

## FORUM

# Environmental heterogeneity, species diversity and co-existence at different spatial scales

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### Abstract

The positive relationship between spatial environmental heterogeneity and species diversity is a widely accepted concept, generally associated with niche limitation. However, niche limitation cannot account for negative heterogeneity–diversity relationships (HDR) revealed in several case studies. Here we explore how HDR varies at different spatial scales and provide novel theories for small-scale species co-existence that explain both positive and negative HDR. At large spatial scales of heterogeneity (e.g. landscape level), different communities co-exist, promoting large regional species pool size and resulting in positive HDR. At smaller scales within communities, species co-existence can be enhanced by increasing the number of different patches, as predicted by the niche limitation theory, or alternatively, restrained by heterogeneity. We conducted meta-regressions for experimental and observational HDR studies, and found that negative HDRs are significantly more common at smaller spatial scales. We propose three theories to account for niche limitation at small spatial scales. (1) Microfragmentation theory: with increasing spatial heterogeneity, large homogeneous patches lose area and become isolated, which in turn restrains the establishment of new plant individuals and populations, thus reducing species richness. (2) Heterogeneity confounded by mean: when heterogeneity occurs at spatial scales smaller than the size of

individual plants, which forage through the patches, species diversity can be either positively or negatively affected by a change in the mean of an environmental factor. (3) Heterogeneity as a separate niche axis: the ability of species to tolerate heterogeneity at spatial scales smaller than plant size varies, affecting HDR. We conclude that processes other than niche limitation can affect the relationship between heterogeneity and diversity.

**Keywords:** Community ecology; Grain; Meta-analysis; Niche limitation; Small and large scale; Spatial heterogeneity.

**Abbreviations:** HDR = heterogeneity–diversity relationship.

### Introduction

The relationship between spatial environmental heterogeneity and species diversity (HDR) is one of the principal concepts of community ecology, but has not yet been studied thoroughly (Wilson 2000). The term “heterogeneity” is rarely defined precisely, leading to additional ambiguity (Sparrow 1999; Lundholm 2009). According to Ettema & Wardle (2002), “spatial heterogeneity is variability in spatial structure, such that spatial distributions are not uniform or random, but aggregated (patchy, clumped).” Although it is widely thought that heterogeneous environments should maintain more species than homogeneous ones, empirical evidence of the true trend of HDR is surprisingly scarce. In a thorough review of the literature of the past century, Lundholm (2009) found only 41 observational and 11 experimental case studies. Contrary to conventional theory, negative HDR relationships have also been reported.

The premise of positive HDR is based on classical niche theory, which expects species to prefer particular resource conditions, and habitat heterogeneity to allow species co-existence. It is possible to distinguish  $\alpha$ - and  $\beta$ -niches (Pickett & Bazzaz 1978; Ackerly & Cornwell 2007).  $\alpha$ -niches are components of the species niche associated with factors occurring

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at small (within community) scales, whereas  $\beta$ -niches refer to the species responses to factors occurring at large spatial scales (Pickett & Bazzaz 1978; Ackerly & Cornwell 2007). Spatial heterogeneity occurs simultaneously at different scales. At larger spatial scales, heterogeneity is expressed mainly as gradients of environmental factors. Individual patches within communities, which can influence species co-existence, can be distinguished at smaller scales (Ettema & Wardle 2002). “Small scale” usually refers to within-community or  $\alpha$ -scale, whereas “large scale” deals with inter-communities or  $\beta$ -scale processes. The border between small and large spatial scale varies among studies, because of different community structures, and remains ambiguous.

Species distribute themselves along environmental gradients or habitat types according to their  $\beta$ -niche, resulting in co-existence of communities, rather than species. For species co-existence, the  $\alpha$ -niche is more important (Silvertown 2004). Additionally, studies at large spatial scales might encompass different vegetation types (e.g. grasslands and forests), which should be analysed separately. For example, grasses and trees probably respond to heterogeneity at different spatial scales, since their root systems exhibit spatial differences (Schenk & Jackson 2002). This difference also leads to diverse associations between heterogeneity and vegetation type (Pärtel et al. 2008).

Lundholm (2009) distinguishes different spatial scale parameters: extent (size of total area within which samples are located); grain (scale at which heterogeneity is measured, i.e. the patch size, generally deemed the average spatial distance between neighbouring environmental measurements); and focal scale (scale at which species diversity is measured, e.g. vegetation sample plot size). Lundholm (2009) studied how HDR might vary according to focal scale. Although grain and focal scale are correlated in some studies, this correlation is not universal. We suggest that grain is more important for species co-existence than other scale parameters. Species respond to environmentally distinct patches rather than abstract heterogeneity indices. Also, the factors causing heterogeneity vary with spatial scale (Pickett et al. 2000; Ettema & Wardle 2002). Abiotic heterogeneity is caused mainly by climate, local topography or parent material (Hodge 2005), and thus occurs at relatively large spatial scales (Pickett et al. 2000). Biotic heterogeneity is typically caused by soil microorganisms (Ettema & Wardle 2002) or herbivores (e.g. Augustine & Frank 2001), or through patchy resource uptake and release by plants

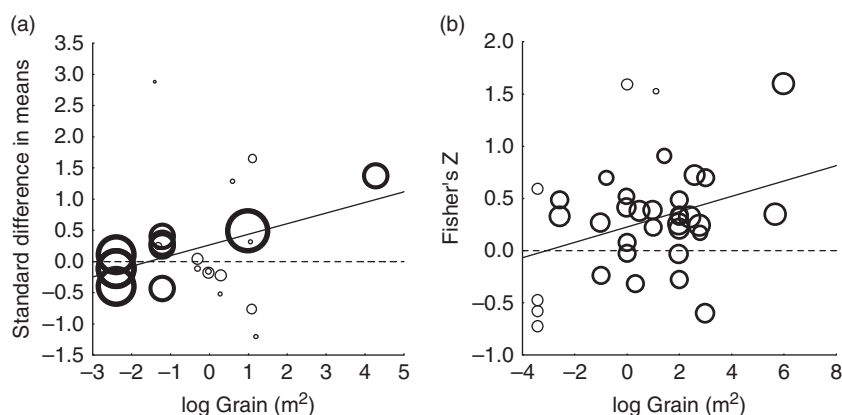
(Wilson 2000). Since biotic processes function mostly at small spatial scales, biotic heterogeneity might be more relevant to species co-existence. However, most case studies consider only abiotic heterogeneity at relatively large scales.

Lundholm (2009) suggests that new theories are needed to account for the diverse results from HDR studies, and that this topic remains unresolved. Here, we explore how different HDR theories are supported using a meta-regression of HDR and spatial scale (grain instead of focal scale), propose novel theories to describe both positive and negative HDR with respect to species co-existence, and provide insights for future research.

## Meta-Analysis and the Effect of Spatial Scale

HDR is expected to be positive at larger spatial scales due to habitat selection (i.e.  $\beta$ -niche differentiation). At smaller scales the limitation of  $\alpha$ -niches would be supported if HDR is also positive. However, non-existent or even negative HDR at smaller spatial scales demands alternative theories to explain how species co-existence is inhibited by heterogeneity (negative HDR at small scale). We used meta-analyses of the experimental and observational studies collected by Lundholm (2009) to test this idea. We applied meta-regressions with mixed effects (unrestricted maximum likelihood model) between HDR pattern and grain (Borenstein et al. 2009). All analyses were performed using Comprehensive Meta-Analysis v. 2 (Biostat Inc.).

Experimental and observational studies were analysed separately. To quantify HDR, different parameters were designated as effect size. Standard difference in diversity means (between homogeneous and heterogeneous treatments) served as effect size for experimental studies and Fisher's  $Z$  (transformed from correlation coefficient in order to obtain normal distribution) for observational studies. If studies provided no correlation coefficient,  $P$ - and  $t$ -values were transformed to Fisher's  $Z$ . Only a single measure of heterogeneity and species diversity was used for each experiment or description, since different measures are usually correlated and can bias statistical tests. If a study was conducted at different sites (observational studies) or varied in configuration of heterogeneity (experimental studies), one data point from each site or different experimental heterogeneity configuration was used. Thus, some studies provided several independent data points.



**Fig. 1.** Meta-regression showing a significant effect of log grain ( $\text{m}^2$ ) on the heterogeneity–diversity relationship (HDR) in (a) experimental studies (effect size expressed as standard difference in means; slope point estimate 0.170,  $Z = 3.5$ ,  $P < 0.001$ ); (b) observational studies (correlation coefficient transformed to Fisher's  $Z$ ; slope point estimate 0.073,  $Z = 2.2$ ,  $P = 0.027$ ). Positive HDR is found mostly at larger spatial scales, whereas negative HDR has been documented more frequently at smaller scales. Circle size is proportional to study weight (inversely proportional to the total variance) in both graphs. Dashed zero lines partition positive and negative HDR.

In deciding which observations to include from multiple measurements, we complied with the following priorities: (1) when different species diversity measures were given, we selected “total species richness” (in a few observational case studies “mean compositional diversity”, “Simpson’s diversity index” and “area–species richness slope” were substituted); (2) when HDR was given at different focal scales (scale at which species diversity was measured), we included the smallest scale, since this is most likely to correspond to the scale at which heterogeneity was measured; (3) of the environmental variables, we favoured those reflecting heterogeneity of soil topography or soil nutrient content. Finally, we included 23 data points from nine experimental studies, and 46 data points from 29 observational studies (details of the studies and parameters are in supporting information Appendix S1).

In meta-analysis there is always the possibility for publication bias – selective publication of studies due to submission, review or editorial decisions (Borenstein et al. 2009). We checked both experimental and observational studies for publication bias but found no statistically significant evidence to confound our meta-regressions of HDR and grain (Funnel plot figures and statistics are in supporting information Appendix S2). Data points from observational studies with no available grain size data were excluded from the meta-regression analysis. Thus, 35 data points from 19 case studies were included. The grain size was log-transformed. The results revealed a significant positive effect of grain size on the HDR in experimental studies (Fig. 1a) and in observational studies (Fig. 1b). Since no positive HDR is evident at smaller grain sizes, we conclude that niche limitation theory is

inadequate to account for the variation of HDR patterns at small spatial scales.

### Novel Theories on the Heterogeneity–Diversity Relationship

The positive HDR at large spatial scale confirms that species have distinct  $\beta$ -niches. We can readily identify species that prefer forests over grasslands, or moist over dry habitats. However, since we found little evidence for limitation of  $\alpha$ -niches at small spatial scales, we provide three novel theories to complement the niche limitation concept (which accounts only for positive HDR). Depending on whether within-community heterogeneity reflects patches with larger or smaller size than plant individuals, we propose a microfragmentation theory (patches larger), a heterogeneity confounded by mean theory (patches smaller), and a heterogeneity as a separate niche axis theory (patches smaller).

### Heterogeneity as Microfragmentation

The detection of positive HDR might be hampered if environmentally homogeneous areas with large species pools become spatially heterogeneous over time (Lundholm 2009). Should environmental heterogeneity increase, the total area of some types of patches within the community would decrease, which might reduce species richness. Kadmon & Allouche (2007) recently constructed an analytical model integrating the effects of habitat size and heterogeneity on species diversity. Contrary to the expectation of

classical niche theory, this model produced unimodal and even negative HDR trends. The authors attributed this variety in trends to stochastic extinction of species due to the loss in area of each habitat type with increasing heterogeneity (number of habitat patches) within a fixed total community area. We extend this idea to small-scale heterogeneity: even if the total area of some patch type remains constant, greater heterogeneity might increase isolation of different patches, a process we call microfragmentation. This process is analogous to habitat fragmentation at the landscape level (e.g. Helm et al. 2006). Similar ideas have been proposed for animal communities. Tews et al. (2004) reviewed the environmental heterogeneity and animal species relationship and found negative HDR in some cases. They proposed that heterogeneous vegetation cover might provide different niches for some species, while leading to habitat fragmentation for others. Habitat fragmentation inhibits both individual fitness and population dynamics due to habitat loss or isolation (Saunders et al. 1991). Our microfragmentation concept can be considered an alternative to niche limitation theory since it accounts for negative HDR, but the joint effects of area loss and increased isolation of different microhabitats remains to be studied. Both microfragmentation and niche limitation theory play a role when the size of environmental patches (grain) is larger than plant individuals.

### Heterogeneity Confounded by Mean

When patches in heterogeneous environments are smaller than plant individuals, then plants are able to forage through the patches and might be unaffected by heterogeneity. Heterogeneity can imply a change in mean of the particular environmental variable (see also Lundholm 2009). Initially homogeneous environments become heterogeneous when patches with new environmental characteristics emerge. If the mean of such patches differs from the initial environment, a change in environment mean likewise develops. For example, litter of scattered coniferous shrubs creates acidic patches in calcareous grasslands. These acidic patches lower the overall soil pH and decrease richness, since acidic soils in temperate regions exhibit relatively small species pools (Pärtel 2002). In contrast, when species pools are larger for environments with changed means, species richness can increase with increasing heterogeneity. Thus, heterogeneity can be confounded by changes in mean, and result in either positive or negative HDR. We presume that such temporal changes are quite common in nature, as

opposed to the theoretical expectations of constant mean environmental values in homogeneous and heterogeneous sites. Therefore, HDR studies should also consider the possible confounding effect of changed means of environmental variables.

### Heterogeneity as a Separate Niche Axis

As an alternative to heterogeneity confounded by mean theory, by which plant species respond not to spatial heterogeneity, but to environmental parameter mean, some plant species (e.g. woody species from temperate regions) exhibit competitive advantage in spatially heterogeneous environments, whereas others (e.g. some herbaceous species) thrive in homogeneous environments (Grime 1994; Schlesinger et al. 1996; Pärtel & Helm 2007). Thus, heterogeneous environments can be an advantage to some dominant species, which causes species richness to decrease with increasing heterogeneity (Lundholm 2009). Moreover, experimental studies have shown that the competitive abilities of species change when soil heterogeneity is altered (Reynolds et al. 1997). Hence, adaptation to spatial heterogeneity could be considered a separate niche axis. Although knowledge of the environmental requirements of species is increasing (e.g. Ellenberg indicator values in Europe), the possibility of defining species pools through species adaptation to spatial heterogeneity remains a future prospect.

### Future Directions

In order to draw explicit conclusions on HDR trends and their underlying processes, more research is needed, especially in species-diverse ecosystems (e.g. temperate calcareous grasslands, rain forests). We encourage research at smaller spatial scales to provide explanations on HDR through species coexistence. Also, more studies are needed to explore the mechanisms underlying HDR.

Observational case studies should also consider processes that could influence the shape of HDR at different spatial scales. Species from diverse communities (e.g. grasslands or forests) can respond dissimilarly at different scales. Thus, choosing an appropriate spatial scale for measuring heterogeneity is important. We stress that grain – the scale at which heterogeneity emerges – is the most informative, especially when grain is comparable to plant size. Climatic, biogeographic and floristic regions could also affect the shape of HDR. For instance, grasslands in temperate regions generally feature more homo-

geneous soils than forests, but the opposite is true in the tropics (Pärtel et al. 2008). Additionally, different disturbance regimes (e.g. grassland management) could affect spatial heterogeneity and influence HDR differently at varying spatial scales (de Bello et al. 2007; Reitalu et al. 2008).

In addition to niche theory, studies should elaborate complementary explanations to account for HDR. We provide theories on heterogeneity, such as microfragmentation, heterogeneity confounded by mean, and heterogeneity as a separate niche axis, but this list is by no means complete.

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## Supporting Information

Additional supporting information may be found in the online version of this article:

**Appendix S1:** Data used in meta-analyses.

**Appendix S2:** Analyses of publication bias.

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