

Microfragmentation concept explains non-positive environmental heterogeneity–diversity relationships

Lauri Laanisto · Riin Tamme · Inga Hiiesalu ·
Robert Szava-Kovats · Antonio Gazol · Meelis Pärtel

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Abstract Although recent studies have revealed that the relationship between diversity and environmental heterogeneity is not always positive, as classical niche theory predicts, scientists have had difficulty interpreting these results from an ecological perspective. We propose a new concept—microfragmentation—to explain how small-scale heterogeneity can have neutral or even negative effect on species diversity. We define microfragmentation as a community level process of splitting habitat into a more heterogeneous environment that can have non-positive effects on the diversity through habitat loss and subsequent isolation. We provide support for the microfragmentation concept with results from spatially explicit heterogeneity–diversity model simulations, in which varying sets of species (with different ratios of specialist and generalist species) were modeled at different levels of configurational

heterogeneity (meaning that only the habitat structure was changed, not its composition). Our results indicate that environmental heterogeneity can affect community diversity in the same way as fragmentation at the landscape level. Although generalist species might not be seriously affected by microfragmentation, the persistence of specialist species can be seriously disturbed by small-scale patchiness. The microfragmentation concept provides new insight into community level diversity dynamics and can influence conservation and management strategies.

Keywords Species diversity · Environmental diversity · Habitat fragmentation · Modeling · Community dynamics

Introduction

What drives and maintains diversity in nature has been an ongoing question in ecology, and we remain far from understanding all the significant processes that dictate diversity patterns. Among the most persistent theories related to the maintenance of diversity has been the ecological relationship between environmental heterogeneity and species diversity (heterogeneity–diversity relationship; hereafter HDR). Although heterogeneity is a remarkably diverse concept, encompassing very different aspects of environment—both biotic and abiotic—at varying spatial and temporal scales, HDR has almost always been described as positive, examples of which exist for plants (Lundholm and Larson 2003), animals (Griffin et al. 2009), and other groups (Gignac and Dale 2005; Whitcomb and Stutz 2007).

Why does environmental heterogeneity increase diversity? Niche-based ecological theories emphasize environmental heterogeneity as one of the main factors that

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L. Laanisto (✉) · R. Tamme · I. Hiiesalu · R. Szava-Kovats ·
A. Gazol · M. Pärtel
Institute of Ecology and Earth Sciences,
University of Tartu, Lai 40, 51005 Tartu, Estonia
e-mail: laanisto@ut.ee

L. Laanisto
Department of Biodiversity and Evolutionary Biology,
National Museum of Natural Science, CSIC,
C/Gutierrez Abascal, 2, 28006 Madrid, Spain

L. Laanisto
Laboratorio Internacional en Cambio Global, UC-CSIC,
Departamento de Ecología, Facultad de Ciencias Biológicas,
Pontifical Catholic University of Chile, Alameda 340,
6513677 Santiago de Chile, Chile

structures ecological communities (Hutchinson 1957; Harrison et al. 2010). It is widely accepted that heterogeneous environments provide more niches than homogenous environments; therefore, heterogeneity can support more diverse communities (e.g., Rosenzweig 1995). Environmental heterogeneity is in some ways incorporated in almost all theories of community ecology, but in evolutionary ecology it is considered one of the most fundamental diversity-maintenance mechanisms (Kassen 2002; Allouche and Kadmon 2009). Even according to the neutral theory, both biotic and abiotic heterogeneity of microenvironments are considered important factors preventing competitive exclusion of species and, therefore, maintaining diversity (Hubbell 2005). This general idea of a ubiquitous positive HDR is both simple and elegant, and it is obvious why so many classical articles and biology and ecology textbooks refer to this theory time and time again (Williams 1964; Huston 1994; Rosenzweig 1995; Begon et al. 2006). However, the ecological literature actually contains surprisingly few case-studies showing any real evidence to support this theory (Lundholm 2009; Reynolds and Haubensak 2009; Tamme et al. 2010; Fahrig et al. 2011).

One likely reason for the scarcity of real and comparable evidence to support positive HDR could stem from both the ambiguity and very liberal interpretation of the term “heterogeneity” (Sparrow 1999; Tamme et al. 2010). While the definitions usually emphasize the aggregated spatial variability as the essence of heterogeneity; e.g., the definition by Ettema and Wardle (2002, p.178): “Spatial heterogeneity is variability in spatial structure, such that spatial distributions are not uniform or random, but aggregated (patchy, clumped).”, there are also strong associations linking heterogeneity directly (and often solely) to environmental diversity (e.g., Hortal et al. 2009). Those two contrasting approaches in determining the effects of environmental heterogeneity on species diversity have historical roots leading back to the 1960s (Cramer and Willig 2005).

Before conducting research, it is necessary to partition environmental heterogeneity into components, and there are several frameworks one can follow. Duelli (1997) suggested dividing habitat heterogeneity into “habitat variability” (number of biotope types per unit area) and “habitat heterogeneity” (number of habitat patches and ecotone length per unit area). Fahrig et al. (2011) advocated a more generalized version of this division, by which heterogeneity is divided into two principal components: “compositional heterogeneity”—a more heterogeneous landscape is a landscape with a greater variety of different cover types; and “configurational heterogeneity”—the complexity of spatial patterns of these cover types. Environmental diversity is just one facet of

heterogeneity and, although we would expect environmental heterogeneity and its diversity to be interacted in most natural systems, the shape of this relationship is unclear and could vary under different conditions (Fahrig et al. 2011). Therefore, by focusing only on environmental diversity and species diversity, we could miss the wider set of heterogeneity effects beyond mere environmental diversity.

One study (Kadmon and Allouche 2007) showing the possibility of non-positive HDRs created some controversy (e.g., Hortal et al. 2009; Kati et al. 2010), although non-positive HDRs had been detected earlier (e.g., Cramer and Willig 2005; Reynolds et al. 2007). Kadmon and Allouche (2007) unified the island biogeography model with niche theory principles in an individual-based model that assumed niche differentiations between individuals of different species. Their model demonstrated that unimodal and even negative HDRs are also possible. A similar study in which coexistence was modeled in fractal landscapes showed that extremely high fractality results in lower species diversity at the landscape scale (Palmer 1992).

Recent meta-analyses by Lundholm (2009) and a corresponding forum paper by Tamme et al. (2010) added cracks to the monolithic positive HDR theory. Lundholm (2009), who made a thorough review of the HDR literature of the past century, reported the meta-results of 41 observational and 11 experimental HDR case-studies of plants with different plot sizes from all over the globe and concluded that, although positive HDRs were most common, there were many cases in which no relationship was found. Further analysis of Lundholm’s dataset found the existence of negative HDRs, which were significantly more common at smaller spatial scales, whereas studies at larger scales (i.e. homogeneous habitat patches were larger) reported predominantly positive HDRs, indicating at least a non-ubiquity of positive HDRs across different spatial scales (Tamme et al. 2010).

Conflicting results from computer simulations, observational fieldwork, and experiments demand new theories explaining why, in some cases, environmental heterogeneity can have a neutral or even negative effect on diversity. Lundholm (2009) primarily suspected artifacts and other methodological errors for non-positive HDRs, though also briefly mentions some ecological possibilities (available energy hypothesis, dispersal limitations, mass effect, etc.). However, Kadmon and Allouche (2007) attributed the variety in HDR trends to stochastic extinction of species due to the loss in area of each habitat type with increasing heterogeneity within a fixed total community. Somewhat similar ideas have also circulated in ecology before. For example, Tews et al. (2004) reviewed the relationship between environmental heterogeneity and animal species, and in some cases (for mammals,

butterflies, birds etc.) found negative HDR or no relationship at all. They suggested that, while heterogeneous vegetation cover might provide different niches for some animal species, it leads to habitat fragmentation for others. Similarly Fahrig et al. (2011) proposed the “intermediate heterogeneity hypothesis”, in which an increase in heterogeneity has a positive effect on diversity only to a certain level, after which the negative effects of fragmentation overshadow the positive effects of heterogeneity to decrease diversity.

As an extension of these ideas, we go even further, supposing that, if the area of each habitat type remains constant, greater heterogeneity might increase isolation of different patches at smaller scales. Since the loss or isolation of habitat constrains the normal functioning of species (Saunders et al. 1991; Duelli 1997; Fahrig 2003), heterogeneity can have a similar kind of influence on diversity on the community level as habitat fragmentation has on the landscape level (e.g., Helm et al. 2006). A similar explanation was also put forward by Palmer (1992), who polemized that high fractality can reduce connectivity and contiguity of similar fractions. We propose the term microfragmentation (first mentioned in Tamme et al. 2010) and define it as follows: Microfragmentation is a community influencing process of changing habitat into a more heterogeneous environment that can have negative effects on the diversity through habitat loss and subsequent isolation. This concept can be considered as an alternative to niche limitation theory, since it accounts for negative or neutral HDR.

The purpose of this study is to draw attention to the much wider field of possible effects of environmental heterogeneity on diversity currently being discussed in the ecological literature. We propose a new concept—microfragmentation—that could provide an explanation to some cases of non-positive HDR. In addition to theoretical considerations, we also modeled HDR in a simple, spatially explicit model system in which species diversity and the “configurational component” of environmental heterogeneity (sensu Fahrig et al. 2011) were simulated within different time limits, varying species habitat preferences, and the spatial scale of heterogeneity. Our main aim was to test whether microfragmentation can cause non-positive HDR and to determine how these relationships vary in different community assemblages and heterogeneity levels.

Materials and methods

To model HDR, we used the freeware application CAPS—an individual-based, spatially explicit stochastic lattice model, which was designed to examine multiple processes responsible for spatial patterns of abundance and diversity

of sessile species in heterogeneous landscapes (Plotnick and Gardner 2002; Gardner and Engelhardt 2008). The general procedure of species dynamics simulation with CAPS includes the following steps: (1) create a habitat map, (2) define species habitat preferences, dispersal and fecundity parameters, (3) define a disturbance regime, and (4) initialize species distributions on the habitat map. We provide a more detailed description of our simulation design, but for full details the reader is referred to Plotnick and Gardner (2002), Gardner and Engelhardt (2008), or the CAPS webpage <http://www.al.umces.edu/CAPS.htm> (where its source code and executables can be downloaded).

Heterogeneity was modeled combining two habitat types of equal overall area but different spatial configuration in a model landscape (Fig. 1). The landscapes were created using chessboard-type combinations of the two habitat types. Different sized patches of habitat type were used to model spatial heterogeneity levels at different spatial scales. We created 2-dimensional 100×100 -node lattice landscapes with wrapped boundaries that allow dispersal “over the edge” (in order to eliminate edge effect), in which each node of the lattice corresponded to a homogeneous habitat site of sufficient size to support a single individual of a sessile species (Gardner and Engelhardt 2008). At the small scale, comparable to an individual (one node), this patchiness represents heterogeneity as the probability that a neighboring node (of the four closest neighbors) is a different habitat. Large patches are much more homogeneous since most nodes are adjacent to nodes of similar habitats.

We generated landscapes with different sized uniform patches: 50×50 nodes (heterogeneity, i.e. the average chance that one of the adjacent nodes represents another habitat type = 0.08 %); 25×25 nodes (0.32 %); 10×10 nodes (2 %); 5×5 nodes (8 %); 2×2 nodes (50 %); and 1×1 nodes (100 %). The temporal scale varied between 500 and 10,000 time steps (e.g., years), with simulation steps of: 500, 1,000, 3,000, 5,000, and 10,000. (Note that each simulation time step represented an independent simulation, not a “pause” in a continuous 10,000 time steps simulation.)

Each node in the landscape could be occupied by only a single adult individual at any point in time. CAPS individuals exhibit three characteristics: habitat preference (niche breadth), relative fecundity, and dispersal ability. We kept fecundity constant for all species in each run of the model, and dispersal was always in a random direction of radius 1, meaning that each individual could disperse at each time step to one randomly chosen adjacent node (of four possible nodes). However, habitat preferences of species varied. We had four principal scenarios for assemblages of virtual communities, which contained species with varying habitat preferences (Table 1).

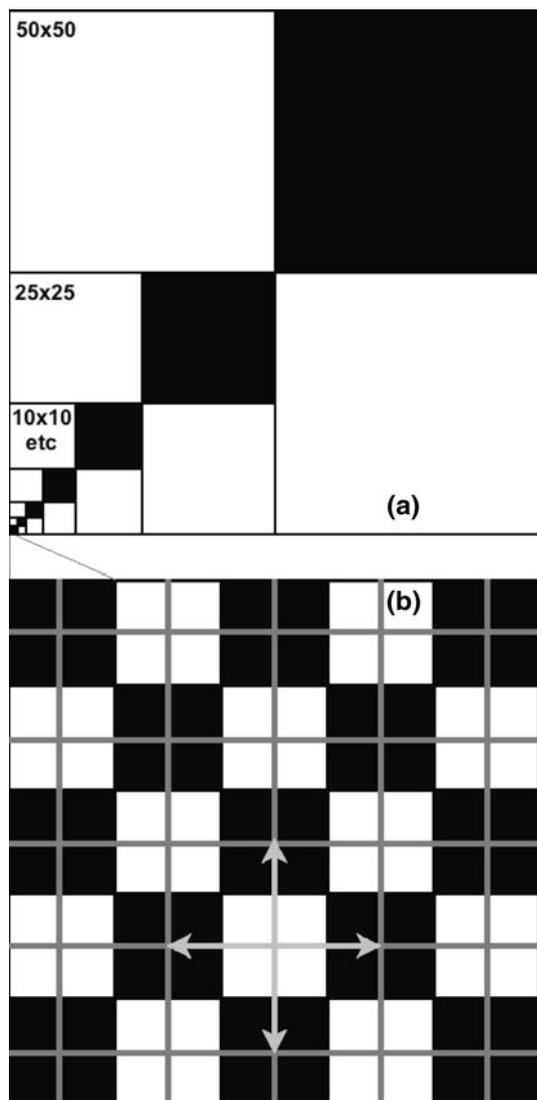


Fig. 1 **a** Chessboard-type combinations of model landscapes (*white* and *black* represent the two habitat types) showing different patterns of heterogeneity used for modeling; **b** expansion of the most heterogeneous model landscape showing where a model individual can disperse (*light gray arrows*) on the nodes of lattice (*intersections of dark gray lines*)

Additionally, there were two different species determination frameworks for each scenario: categorical and continuous species preferences, where categorical assemblages contained species that were either fully capable or completely incapable of inhabiting certain habitat type. For the continuous framework, species preferences had a continuous fitness span from 1 to 9 (see Table 1), making them capable of surviving in unfavorable habitat types, yet not capable of successfully competing with specialist species preferring a given habitat type.

For all datasets, the local species pool always contained 30 species, which were distributed across the habitat so that at the beginning of a simulation every node was filled with

Table 1 Model community assemblages by scenario and framework showing the initial number of specialist species (for habitat A + B) and generalists species in simulations

Scenario and framework	No. of specialists	No. of generalists
S 1—categorical	15 + 15	0
S 1—continuous	15 + 15	0
S 2—categorical	10 + 10	10
S 2—continuous	10 + 10	10
S 3—categorical	5 + 5	20
S 3—continuous	5 + 5	20
S 4—categorical	0	30

a randomly drawn viable individual. The initial random number of seeds was divided with 30 (the number of species) so there were equal amounts of seeds of all the species at the beginning of each simulation. In addition to environmental heterogeneity and species preferences to certain habitats, community diversity was also regulated by random disturbance, which removed 10 % of the population at each time step. The empty node was then filled with the descendant of the individual filling one of the nearby nodes that had the best fitness for the habitat type of the empty node compared with the rest of the neighbors.

We recorded the outcome diversity of every simulation (an example of the .ini file is in Online Resource 2), and for each unique set of variables (scale of heterogeneity, scale of time, and type of community), we performed ten simulations that differed only by the random initial seed number. The richness in every set of variables was the average of those ten simulations. Diversity was expressed as Simpson's Reciprocal index, which has been commonly used in comparable HDR studies (e.g., Lundholm 2009; Smith and Lundholm 2012).

Scenarios were constructed as follows:

Scenario 1—only specialists, in which 15 species preferred habitat A and the other 15 species preferred habitat B. For categorical species preferences, habitat A species could not survive in habitat B and vice versa; for continuous species preferences, habitat A species could also survive (their fitness was 1 out of 9) in habitat B and vice versa. Note that species preferring habitat A are not capable of successfully competing with habitat B specialists.

Scenario 2—mostly specialists, in which 10 species preferred habitat A, 10 species habitat B and 10 species were equally capable of living in both habitat types. Similarly, for categorical species preferences, habitat A species could not survive in habitat B and vice versa, while generalists were equally capable of living in both habitats; for continuous species preferences, habitat A species could also survive (their fitness was 1 out of 9) in habitat B and vice versa. Generalist species fitness for both habitats was

8, which was slightly lower than specialist species whose fitness in preferred habitat was 9. (The reason for choosing such fitness levels for continuous species was in virtue of illustrative power of the results. Simulations with different fitness levels similar produced HDRs.)

Scenario 3—mostly generalists. This scenario was principally similar to scenario 2, but contained 20, rather than 10 generalist species, and accordingly just 10 specialist species—5 preferring habitat A and 5 habitat B. Continuous species preferences were the same as in Scenario 2.

Scenario 4—only generalists. In this case all 30 species were equally capable of living in both habitats. We had only a categorical framework for this scenario as a continuous framework would have been substantially identical to the categorical framework.

Results

The relationship between small-scale environmental heterogeneity and diversity is not always positive (Figs. 2, 3, 4, 5;

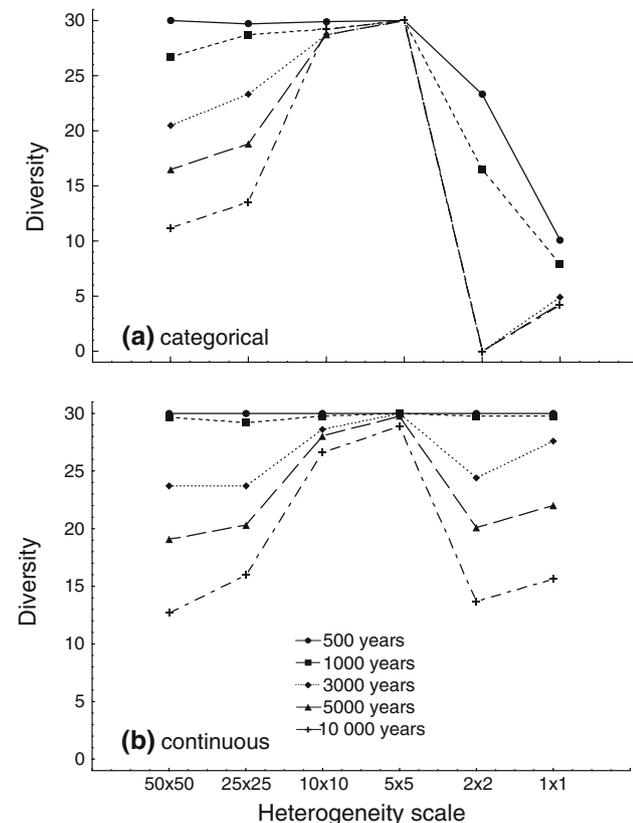


Fig. 2 Results of diversity simulations for *Scenario 1: only specialists*. Heterogeneity scale corresponds to patch sizes in model landscapes (low heterogeneity at left and high heterogeneity at right); diversity is measured as Simpson’s Reciprocal index. Results of **a** categorical and **b** continuous framework (see “Materials and methods” for details). Lines show results for varying time frames

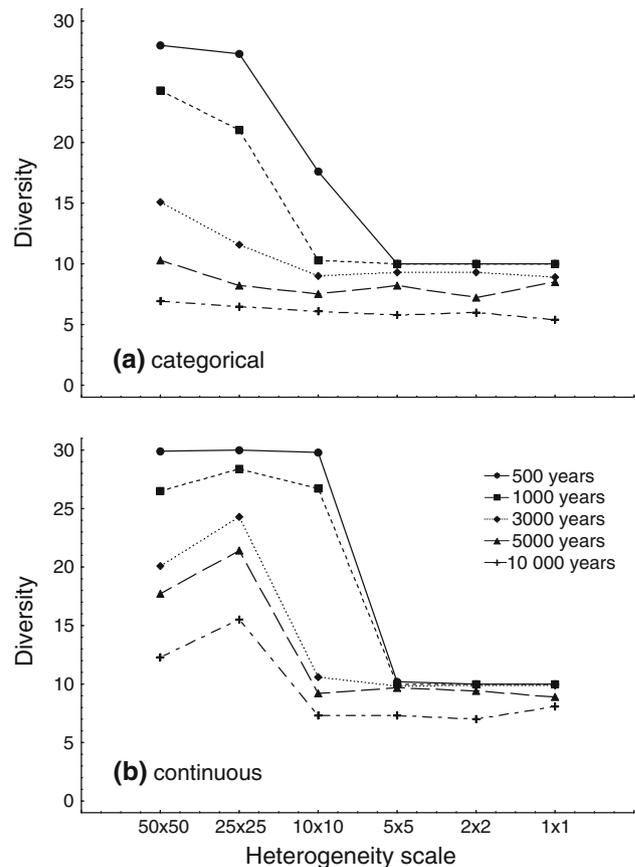


Fig. 3 Results of diversity simulations for *Scenario 2: mostly specialists* for **a** categorical and **b** continuous framework. See Fig. 2 for details

for raw datasets, see Online Resource 3). Fully specialist species communities (*Scenario 1*) exhibited mostly unimodal relationships with the highest diversity at medium heterogeneity levels (Fig. 2). Communities consisting of mainly specialists and few generalists (*Scenario 2*) led to predominantly negative relationships between diversity and heterogeneity (Fig. 3). In generalist-dominated communities with few specialists (*Scenario 3*), habitat heterogeneity featured mainly neutral or negative effects on diversity (Fig. 4). In solely generalists communities (*Scenario 4*), heterogeneity had no effect on diversity whatsoever (Fig. 5). The complete results for species richness—habitat heterogeneity, and evenness—habitat heterogeneity relationship are presented in Online Resource 1.

Scenario 1—only specialists. Specialist-only scenarios had quite similar dynamics for all time steps and for both categorical and continuous frameworks HDR (Fig. 2), although for shorter simulation steps, diversity dynamics is considerably “flatter”, especially in the continuous framework. Initially, diversity increases with heterogeneity—the smaller the habitat patches, the greater the diversity, peaking at two medium patch sizes (10 × 10 and 5 × 5).

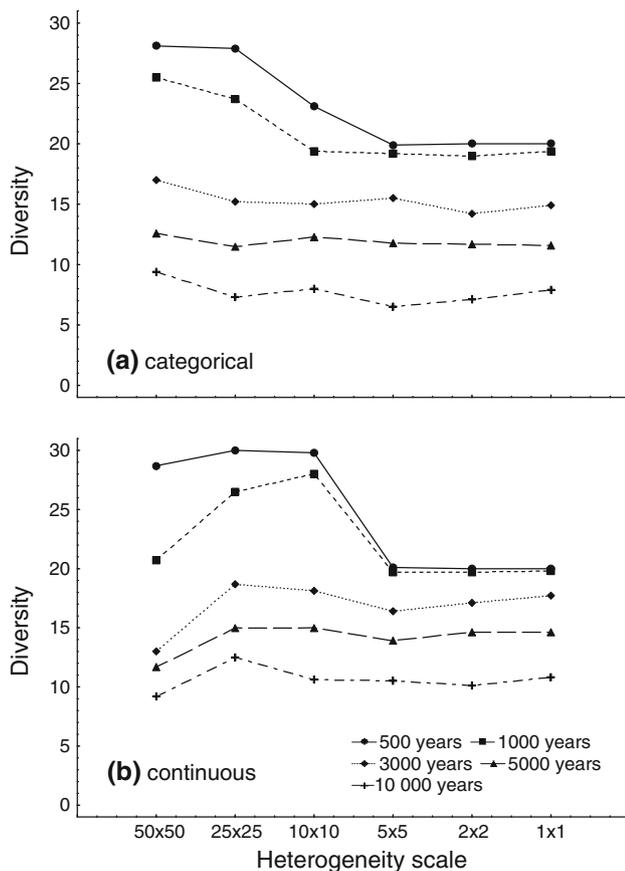


Fig. 4 Results of diversity simulations for *Scenario 3: mostly generalists* for **a** categorical and **b** continuous framework. See Fig. 2 for details

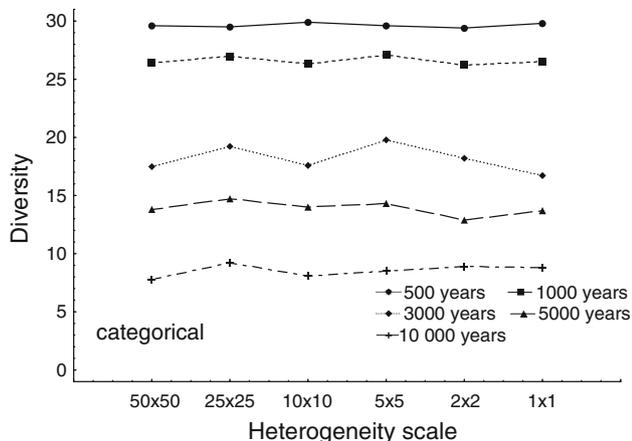


Fig. 5 Results of diversity simulations for *Scenario 4: only generalist* for categorized framework (the continuous framework was not simulated). See Fig. 2 for details

Thereafter, there is a negative effect of heterogeneity on diversity as habitat patch size decreases. Species in categorical framework almost die out, especially in longer simulation steps. More species survive under continuous

framework but still lose richness, once more for longer simulation steps.

Scenario 2—mainly specialists. In simulations with 20 specialist and 10 generalists, species heterogeneity exhibits mostly negative or neutral effects on diversity (Fig. 3). In categorical framework, specialists tend to die out in almost all communities and only generalists survive and attain a stable diversity plateau with patch sizes 10×10 or smaller. Species in continuous framework show a slight positive trend in transition from 50×50 to 25×25 patch size, but by 5×5 patch size diversity has reached a similar plateau as categorical species.

Scenario 3—mainly generalists. When community consists of 20 generalists and 10 specialists, heterogeneity has little effect on diversity (Fig. 4). The overall dynamics is rather similar to Scenario 2, but as there are more generalist species involved, the effects of heterogeneity are “flatter”. There is some variation in continuous framework, yet a certain level of diversity in categorical framework is maintained throughout all patch sizes.

Scenario 4—only generalists. In strictly generalist scenarios, heterogeneity has no effect on diversity whatsoever (Fig. 5). Similar to the categorical framework of mainly generalists scenario, a certain level of diversity is maintained throughout all patch sizes and diversity depends on time.

Discussion

The outcome of simulations combining differently configured species assemblages, heterogeneity levels (i.e. variable patch size) and community development stages show that the relationship between heterogeneity and diversity is not always positive (Figs. 2, 3, 4, 5). Furthermore, our proposed concept—microfragmentation—can explain these results. Although other studies (e.g., Tews et al. 2004; Kadmon and Allouche 2007; Smith and Lundholm 2012) have reported somewhat similar results, our study is significantly advanced in several ways. In addition to attributing non-positive HDR to a new and comprehensive idea, we also distinguished the effects of the “configurational component” of environmental heterogeneity (sensu Fahrig et al. 2011) on species diversity from those of the “compositional component” of environmental heterogeneity (sensu Fahrig et al. 2011), and our spatially explicit model landscapes included both specialist and generalist species, which reacted differently to changes in small-scale heterogeneity.

The effects of environmental heterogeneity on species richness or diversity are usually observed in systems in which changes in heterogeneity entail similar shifts in environmental diversity (e.g., Lundholm and Larson 2003;

Gignac and Dale 2005). This is no different for artificial systems: for example, Kadmon and Allouche (2007) increased heterogeneity by adding patches of new habitat types to the system, i.e. by also increasing environmental diversity. Similarly, a recent modeling study by Smith and Lundholm (2012) did not differentiate between the effects of environmental heterogeneity and environmental diversity. Although they varied spatial configuration of heterogeneity, they also included different values of environment in their model systems and measured environmental heterogeneity in quadrats differing essentially in the configuration as well as in the number of different types of habitat patches. Therefore, estimating the configurational component of environmental heterogeneity is problematic, as it is not readily distinguishable from the effect of environmental diversity or the compositional component on diversity (Kassen 2002; Cramer and Willig 2005; but see, for example, Bell et al. 2000; Reynolds et al. 2007 for successful effect separations). Moreover, researchers themselves use the terms “environmental heterogeneity” and “environmental diversity” in a broad and overlapping sense, which generates additional confusion to discussions on the shape of HDR (Sparrow 1999; Cramer and Willig 2005; Fahrig et al. 2011).

Although environmental heterogeneity and diversity, i.e. both components of heterogeneity, are frequently correlated in natural systems (Kallimanis et al. 2008), the underlying cause and effect of these two phenomena could actually be transposed and the positive effect of the combination of small-scale heterogeneity and diversity on species richness may stem from the effect of environmental diversity. Thus, it is important to distinguish these effects in order to evaluate correctly how small-scale heterogeneity affects species diversity in communities. That is why the changes in configurational heterogeneity in our spatially determined model systems did not entail changes in environmental diversity (there were always only two habitat types), nor in the total area of habitat types (both habitat types always covered half of the landscape). This means that only the configurational aspect of environmental heterogeneity had an effect on the model system diversity. This approach clearly shows that the “pure effect” of configurational heterogeneity on species diversity can be non-positive (Figs. 2, 3, 4, 5).

All model simulations are obviously crude simplifications of reality, and the choice of model parameters and their values usually serves as the main source of criticism. The tersest counter argument to the model by Kadmon and Allouche (2007) was published by Hortal et al. (2009) addressing the “roughness” of modeled species fitness landscapes. Kadmon and Allouche (2007) used non-overlapping sets of species for each habitat type in their spatially implicit model systems. Hortal et al. (2009) were critical of

this approach, asserting that it is unreasonable to assume—at least for island communities—that species can inhabit only one habitat type, and further claiming that most species are either generalists or at least capable of living in several habitat types, thus rendering the model proposed by Kadmon and Allouche (2007) overly unrealistic.

In nature, both specialist and generalist species usually occur in communities with different environmental heterogeneity (Cramer and Willig 2005; Manthey et al. 2011); our model landscapes accommodate this reality, containing both species types, within different frameworks (categorical and continuous). The results demonstrate that heterogeneity had different effects on the diversity of specialists and generalists (Figs. 2, 3, 4, 5). While generalists remained largely unaffected by direct changes in heterogeneity, the impact on specialists was rather strong. This disparity comes as no surprise, because generalists, who can survive in different conditions, should be better adjusted to live in heterogeneous landscapes than specialists (Tienderen 1991; Tews et al. 2004; Hortal et al. 2009). Generalists were influenced by heterogeneity indirectly, i.e., through the dynamics of specialists who were affected directly. In *Scenario 4*, which was devoid of specialists, the model represented a somewhat idealistic neutral community model, in which the “functional equivalence” (Hubbell 2005) caused community diversity to be driven only by random processes. Moreover, generalists are considered better colonizers and less prone to stochastic extinction (Kotiaho et al. 2005; Hortal et al. 2009). Both of these tendencies can also be seen in our simulations, especially in the categorical model framework, in which the maximum adaptation for one habitat type was equal for both generalists and specialists.

Another critical issue in studying diversity patterns in both nature and model simulations is dispersal dynamics, which is known to play an essential role in shaping diversity patterns in heterogeneous environments (Palmer 1992; Berkley et al. 2010). In our model, species could spread only to nearby nodes that had been vacated by random disturbance. One reason for applying such dispersal constraints was to accentuate heterogeneity effects on dispersal. This kind of situation is actually also quite common in nature; for example, gaps, especially in herbaceous plant communities, are usually filled by local and nearby species that are capable of colonizing free space very quickly, partially due to their clonality. Outside species are rarely introduced to the community (Reynolds et al. 2007; Laanisto et al. 2008). However, when the environment is highly heterogeneous, i.e. containing many different types of habitat patches, the diversity maintaining the interconnecting network of local species can be more readily overwhelmed by outside species due to the micro-fragmentation effect, and, depending on the nature of

newly dispersed species, the effect on diversity can be either positive or negative (Davies et al. 2005). Additionally, the effect and importance of resource heterogeneity may already be dampened by local dominant species that can establish over a wide range of resource availability prior to dispersal of new species, (Baer et al. 2004).

Although our model landscapes contained only two habitat types, microfragmentation still exhibited a clear non-positive effect on species diversity (Figs. 2, 3, 4, 5). In nature, variability of small-scale heterogeneity and diversity in one landscape can be much greater, and, according to classical niche theory, which dictates positive HDRs, should result in less competition by means of the competitive exclusion principle (Armstrong and McGehee 1980; Hubbell 2005) and more available niches due to higher environmental diversity (Huston 1994; Rosenzweig 1995; Hortal et al. 2009). To expand on this, the negative effect of microfragmentation should likewise be stronger, as isolation between similar patches is greater and the relative area of different habitat types is reduced, weakening the connectivity between patches, as space is a limiting factor (Palmer 1992; Cramer and Willig 2005; Helm et al. 2006; Kadmon and Allouche 2007; Tamme et al. 2010). Therefore, diversity dynamics in general depends strongly on whether the species are specialists or generalists, as species with narrow niches are more strongly dependent on the environment (Smith and Lundholm 2012).

Smith and Lundholm (2012) recently studied HDR in simulated communities with varying environmental geometry, species preferences, and dispersal distances. Although they found that increasing the configuration (fractal dimension) of environmental conditions generally has a negative effect on HDR, the relationship per se was rarely negative. Contrary to our results, they found no support for the microfragmentation concept, since most negative HDRs were revealed when species exhibited wide niche breadth and high dispersal distances in highly fractal landscapes. However, this may be an artifact of the confounding effects of environmental heterogeneity and environmental diversity, explained above. Smith and Lundholm (2012) used standard deviation of environmental values within quadrats as a measure of heterogeneity, but this measure is not dependent on the fractal dimension of the landscape (Palmer 1992), making the influence of patch size indistinguishable. However, the microfragmentation concept relies on the size of habitat patches as decreasing the effect of species diversity (Tamme et al. 2010). In our simulations, the negative effect of heterogeneity can clearly be attributed to a decrease in habitat patch size, hence the microfragmentation concept is applicable to explain these results. We realize that in field studies sampling methods fail to distinguish environmental heterogeneity and environmental

diversity, and that measuring patch size would be time-consuming and difficult, although the distance between environmental samples gives us some sort of information of patch size on the same scale we study HDR.

Consequently, the crucial factor shaping the HDR is to understand when and in what conditions heterogeneity could become fragmentation (Fahrig et al. 2011). Heterogeneity and fragmentation are usually considered to be distinct effects, although their natures are actually very similar, and habitat fragmentation can be considered habitat heterogeneity in its simplest form (Franklin et al. 2002). Both fragmented and heterogeneous areas consist of varied patches with different soil types, vegetation types, etc. (Saunders et al. 1991), and their essential difference is related more to species characteristics, i.e. whether it is limited to living in only one type of patch, its vagility, etc. (With and Crist 1995). Often the functional distinctions between different habitat types that truly dictate the fitness of organisms are subtle and not readily apparent, and this can generate an “invisible mosaic” accountable for species responses (Fahrig et al. 2011). This brings us to the “roughness” of adaptive landscapes of species inhabiting such patches and habitats.

“Choosing” to be either specialist or generalist is undoubtedly a trade-off between being able to inhabit different habitat types and being able to compete successfully (Cousins and Eriksson 2001; Cramer and Willig 2005). As different patterns in heterogeneity dynamics have been found for different habitat types, stemming from differences in geological history (Partel et al. 2008), we can also assume differences in environmental heterogeneity preferences, both at the global and local scale, for different taxonomic groups. The general notion from our model systems indicates that specialist species are much more fragile than generalists in very patchy/heterogeneous conditions—all their troubles pointing directly to within-community isolation, i.e. microfragmentation issues. Rare species tend to be specialists, inhabiting areas with very specific conditions (Cousins and Eriksson 2001), and, in order to better manage their survival, it might be a good idea not to protect only the most heterogeneous habitats; although the overall species richness in the conservation area could be greater (Kati et al. 2010), the risk of losing valuable specialists could also be greater.

Our results clearly demonstrate that the effects of environmental heterogeneity on species diversity are not always positive, and can be explained by the microfragmentation concept, stating that community level diversity might be reduced by increasing environmental heterogeneity due to the isolation of suitable patches. However, different aspects and variations in this novel idea still need to be mapped and analyzed with both theoretical and practical considerations.

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