatic systems, (2) used landscape metrics to understand metacommunity patterns, and (3) empirical studies or experiments conducted at the landscape scale, excluding laboratory experiments. A PRISMA flow diagram showing the process of literature search and filtering criteria is available at Online Resource 1.

We classified studies according to five criteria: (1) taxonomic group, (2) aquatic system, (3) landscape metric(s), (4) response variable(s), and (5) whether the effect of landscape separated from other variables was reported. Aquatic systems were classified as lakes, ponds (ponds and pools), and wetlands. Landscape metrics were classified into patch- or landscape-level [sensu 25, 26]. We considered patch size and isolation as patch-level metrics, whereas landscape composition and configuration were considered as landscape-level metrics. While landscape composition represents the assemblage of landscape units that composes a landscape (e.g., amount of native habitat, matrix types), landscape configuration represents the spatial arrangement of landscape units [25]. Therefore, landscape metrics such as number/density of patches [8, 26] and landscape connectivity [27, 28] were considered as landscape configuration metrics. One study

reported the proportion of road cover within a 500-m radius around the pond as a measure of patch isolation [29]. However, we considered it as a measure of landscape composition.

We did not consider spatial eigenfunction analysis (e.g., Moran or Asymmetric Eigenvector Maps) as a measure of landscape configuration, despite its derivation from a connectivity network, which considers hypothetical connectivity among patches (e.g., minimum spanning tree, k-nearest neighborhood). While landscape-level metrics consider all patch types or classes over the entire landscape [30, 31], spatial eigenfunction analysis only considers the sampled patches. Likewise, we did not consider a binary variable, such as "hydrological connectivity" (0: individual lakes not connected to the hydrographical network; 1: connected to rivers and streams) reported in one article [32], as a measure of landscape configuration.

Response variables were classified into alpha (or local diversity) and beta diversity (variation in species composition among communities), both subdivided into taxonomic, functional, and phylogenetic facets. The effect of landscape on metacommunities was classified into three different levels: (1) studies that assessed the effect of landscape on diversity measures separated from other variables (e.g., local environmental variables); (2) studies that reported the individual effect of specific landscape metrics (e.g., patch size, connectivity) on diversity measures; (3) studies that reported the directionality of the relationship between landscape metrics and diversity measures.

Results

We found 32 articles that evaluated the effect of landscape patterns on metacommunities in lentic environments, published from 2006 to 2018 (Online Resource 2). A range of taxa were studied, including plants, invertebrates, and vertebrates (Fig. 1a). Among animals, studies with invertebrates ($N = 17$) were more common than with vertebrates ($N = 15$), with insects being the most studied group ($N = 12$) (Fig. 1b, c). Among vertebrates, amphibians ($N = 11$) and fish ($N = 5$) were the most studied groups (Fig. 1c). Ponds (ponds and pools; $N = 17$) were more studied than wetlands ($N = 8$) and lakes ($N = 8$). Patch-level metrics ($N = 29$) and landscape-level metrics ($N = 28$) were similarly reported. Patch size was the most used landscape metric ($N = 21$), followed by metrics of landscape composition ($N = 15$) and landscape configuration ($N = 13$). Beta diversity ($N = 32$) was more common than alpha diversity ($N = 22$) as a response variable. Most studies evaluated taxonomic ($N = 26$, $N = 18$; respectively for beta and alpha diversities), rather than functional ($N = 4$, $N = 3$) or phylogenetic ($N = 2$, $N = 1$) diversities.

Most studies reported the effect of landscape separated from other variables ($N = 24$, Online Resource 2). In the remaining studies ($N = 8$), the landscape and local variables were considered as a single environmental component. This was done by summarizing them using a principal component analysis (PCA, $N = 4$) or using a matrix of landscape and local variables ($N = 4$). Among the studies that reported the effect of landscape separated from other variables, 20 provided the individual effect of landscape metrics (e.g., patch size, connectivity, forest cover) and four summarized different landscape metrics using a PCA or reported the amount of variance explained by the component "landscape" (Online Resource 2). Eighteen out of these 20 studies reported the directionality of the relationship between landscape metrics and diversity measures (Table 1).

The relationship between patch size and alpha diversity was more positive ($N = 6$) than negative ($N = 2$) or neutral ($N = 4$; Table 1). Similarly, more studies found positive ($N = 3$) than negative ($N = 1$) or neutral ($N = 1$) relationships between landscape configuration and alpha diversity (Table 1). Conversely, a similar number of studies found negative ($N = 4$) and neutral ($N = 3$) relationships between landscape composition and alpha diversity and positive ($N = 3$) and negative ($N = 2$) relationships between landscape configuration and beta diversity (Table 1). For example, Zealand and Jeffries [33] found no relationship between pond area and snail species richness. Also, farther ponds were less similar in terms of vegetation structure and snail community composition (Fig. 2).

Discussion

Our current understanding of the effects of landscape metrics on metacommunities in lentic systems is clearly biased towards animals (especially insects and amphibians), ponds (ponds and pools) and beta diversity. Insects and amphibians have been largely evaluated in metacommunity studies in lentic systems worldwide [29, 34–36]. Compared to vertebrates, insects are more abundant and speciose and easier to sample and to manipulate [37]. Amphibians can be useful models for studying environmental changes because of their life-history traits, such as their role in aquatic food webs, high sensitivity to environmental changes, and easiness to use in experimental manipulations [38]. Ponds—the most studied aquatic system—can be good model systems for research in ecology because they are abundant, have discrete boundaries (as aquatic "islands"), are relatively easy to sample due to their small size, and span a broad range of ecological gradients [39, 40]. Finally, beta diversity (especially the taxonomic facet) was more studied than alpha diversity. Beta diversity can be more informative as it encompasses information on both the variation in species identities and abundance [41, 42], whereas
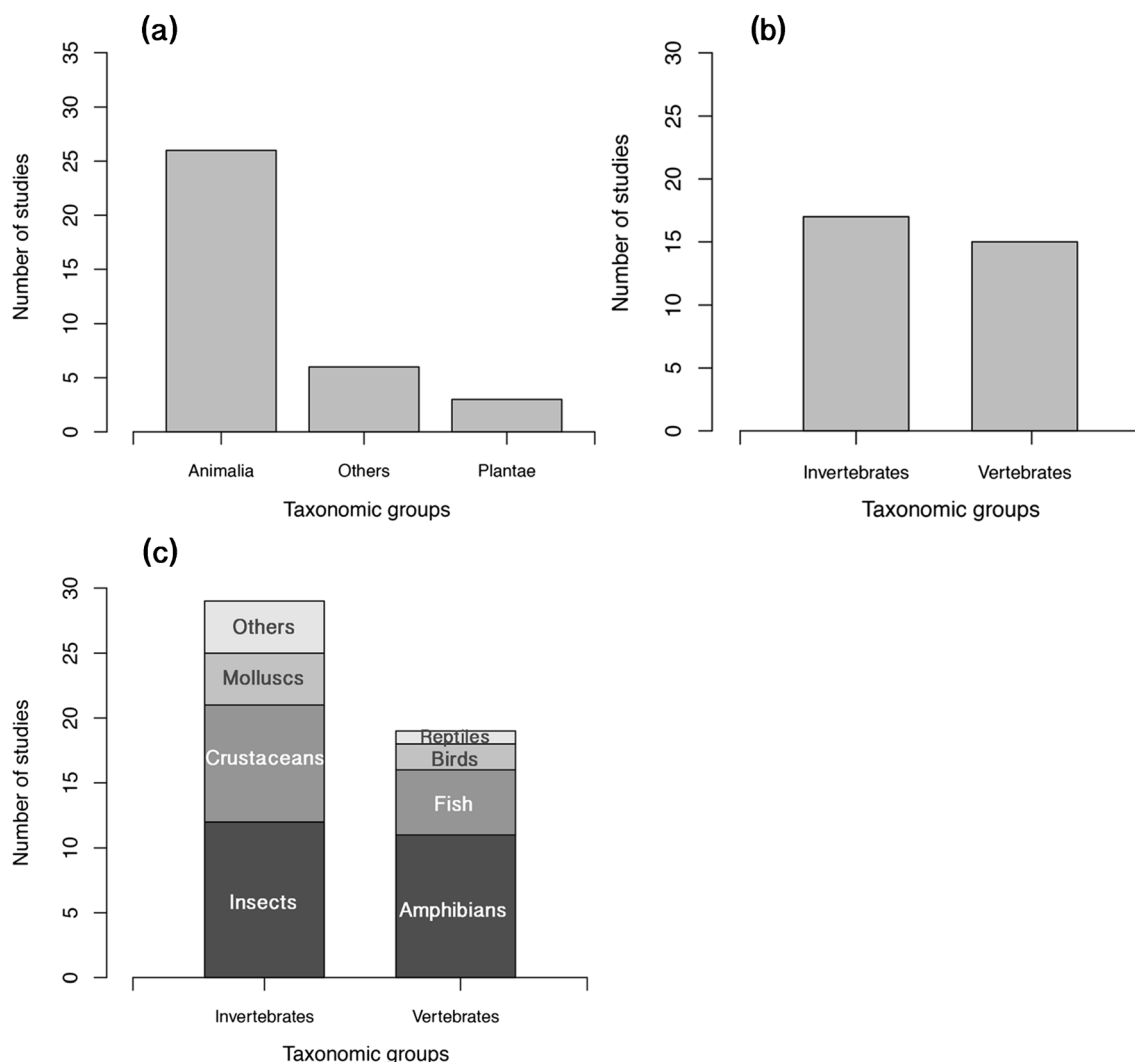
Fig. 1 Taxonomic groups studied in the articles that evaluated the effect of landscape on metacommunities. The number of studies in each group is indicated for realm (**a**), invertebrates and vertebrates (**b**), and groups of vertebrates and invertebrates (**c**). The category "others" includes the realms Monera, Chromista, and Protista in panel **a** and the groups of invertebrates Oligochaeta, Hirudinea, and Rotifera. Some articles included more than one biological group

alpha diversity usually is summarized in species richness or diversity indices. Most studies partitioned the variation in species composition matrix with redundancy analysis (RDA) [43]. The analysis of species composition using RDA (the so-called raw data approach) has been conceptualized as a measure of beta diversity by some [41] on the basis that it

Table 1 Summary of the results of landscape metrics in the evaluated studies. + positive effect, − negative effect, 0 no clear effect detected. Numbers in square brackets indicate the articles at Online Resource 2

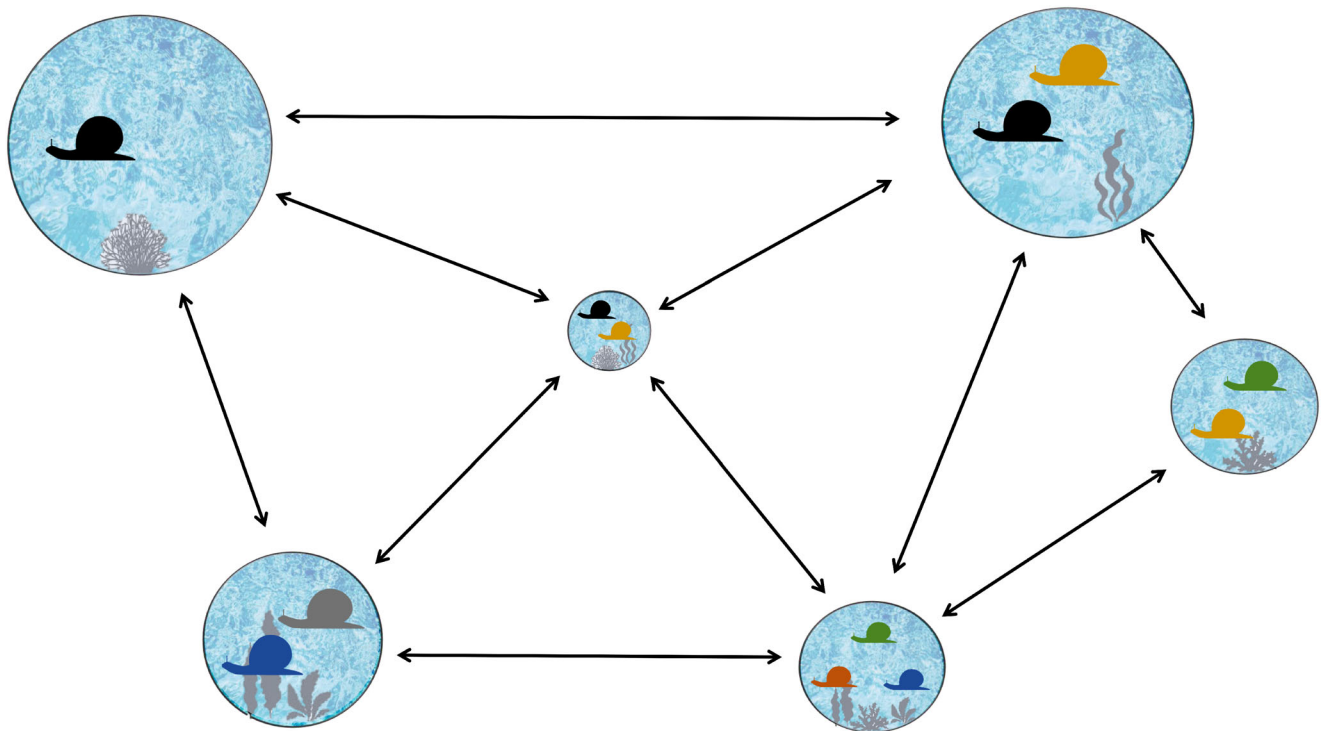| Diversity measure	Patch size	Patch isolation	Landscape configuration	Landscape composition
Alpha diversity (taxonomic)	+ [1, 6, 8, 11, 20, 30]	+ [4]	+ [8, 10, 20]	+ [6]
	− [6, 23]	− [8]	− [8]	− [1, 6, 7, 28]
	0 [5, 6, 11, 23]	0 [18]	0 [10]	0 [6, 18, 24]
Alpha diversity (functional)			+ [9]	
			0 [9]	
Beta diversity (taxonomic)	+ [23]		+ [2, 12]	+ [18]
	− [2, 18]		− [5, 12, 22]	− [28]
	0 [22]	0 [22]		0 [7, 18]

Fig. 2 Scheme illustrating the main results found in Zealand and Jeffries (2009). Pond area had no effect on snail species richness, but closer ponds were more similar in terms of vegetation structure and snail community composition

assesses the variation in species composition among sites. RDA is a distance-based ordination technique that takes the Euclidian distance between sites and allows calculating its total variance, and also the contribution of each site (LCBD) and each species (SCBD) to the total variance [44].

Most studies reported the effect of landscape separated from other variables. However, the chosen metrics (patch- and landscape-level) varied widely as well as their effects on metacommunity structure. Patch size was the most used landscape metric (mostly with positive effect on alpha diversity), probably because the increase in richness with spatial scale (the species–area relationship, SAR) is one of the most robust and popular patterns in ecology [45–48]. For example, Parris [29] reported a strong and positive effect of pond size on amphibian species richness. Likewise, Özkan et al. [49] found a strong and positive relationship between lake area and the richness of the main phytoplankton groups. However, Zealand and Jeffries [33] found no significant relationship between the number of snail species and pond area.

The use of different land uses classes (e.g., urban areas, native forest areas, agriculture areas) and measures of landscape configuration (e.g., number of patches, landscape connectivity, distance among patches) preclude a proper assessment of the effect of landscape structure on metacommunities. Parris [29] found a strong and negative effect of the proportion of road cover in a buffer of 500-m radius around ponds on amphibian species richness. Wetlands embedded within urban areas supported 60% lower species richness of amphibians

and aquatic reptiles and 33% lower richness of aquatic insects, mollusks, and crayfish relative to wetlands embedded within grassland areas [50]. However, land use was a poor predictor of the variation of phytoplankton richness in lakes [49] and abundance of tadpole species [51]. Connectivity had a positive effect on species richness of insects with high-flying ability in wetlands [52] and on species turnover of larval amphibians [27], but it had a context-dependent effect on a seasonal flood-plain fish metacommunity [53].

Although we recognized that some studies did not have the specific aim to assess the role of landscape metrics on metacommunity structure, we identified two problems that precluded a proper evaluation of how landscape variables shape metacommunities in lentic environments. First, some studies [54, 55] summarized a set of environmental variables (including landscape metrics and local variables) using PCA and entered them in downstream ordination analysis, hampering our ability to evaluate the role of landscape separated from other variables. Second, other studies [56, 57] summarized different landscape metrics as a single variable, making it impossible to evaluate the real contribution of each landscape metric. The use of non-mixed landscape metrics allows a proper link to ecological theory. For example, differences in patch size can cause nested patterns, with species on smaller and less habitat–diverse patches being subsets of those on larger and more diverse ones [58, 59]. Conversely, land cover changes can cause species turnover for a range of taxa world-wide [60, 61]. Furthermore, matrix characteristics can

influence species dispersal, determining metacommunity structure [51]. Therefore, by not showing the individual effect of each landscape metric, we likely lose important information on ecological processes that drive species distribution patterns.

The integration of metacommunity and landscape ecology can be done using analytical tools commonly used by metacommunity ecologists. The commonly used variation partitioning applied to linear models (e.g., multiple regressions and redundancy analysis) can disentangle the effects of a set of predictors, such as environmental, connectivity, and spatial variables on biodiversity patterns. Accordingly, Monteiro et al. [62•] compared two variation partitions applied to a marine polychaete metacommunity to show that the addition of a patch connectivity component (a species-specific measure) improved about 40% the amount of variation explained compared to the traditional approach (using only environmental and eigenfunction analysis). This simple approach allows the comparison of the amount of variance explained by spatial and connectivity components, but few studies analyzed here used a similar approach [56, 57]. Similarly, landscape resistance can be easily included in metacommunity analyses to better understand how landscape affects metacommunity structure [22, 23]. On a side note, the landscape resistance approach relies on distance-based analyses (e.g., Mantel test), requiring the computation of dissimilarity measure from the raw response data, an approach criticized by Legendre et al. [41]. Our results indicated that two studies used this approach [8, 53], although in Benito et al. [8], landscape resistance was summarized by Moran eigenvector maps.

The landscape contrast approach (ordered from low to high contrast: homogeneous = 1, gradient = 2, mosaic = 3, binary = 4) developed by Biswas and Wagner [21] and operationalized by Ryberg and Fitzgerald [12] was not used by any study we analyzed, despite its interesting framework that explicitly links landscape patterns to metacommunity archetypes. In a review of 123 empirical metacommunities studies, Biswas and Wagner [21] found that only 22% were explicit about their underlying landscape model assumptions, and that landscape contrast has limited power in predicting metacommunity archetypes. However, this result might not reflect the actual role of the landscape in determining metacommunity structure, as the definition of landscape models based on landscape contrast might be an oversimplification.

Conclusion

In sum, our analysis shows that the merging of landscape and metacommunity ecology although desirable is still poorly developed. Work to date has primarily attempted to establish a link between general landscape metrics and distribution patterns within the conceptual framework of metacommunity ecology. This has primarily been done in ways that ask if landscape metrics explain any fraction of community variation in addition to those included in metacommunity studies. These studies point to a promising avenue for further research, but currently, analyses have not identified specific predictions related to these effects of landscape metrics on metacommunity structure (with the exception of Biwas and Wagner [21] and Ryberg and Fitzgerald [12]). Furthermore, the link to metacommunity ecology has remained rather simplistic by focusing on metacommunity archetypes (descriptions that apply to entire metacommunities) rather than parsing out variation within metacommunities (descriptions that might apply to species with different traits or patches with different landscape attributes). Further work on such predictions (e.g., [63]) should help solidify insights into the interplay between landscape and metacommunity ecology.

The explicit inclusion of landscape variables is one of the ways to move metacommunity ecology towards a 2.0 version, since it helps metacommunity to become spatially explicit, as pointed out by Leibold and Chase [64]. It would add not only both a landscape context to the study of dispersal but also an exercise of synthesis across disciplines. We recommend that future studies on the role of landscape in structuring metacommunities should (1) avoid summarizing landscape metrics with other environmental variables or several landscape metrics into a single variable, likewise, avoid entering principal components into variation partitioning to measure the amount of variation explained by the "landscape." In this case, it is better to use separate metrics that would allow testing the specific contribution of each variable, for example, using a marginal test [65]; (2) use a proper landscape metric (e.g., patch size, connectivity) in order to obtain a better match with the ecological question of the study; (3) use one of the approaches discussed in the previous paragraph that can operationalize studies aiming to understand the role of landscape on metacommunity patterns. In conclusion, there is a clear need for better practices to understand how landscape patterns affect metacommunity structure in lentic systems.

Compliance with Ethical Standards

Conflict of Interest On behalf of all authors, the corresponding author states that there is no conflict of interest.

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