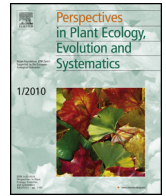




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Environmental heterogeneity drives fine-scale species assembly and functional diversity of annual plants in a semi-arid environment



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ABSTRACT

Spatial environmental heterogeneity is considered a fundamental factor for the maintenance of plant species richness. However, it still remains unclear whether heterogeneity may also facilitate coexistence at fine grain sizes or whether other processes, like mass effects and source sink dynamics due to dispersal, control species composition and diversity at these scales. In this study, we used two complimentary analyses to identify the role of heterogeneity within 15 m × 15 m plots for the coexistence of species-rich annual communities in a semi-arid environment along a steep precipitation gradient. Specifically, we: (a) analyzed the effect of environmental heterogeneity on species, functional and phylogenetic diversity within microsites (alpha diversity, 0.06 m² and 1 m²), across microsites (beta diversity), and diversity at the entire plot (gamma diversity); (b) further we used two null models to detect non-random trait and phylogenetic patterns in order to infer assembly processes, i.e. whether co-occurring species tend to share similar traits (trait convergence) or dissimilar traits (trait divergence). In general, our results showed that heterogeneity had a positive effect on community diversity. Specifically, for alpha diversity, the effect was significant for functional diversity, and not significant for either species or phylogenetic diversities. For beta diversity, all three measures of community diversity (species, functional, and phylogenetic) increased significantly, as they also did for gamma diversity, where functional measures were again stronger than for species or phylogenetic measures. In addition, the null model approach consistently detected trait convergence, indicating that species with similar traits tended to co-occur and had high abundances in a given microsite. While null model analysis across the phylogeny partly supported these trait findings, showing phylogenetic underdispersion at the 1m² grain size, surprisingly when species abundances in microsites were analyzed they were more evenly distributed across the phylogenetic tree than expected (phylogenetic overdispersion). In conclusion, our results provide compelling support that environmental heterogeneity at a relatively fine scale is an important factor for species co-existence as it positively affects diversity as well as influences species assembly. Our study underlines the need for trait-based approaches conducted at fine grain sizes in order to better understand species coexistence and community assembly.

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1. Introduction

Spatial environmental heterogeneity is a fundamental factor affecting the coexistence of plant species (Chesson, 2000). The unequal distribution of water, nutrients and light provides niches for species with different environmental preferences and ecological strategies. Although the positive effect of environmental hetero-

geneity on species richness as well as the influence on species assembly is well documented in the literature (Adler et al., 2013; Götzenberger et al., 2012; Stein et al., 2014), the underlying mechanisms of how heterogeneity facilitates plant coexistence are still poorly understood. For instance, it was commonly accepted that species richness increases with heterogeneity, since heterogeneous habitats provide more niches than homogenous ones (MacArthur and MacArthur, 1961). However, this view has been recently challenged, suggesting that the effect of heterogeneity on species richness is highly scale-dependent with an increasing positive effect with grain size, i.e. the spatial scale the vegetation is recorded (Giladi et al., 2011; Lundholm, 2009; Stein et al., 2014; Tamme et al., 2010). At small spatial grains, high environmental heterogeneity leads to the loss of effective habitat area for species and micro-fragmentation with subsequent species loss (Kadmon and Allouche, 2007; Laanisto et al., 2012). Therefore, heterogeneity may have a unimodal or even negative effect on species richness (Gazol et al., 2013; Kadmon and Allouche, 2007; Laanisto et al., 2012). In contrast, theory of community assembly assumes that the fingerprint of environmental heterogeneity on species sorting, i.e. the co-occurrence of species, becomes less important with decreasing grain size (Götzenberger et al., 2012; HilleRisLambers et al., 2012). As a result, species sorting appears increasingly random with decreasing grain size (Chase, 2014; Weiher et al., 2011). Hence, whether heterogeneity is considered as important factor for species co-existence depends on the investigated spatial grain size and response variable, i.e. species diversity or species sorting. Therefore, the joint analysis of these two response variables may provide a better understanding of the effect of heterogeneity on the coexistence of plant species.

Trait-based approaches are increasingly used to infer mechanisms of species coexistence and improve understanding of species distributions (Cornwell and Ackerly, 2009; Dainese and Sitzia, 2013; Götzenberger et al., 2012; May et al., 2013a). Environmental heterogeneity should lead to predictable species assembly from a larger species pool (Keddy, 1992). Since all species in a given location experience the same environmental conditions, co-occurring species are assumed to exhibit similar ecological strategies and share similar traits (Cornwell et al., 2006; Keddy, 1992). The exclusion of species with dissimilar or non-adapted traits from the site may arise either because these species may not survive under those conditions (environmental filtering *sensu strictu*; e.g. Kraft et al., 2015; Mayfield and Levine, 2010) or due to the species weak competitive ability under the particular environmental conditions ('weaker competitor exclusion' *sensu de Bello et al., 2012*). While disentangling these processes may be challenging (Kraft et al., 2015; Mayfield and Levine, 2010; but see de Bello et al., 2012), they both lead to trait convergence in species assemblages (Mayfield and Levine, 2010). In contrast, the concept of 'limiting similarity' (MacArthur and Levins, 1967) entails that competitive interactions lead to trait divergence, because species with similar ecological strategies experience strong niche overlap and may thus not coexist in the long run (Cornwell and Ackerly, 2009; MacArthur and Levins, 1967). In order to reveal species assembly processes, an extension to trait-based approaches is the detection of distinct phylogenetic patterns of co-occurring species (Webb et al., 2002). The phylogenetic relationships between species may serve as a predictor for their ecological strategy, since closely-related species are expected to share similar traits (Blomberg et al., 2003). If this assumption is met, the same processes entailing trait convergence should lead to phylogenetic underdispersion, i.e. closely-related species tend to co-occur, whereas limiting similarity should lead to phylogenetic overdispersion, i.e. distantly-related species tend to co-occur (Webb et al., 2002). The application of phylogenetic relationships to infer community assembly processes receives frequent criticism, since the same phylogenetic pattern can be generated

by different processes (Cavender-Bares et al., 2009; Gerhold et al., 2015). However, assembly processes may affect traits differently (e.g. Spasojevic and Suding, 2012) and trait-based approaches frequently use the same easy-measurable 'key functional traits'. Complex traits are often not feasible to measure for species-rich communities, but these can be well phylogenetically conserved (de Bello et al., 2015). Therefore, "a combination of key measured traits and phylogeny may better assure that different axes of differentiation between species are being considered" (de Bello et al., 2015).

The detection of both trait patterns and phylogenetic patterns varies with the scale under consideration (Kraft and Ackerly, 2010; Swenson et al., 2007). Environmental filters presumably act at larger scales, which should lead to the detection of trait convergence (Cavender-Bares et al., 2009). At finer grains, species assembly is assumed to be driven by limiting similarity or by stochastic dispersal events (Götzenberger et al., 2012; Weiher et al., 2011). Some small-scale studies confirmed limiting similarity by detecting trait divergence (Bernard-Verdier et al., 2012; de Bello et al., 2013), while others found random trait pattern (Thompson et al., 2010). However, Adler et al. (2013) argued that trait divergence may be the result of environmental filtering at even finer grain sizes. Consequently, trait pattern should be analyzed at different spatial scales, in order to identify the effect of environmental heterogeneity on species assembly.

The framework of alpha, beta and gamma diversity (Whittaker, 1972) enables analysis of the effect of heterogeneity on species diversity at different spatial grain sizes simultaneously. Since the study presented in the current article focuses on describing patterns at fine scales, we define gamma diversity as the species pool at a plot-scale (i.e. 15 m × 15 m), alpha diversity as the diversity within microsites (two grain sizes, 0.06 m² and 1 m²) and beta diversity as turnover among microsites. Environmental heterogeneity, measured at the plot-scale, may positively affect alpha, beta and gamma diversity through different mechanisms. Gamma diversity may increase with heterogeneity, as heterogeneous environments offer more opportunities for niche differentiation and species sorting across environmental variation. In line with that, species turnover between microsites should increase with environmental heterogeneity, if environmental differences between microsites favor distinct species, as the concept of 'environmental filtering' would suggest (see above). In contrast, diversity within microsites may increase either due to a higher environmental heterogeneity within the microsite (if there is a correlation between microsite and plot-scale environmental heterogeneity) or simply due to the inflow of species from the surrounding area through spatial mass effects (Shmida and Wilson, 1985). Hence, the positive effects of environmental heterogeneity include niche-based as well as dispersal-based mechanisms. Negative effects of heterogeneity on species richness may emerge due to high extinction risk, e.g. demographic stochasticity, of small populations (Kadmon and Allouche, 2007). Depending on which mechanisms act, heterogeneity may affect functional and species diversity differently (as observed by Meynard et al., 2011), since species may be functional redundant. Therefore, comprehensive analyses of the effect of environmental heterogeneity on species, functional and phylogenetic diversity at different spatial grain sizes may help to reveal the underlying mechanisms of environmental heterogeneity effects on the maintenance of species richness and to link results of species assembly studies.

Finally, the effect of heterogeneity on diversity and species assembly may depend on the position along environmental gradients. Yang et al. (2015) proposed a model in which heterogeneity has a positive effect on species richness at the extreme ends of a stress-productivity gradient and a hump-shaped effect at the intermediate position. With respect to species assembly, Price

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