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PERSPECTIVE

Landscape contrast: a solution to hidden assumptions in the metacommunity concept?

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Abstract The metacommunity concept provides a spatial perspective on community dynamics, and the landscape provides the physical template for a metacommunity. Several aspects of landscape heterogeneity, such as landscape diversity and composition, and characteristics of the matrix between habitat patches such as habitat connectivity, and geometry of habitat patches, may moderate metacommunity processes. These aspects of landscape heterogeneity are rarely considered explicitly in the metacommunity discussion, however. We propose landscape contrast (i.e., the average dissimilarity in habitat quality between neighboring patches) as a key dimension of landscape heterogeneity. The concept of landscape contrast unifies discrete and continuous landscape representations (homogeneous, gradient, mosaic and binary) and offers a means to integrate landscape heterogeneity in the metacommunity concept. Landscape contrast as perceived by the organisms affects several fundamental metacommunity processes and may thus constrain which metacommunity models may be observed. In a review of empirical metacommunity studies ($n = 123$), only 22 % of studies were explicit about their underlying landscape model assumptions, with striking differences among taxonomic groups. The assumed landscape model constrained, but did not determine, metacommunity models. Integration and explicit investigation of landscape contrast effects in metacommunity studies are likely to advance ecological theory and facilitate its application to real-world conservation problems.

Keywords Connectivity · Dispersal · Ecological theory · Environmental filtering · Landscape heterogeneity · Landscape model · Matrix · Metacommunity models · Species interaction

Introduction

The metacommunity concept regards metacommunities as sets of local communities connected by dispersal and thus offers a spatial perspective of community dynamics (Gilpin and Hanski 1991; Leibold et al. 2004). Metacommunity models describe metacommunity dynamics as a function of three ecological processes (Table 1): environmental influences, termed "environmental filtering", dispersal among patches, and species interactions. Four general metacommunity models are commonly distinguished, which differ in the relative importance of these three metacommunity processes (Fig. 1a) and are termed as: patch dynamics, species sorting, mass effect and

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Table 1 Definition of metacommunity processes and models

Term	Definition
Metacommunity processes	
Environmental filtering	Environmental conditions govern species' occurrence
Species interactions	Competition among species for resources or space governs species' occurrence. Other interactions, such as facilitation, are not commonly considered in metacommunity studies
Dispersal	Propagules or offspring move permanently from their natal site to another location.
Metacommunity models (Source Leibold et al. 2004)	
Patch dynamics	"[..] Patches are identical and that each patch is capable of containing populations but may be occupied or unoccupied. Local species diversity is limited by dispersal. Spatial dynamics are dominated by local extinction and colonization"
Species sorting	"[..] Emphasizes the resource gradients [..]. Patch quality and dispersal jointly affect local community composition. This perspective emphasizes spatial niche separation above and beyond spatial dynamics. Dispersal allows compositional changes to track changes in local environmental conditions"
Mass effect	"[..] Species can be rescued from local competitive exclusion in communities where they are bad competitors, by immigrate from communities where they are good competitors. This perspective emphasizes the role that spatial dynamics affect local population densities"
Neutral	"[..] All species are similar in their competitive ability, movement and fitness (Hubbell 2001). Population interactions among species consist of random walks that alter relative frequencies of species"

neutral dynamics (Leibold et al. 2004; Holyoak et al. 2005).

A landscape is the physical template a metacommunity occupies. Several aspects of landscape heterogeneity may be relevant for metacommunity dynamics, including landscape composition and configuration, matrix characteristics, connectivity, and the diversity and geometry of habitat patches, yet these are rarely considered explicitly. This is surprising given that landscape heterogeneity alters ecological processes that govern and distinguish metacommunity models (Danielson 1991; Dunning et al. 1992; Wiens et al. 1993; With and Crist 1995; Turner 1989; Hoopes et al. 2005; Wagner and Fortin 2005; Jacobson and Peres-Neto 2010). For instance, in pond breeding amphibian metacommunities, matrix characteristics strongly moderated amphibian dispersal, effectively determining the metacommunity model, e.g. species sorting versus mass effect (Richter-Boix et al. 2007). In molluscan metacommunities in lakes, Heino and Muotka (2006) found that landscape position was a more important predictor of species composition than local site conditions, thus challenging the common assumption that local site conditions are the sole determinant of environmental filtering (see also Palmer 1994; With and Crist 1995). The goal of this essay is to argue for explicit integration of landscape heterogeneity into the metacommunity concept.

Because real systems are spatially and temporally heterogeneous (Wiens 2000), the application of theoretical ecological models to real systems requires incorporating heterogeneity (Wagner and Fortin 2005). Metapopulation theory is a good example of a spatially implicit ecological theory that has greatly benefitted from explicit consideration of heterogeneity. Landscape heterogeneity has been integrated into metapopulation theory by incorporating habitat fragmentation and landscape connectivity, landscape structure, and landscape-dependent spatial demography (e.g. Hanski 1994; Gustafson and Gardner 1996; With et al. 1997; Hanski and Ovaskainen 2000, 2003 Ovaskainen and Hanski 2001, 2004; Fahrig 2007; see review by With 2004), thus gaining both theoretical robustness and practical relevance.

Most of the current literature considers metacommunities either as spatially implicit (McGill et al. 2006), where e.g. a set of local communities is linked by an overall migration rate *m*, or as spatially explicit using simplistic assumptions, e.g., where dispersal rates depend on distance between local communities alone. Such assumptions may be unrealistic, as illustrated by Altermatt et al. (2011) who showed that dispersal between patches may vary with direction. Many papers highlight the importance of spatial processes and heterogeneity in species interactions and dispersal (Hoopes et al. 2005; Holt and Hoopes

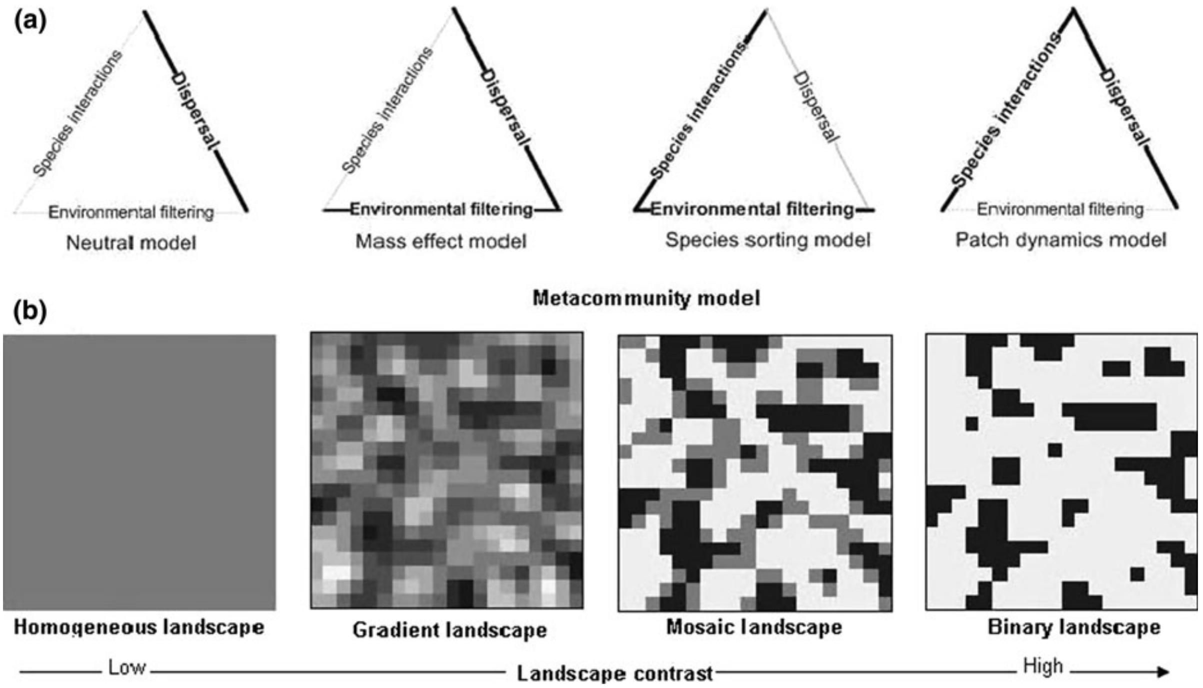

Fig. 1 Conceptual diagram showing **a** four common metacommunity models (patch dynamics, species sorting, mass effect, and neutral model) and **b** four landscape models (homogeneous, gradient, mosaic, and binary model) along the unifying dimension of landscape contrast. For each metacommunity model, the line width of triangle edges reflects the relative importance of the three metacommunity processes (environmental filtering, species interactions and dispersal). See Table 1 for the definitions of metacommunity models and processes

2005), but the role of spatial heterogeneity in metacommunity structure (Davies et al. 2009) often remains implicit. Very little discussion (Holt et al. 2005) and progress has been made in expanding the metacommunity concept to include heterogeneous landscapes (Hoopes et al. 2005; Holt and Hoopes 2005; Davies et al. 2009).

Concepts of landscape heterogeneity

A further complicating issue is the diverse conceptualizing of what constitutes landscape heterogeneity. As a minimum definition, a landscape is an area that is spatially heterogeneous with respect to at least one factor of interest (Turner 1989; Turner et al. 2001). In the metacommunity context, a landscape corresponds to the spatial extent of the metacommunity, and the spatially heterogeneous factor of interest is habitat quality as perceived by the study organisms. Environmental heterogeneity may occur at any spatial or temporal scale (Allen and Hoekstra 1992; Turner 1989; Wiens 2000), and can be discrete or continuous (Li and Reynolds 1995; McIntyre et al. 2000; McGarigal and Cushman 2005; Wagner and Fortin 2005; Talley 2007). Based on the type of spatial heterogeneity, landscapes are commonly conceptualized in four different ways (McGarigal and Cushman 2005; Bolliger et al. 2007; Talley 2007; McGarigal et al. 2009): (1) homogeneous, (2) gradient (continuous gradient of habitat quality), (3) mosaic (different categories of habitat quality), and (4) binary landscape models (habitat versus inhospitable matrix). The homogeneous landscape model may be seen as a null model, while the gradient model provides a continuous representation of landscape heterogeneity; and the binary and mosaic models are discrete representations of landscape patches and heterogeneity.

We propose that these four landscape models represent points along a continuum of *landscape contrast* (Fig. 1b). We define landscape contrast as the average dissimilarity in habitat quality between adjacent patches (sensu edge contrast; McGarigal 2002;

McGarigal et al. 2002). That is, in a low contrast landscape, habitat quality is more similar between adjacent patches than in a high contrast landscape. Categorical landscape models ignore within-patch heterogeneity and emphasize contrast between adjacent patches. Figure 1b illustrates how the same landscape can be represented (from low to high contrast) as: homogeneous, gradient, mosaic or binary. Starting from a gradient landscape, classification of habitats with multiple thresholds of habitat quality results in a mosaic landscape and a single threshold in a binary landscape, effectively maximizing contrast. On the other hand, reduction of contrast ultimately results in a homogeneous landscape.

Scientists often assume a landscape model implicitly with little consideration of the study organisms or the study system. However, the a priori choice of landscape model may constrain results and conclusions. For instance, when Talley (2007) studied the processes governing long horn beetle distributions in California; she reached different conclusions depending on the landscape model assumptions used in the statistical model. When using a patch model, she found empirical support for patch dynamics and source-sink metapopulation models, but when using a gradient model, she found support for gradient-based distribution. This example suggests underlying assumptions about the type of landscape model may potentially constrain which ecological processes dominate and thus which metacommunity models may be observed (Talley 2007).

Here we review the empirical metacommunity literature to quantify how metacommunity ecologists working on different taxonomic groups conceptualized landscapes and to what degree the observed metacommunity models appear to be constrained by the chosen landscape models. We then discuss in detail how landscape heterogeneity may affect metacommunity processes and highlight some conceptual and practical issues regarding conceptualization and integration of landscape heterogeneity in the metacommunity concept.

Methods

A total of 123 papers fulfilled our search criteria (i.e., empirical study on metacommunity assembly) and thus were included in this study (Supplementary Material; Appendix A). These papers were found either through a keyword search on “metacommunity” in the ISI Web of Knowledge^{SM} —Science Citation Index database or by backward and forward searching from two seminal papers (Leibold et al. 2004; Cottenie 2005). From each of the selected papers, we extracted the following information: (1) Was the landscape model explicitly stated? (2) What landscape model was used? (3) What organism did the study consider? (4) What type(s) of metacommunity model did the study observe? Answers to questions 2 and 4 were not explicit in many papers; therefore, we developed rules a priori that allowed us to identify implicit assumptions consistently and classify studies accordingly.

If the landscape model was implicit, we used the following protocol: *binary landscape*—when there was habitat versus non-habitat only, *mosaic landscape*—when there were categories of habitat (i.e., discrete habitat types with different levels of habitat quality), *gradient landscape*—when habitat quality or environmental variables were on a continuous scale, and *homogeneous landscape*—when there was no indication of environmental variability or differences in habitat quality (Supplementary Material; Appendix A). If the study explicitly stated habitat configuration as patch, mosaic, gradient or homogeneous, we classified the landscape model accordingly.

Similarly, when the metacommunity model (Table 1) was not explicitly stated, we adopted the following criteria: s*pecies sorting model*—when environmental filtering was mentioned as the dominant process, along with dispersal and competition, *mass effect model*—when dispersal was identified as the dominant process along with environmental filtering and competition, *neutral model*—when dispersal was the only important process, and *patch dynamics model*—when dispersal and competition (colonization—extinction) were the dominant processes. If more than one metacommunity model was observed in a study, we counted the study more than once.

Results

How do metacommunity ecologists conceptualize the landscape?

Only 21.9 % of studies were explicit about the underlying landscape model. Studies of higher order organisms, such as plant and fish communities, were more likely to be explicit in landscape models compared to studies of lower order organisms such as most invertebrate, plankton and algal communities (Fig. 2).

A majority of studies (61.8 %) assumed a mosaic landscape model, followed by gradient (28.5 %), binary (7.3 %) and homogeneous landscape models (2.4 %). We did not notice any organismal bias in choice of landscape models (Fig. 3). Collectively, most taxonomic groups were studied under at least three of the four different landscape models (Fig. 3).

Are metacommunity models constrained by landscape models?

Species sorting was the dominant metacommunity model in the surveyed studies (56.9 %), followed by mass effect (26.8 %), patch dynamics (13.8 %) and neutral metacommunity models (2.4 %). For most taxonomic groups, three of the four different metacommunity models were reported in the empirical literature (Fig. 4).

There was a moderate, highly significant association (Fig. 5; Spearman $\rho = 0.32$, p-value <0.001) between

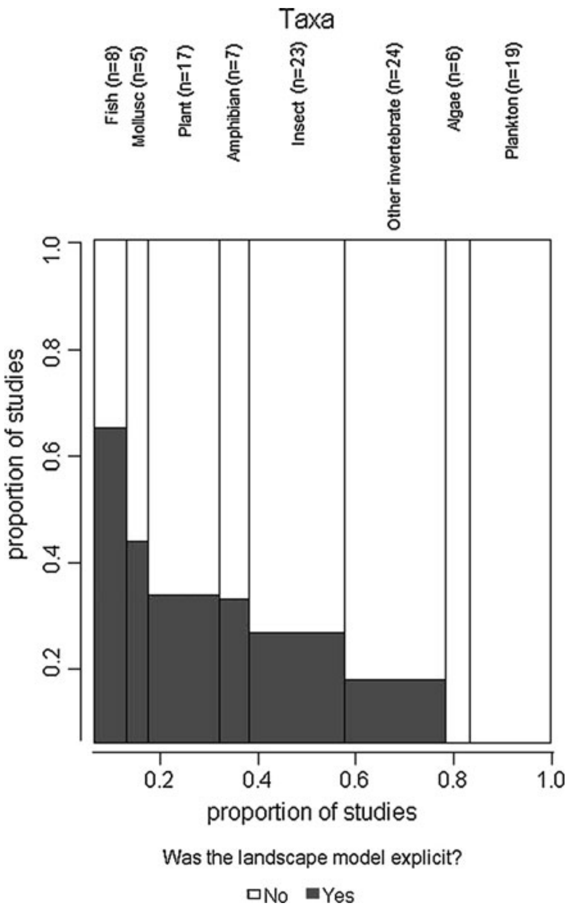

Fig. 2 Mosaic plot showing the proportion of studies where the landscape model was explicit. Each gray vertical bar shows, for a specific taxonomic group, the proportion of empirical metacommunity studies that explicitly reported the underlying landscape model. The width of each bar is proportional to the number of studies per taxon ($n = 109$). Results not shown for a total of 14 taxa with fewer than 5 valid studies

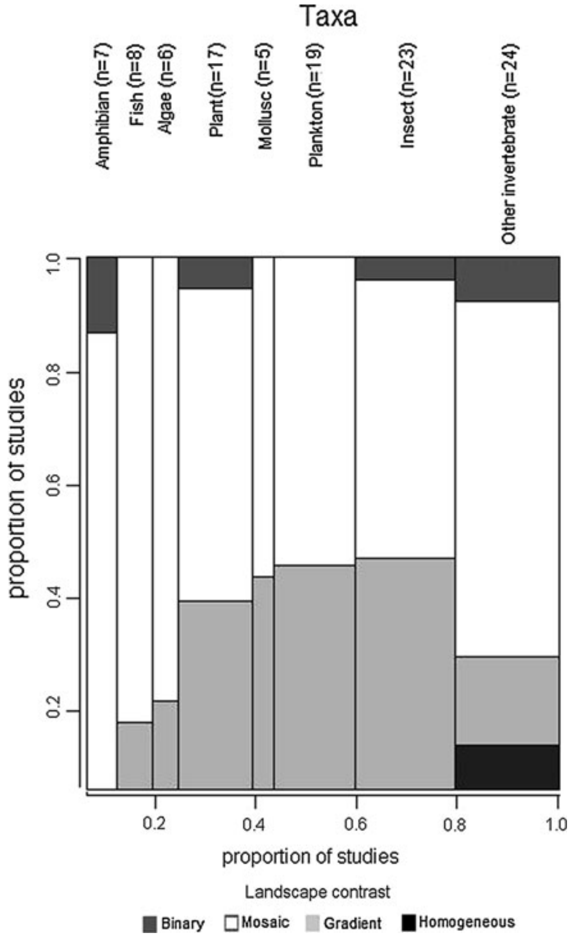

Fig. 3 Mosaic plot of the relative frequency of landscape models for different taxonomic groups. Bar widths are proportional to the number of studies per taxon ($n = 109$). The height of each bar segment corresponds to the relative frequency of a landscape model among studies for the taxon. Results not shown for a total of 14 taxa with fewer than 5 valid studies

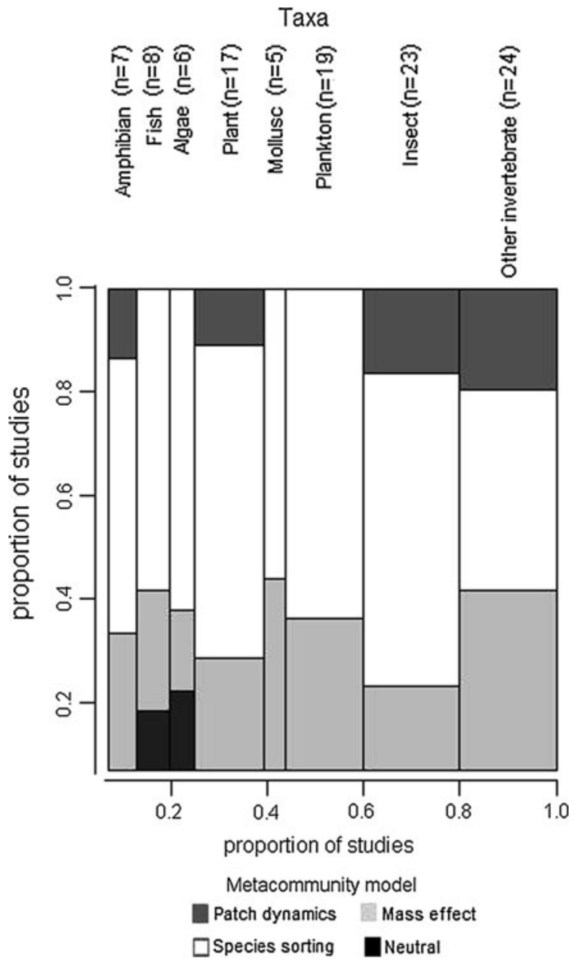

Fig. 4 Mosaic plot of the relative frequency of metacommunity models for different taxonomic groups. *Bar* widths are proportional to the number of studies per taxon ($n = 109$). The height of each *bar* segment corresponds to the relative frequency of metacommunity models among studies for the taxon. Results not shown for a total of 14 taxa with fewer than 5 valid studies

landscape model (ordered from low to high contrast: homogeneous = 1, gradient = 2, mosaic = 3, binary = 4) and metacommunity model (ordered according to the expected relative importance of metacommunity processes from low to high contrast, Fig. 1) neutral = 1, mass effect = 2, species sorting = 3, patch dynamics = 4). Collectively, these results suggests that landscape contrast does affect the relative importance of metacommunity processes, but only to a certain degree, i.e., the metacommunity model cannot be predicted from the landscape model alone.

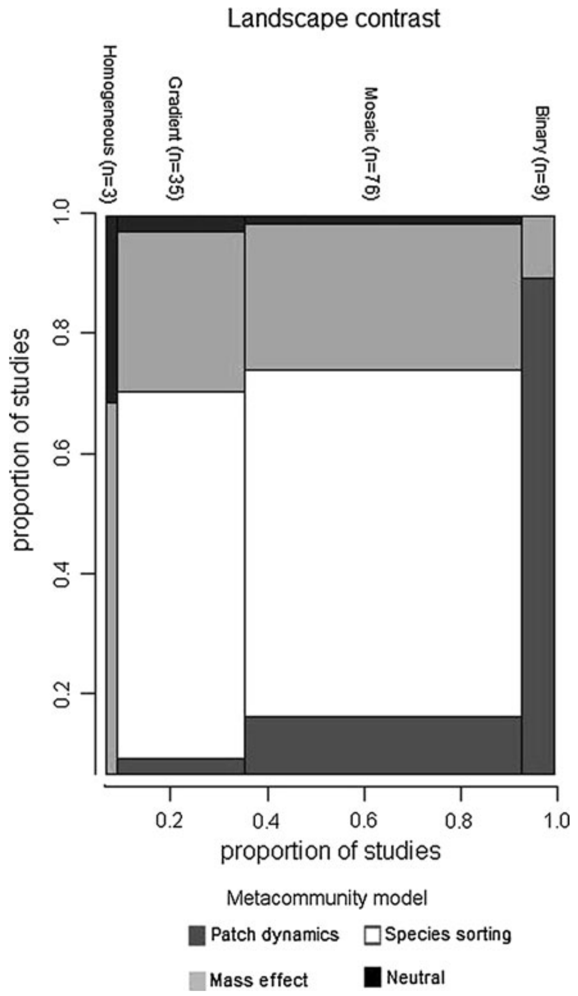

Fig. 5 Mosaic plot of the relative frequency of metacommunity models for different landscape models. *Bar widths* are proportional to the number of studies per landscape model ($n = 123$). The height of each bar segment corresponds to the relative frequency of metacommunity models among studies with a given landscape model

Discussion

Why does landscape heterogeneity matter for the metacommunity concept?

Landscape effects on dispersal

Metacommunity studies typically assume that dispersal is a simple function of geographic distance (diffusion process). In real landscapes, dispersal may be affected by matrix characteristics (e.g., resistance to movement or mortality may vary among land-use/

land-cover types) and the size and shape of patches (Fahrig and Merraim 1994; Hardt and Forman 1989; Kuefler et al. 2010; see Jacobson and Peres-Neto 2010). For instance, in a mark-recapture study of butterfly species commonly inhabiting meadows, Ricketts (2001) evaluated the effect of two matrix types (conifer and willow thicket) on the dispersal of six butterfly species. The author found that depending on the species, a conifer matrix was 3–12 times more resistant than a willow thicket matrix. Hardt and Forman (1989) evaluated the effect of patch shape on colonization of woody plant species in reclaimed mine strips and found that transects along a concave boundary had 2.5 times higher colonization than transects along a convex boundary.

The effects of matrix resistance, patch size and shape, and corridors on active or passive dispersal (Johnson et al. 1992; Fahrig 2003; Arellano et al. 2008; Ockinger and Smith 2008) may further depend on organisms' traits (Dupre and Ehrlen 2002; Schleicher et al. 2011). For instance, animals often show habitat selection where landscape features such as patch size, shape, and contrast among neighboring patches can greatly influence behavior of animals (e.g. Hardt and Forman 1989; Kuefler et al. 2010), and thus affect dispersal. In animal-dispersed plants, dispersal depends on animal movement behavior. In other forms of passive dispersal, such as plants dispersed by wind or water, the distribution of patches (and their shapes) across the landscape may moderate the flow of wind or water and create complex dispersal patterns (e.g., Haddad 1999; Ozinga et al. 2004; Wright et al. 2008; Bolli 2009). Dispersal probabilities between two habitat patches may further depend on the direction, which may have a profound effect on metacommunity dynamics especially if directional bias interacts with disturbance (Altermatt et al. 2011).

Landscape effects on environmental filtering

Metacommunity models assume that a species' physiological ability to tolerate the abiotic environment (fundamental niche) primarily limits its occurrence in a particular habitat type (Keddy 1992; Muller-Dombomis and Ellenberg 2002). Because a species' distribution may further be limited by superior competitors, the realized niche is often only a subset of the fundamental niche. The processes of environmental filtering and species interactions are thus intrinsically linked and difficult to disentangle from observational studies.

Landscape composition (diversity of habitat types) and configuration (spatial arrangement of habitat) may affect the distribution of species with different niche requirements (e.g., habitat specialists versus habitat generalists) beyond the filtering effect of local site conditions (Wiens et al. 1993; With and Crist 1995; With and King 2001). For a habitat specialist that requires the proximity of multiple habitat types to complete its life cycle (e.g., amphibians), the presence and juxtaposition of required habitat types in a landscape may moderate population persistence—this process is called landscape complementation (Tilman 1982; Petit 1989). Habitat generalists are likely to profit from landscape supplementation, where availability of the primary habitat type is supplemented by other suitable habitat types. The supplementary habitat provided by diverse habitat types may thus allow their persistence in the landscape (Whitcomb et al. 1977; Tilman 1982) even in the event of disturbance or habitat loss and fragmentation (With and Crist 1995). On the other hand, species may persist in a low quality (sink) habitat despite reduced fitness if nearby high-quality habitat acts as a continuous source (Pulliam 1988; With and King 2001).

Landscape effects on species interactions

The metacommunity literature demonstrated that if several species can tolerate similar physical environments, species interactions favor the superior competitors (competitive exclusion). Metacommunity models typically assume that species interactions are an intrinsic property of species, and thus species interactions can be represented by the interactions of the average individual and are constant in space and time. However, species interactions may vary spatially with environmental site conditions (Hoopes et al. 2005). For instance, in a simulation study, Graniero (2007) showed that species in resource-poor habitats experience reduced competition compared to intense competition in high quality habitats. Thus, the presence of habitat types with different levels of habitat quality may directly affect species interactions (Danielson 1991).

In a dynamic landscape, a species' presence in habitats adjacent to a disturbed focal patch may allow the species to disperse to the focal patch quickly and thus provide competitive advantage through priority effect (Du Rietz 1921; Gause 1937). Resource fluctuation in space and time may further moderate the strength of species interactions (Kordas and Dudgeon 2010) and may even favor dominance of an inferior competitor through priority effect (Du Rietz 1921; Gause 1937) or spatial mass effect (Shmida and Ellner 1984).

Linking landscape and metacommunity ecology through landscape contrast: some conceptual and practical issues

Metacommunity models differ in the presumed relative importance of dispersal, environmental filtering and species interactions. Landscape heterogeneity effects on metacommunities likely extend beyond modification of dispersal rates, as species-specific competitive ability and reproductive success will vary between cover types, thus modifying environmental filtering and species interactions in addition to dispersal. Aligning the sequence of metacommunity models along the unified dimension of landscape contrast (Fig. 1), by considering how landscape contrast may affect the relative importance of metacommunity process (Fig. 6), helps synthesize these various ideas. For instance, because species in neutral communities do not benefit differentially from habitat heterogeneity, homogeneous landscapes are the most likely landscapes for neutral dynamics in which dispersal is the only acting metacommunity process. Metacommunity models that include environmental filtering and species interactions (e.g., patch dynamics, species sorting and mass effect models) may not be the most appropriate in homogeneous landscapes. Similarly, any metacommunity model that includes environmental filtering (i.e., species sorting and mass effect models) may not be the most appropriate in binary landscapes, because this landscape model only considers habitat versus inhospitable matrix without differentiating habitat quality. Thus, patch dynamics and neutral models are the most likely metacommunity models in binary landscapes.

Species sorting and mass effect dynamics occur when species can establish across a range of habitat types, and thus are most likely to be observed in mosaic or gradient landscapes. In mosaic and gradient landscapes, all three processes may be relevant, and thus, all metacommunity models are potentially applicable. However, the metacommunity model reflects how organisms perceive landscape contrast, so that the dynamics of different organisms in the same physical landscape may follow different metacommunity models (Fig. 5). Because the choice of landscape model may constrain metacommunity models, the choice should be done carefully and be made explicit.

The concept of landscape contrast offers a means to integrate discrete and continuous forms of spatial environmental heterogeneity as a unified dimension into the metacommunity concept. The dimension of landscape contrast considers how organisms may perceive the landscape, ordering landscape models

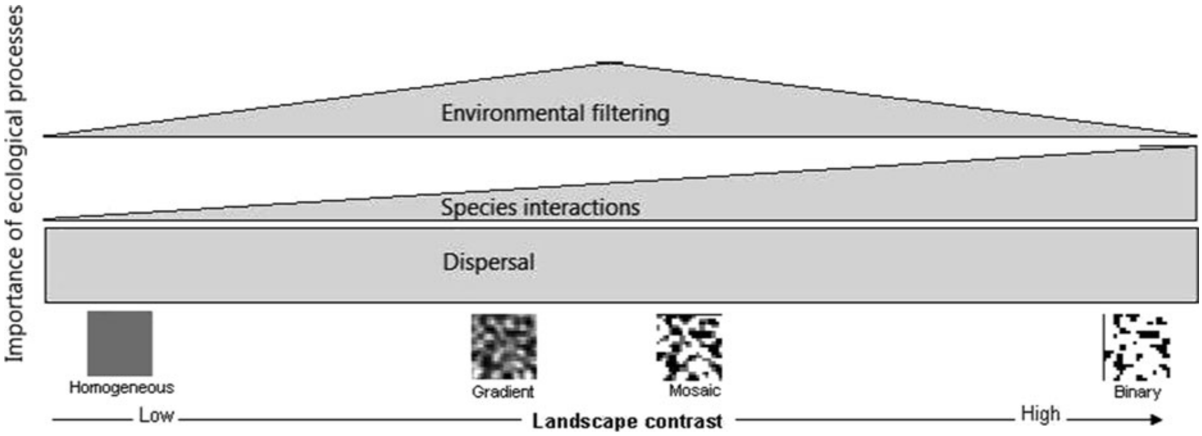

Fig. 6 Conceptual diagram illustrating how the importance (proportional to bar width) of metacommunity processes may be expected to vary with landscape contrast: dispersal is important in all landscapes, environmental filtering is important in intermediate contrast landscapes, and species interactions are important in high to intermediate contrast landscapes

from low to high contrast. This differs from the traditional view such as ordering from simple to complex data models (homogeneous, binary, mosaic, gradient) as is often done implicitly or explicitly in landscape ecology. Ecological complexity (biotic and abiotic) may thus be highest at intermediate contrasts (e.g., mosaic and gradient models) but relatively small at low or high contrasts (e.g., homogeneous and binary models).

However, relevance and representation of landscape heterogeneity depends on the processes under consideration and the organisms involved (Wiens 1989; Holt 2008). The smaller the gap between scientists' perception and organisms' perception of landscapes, the more appropriate a chosen conceptual model will be. How the difference in the conceptualization of a landscape could affect the observable metacommunity model and whether that observation varies with organisms (e.g., habitat specialist vs. habitat generalist) may be a worthy topic for future research using computer simulation. By changing the contrast of a landscape and converting it to different landscape models, one can systematically evaluate the effects of landscape contrast on ecological processes (Fig. 6).

In experimental or theoretical studies, integration of landscape contrast into the study design would increase interpretability and avoid confounding variables. For instance, Matthiessen et al. (2010) studied the effects of environmental heterogeneity on metacommunity diversity in marine benthic microalgae. The authors contrasted diversity in two experimentally manipulated environmental settings, with and without light gradient. Because the control (no light gradient among patches) was not repeated at different light levels (i.e., varying contrast between habitat and matrix), it was not possible to empirically disentangle the effects of homogeneity and habitat quality.

In real systems, appropriate conceptualization of landscapes is challenging and will require the knowledge of an organism's perspective (McIntyre et al. 2000; Talley 2007). What is a patch is often unclear and largely assumed (McIntyre et al. 2000). Definition of a patch may vary with organisms because different organisms that occupy the same physical area may not perceive landscape heterogeneity in the same way. Patch area may be confounded with patch quality (Wiens 1989). For instance, Ellis et al. (2006) studied dynamics of mosquito metacommunities in water-filled tree holes. In a simplified view, the study system can be considered as a binary landscape where tree holes are habitat patches and the volumes of water in tree holes represents patch size, as it may limit the number of individuals. From a mosquito perspective, differences in water volume may represent differences in habitat quality (Gilbert et al. 2008). Thus whether the volume of water in a tree hole represents patch area or patch quality is subject to debate, as both may correlate with species abundance.

The challenges associated with the conceptualization of landscape contrast may vary with study systems and patterns of interest. While landscape ecology has primarily evolved from a terrestrial perspective, 68.3 % of the 123 surveyed metacommunity studies were from aquatic systems (microcosms: 0.8 % and terrestrial systems: 30.9 %). Terrestrial systems are primarily treated as two-dimensional, whereas aquatic systems may be seen as ranging from one-dimensional (stream) to three-dimensional systems (horizontal and vertical stratification of water body).

Also, the boundaries between discrete and continuous landscapes may be blurred, as in the example of the Belgian "De Maten" pond system. This well studied metacommunity represents a collection of ponds (patches) connected by streams (corridors) across an inhospitable terrestrial matrix. Although the concept of a patch-corridor-matrix system may imply a mosaic view with three discrete levels of habitat quality, this landscape is best conceptualized with a gradient model as the streams vary in concentrations of submerged macrophytes, which creates a gradient in habitat quality for zooplankton.

In conclusion, we argue that landscape spatial heterogeneity affects metacommunity processes, and that the chosen landscape model may constrain the range of metacommunity models likely to be observed. Thus, we suggest an explicit integration of landscape spatial heterogeneity in future theoretical and empirical metacommunity studies. Our proposed unification of four different conceptual landscape models into a single dimension of landscape contrast will facilitate development and refinement of ecological theories relevant to real landscapes and thus narrow the gaps between theoretical work, empirical research and application of the metacommunity concept.

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