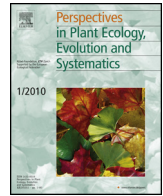




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Environmental heterogeneity drives fine-scale species assembly and functional diversity of annual plants in a semi-arid environment



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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

et al. (2014) showed in an elegant experiment that with increasing small-scale heterogeneity and productivity niche overlap (i.e. trait convergence) increased, due to the suppression of slow-growing species. However, we are not aware of any studies that analyze the heterogeneity's effect on both species diversity and species assembly along stress-productivity gradients.

In this study, we use two complimentary analyses with different research approaches in order to reveal how environmental heterogeneity affects species coexistence. Specifically, we: i) identify trait- and phylogeny-based assembly processes that structure co-occurrence and species abundances in microsites; ii) analyze whether increasing plot-scale environmental heterogeneity feature a higher species diversity within and across microsites (alpha and beta diversity, respectively) as well as a higher plot-scale species diversity (gamma diversity). Our study system is located at the transition zone between Mediterranean and desert ecosystems along a steep precipitation gradient in Israel. The fragmented semi-steppe batha and grassland vegetation in this area features a high proportion (79%) and diversity of annual plants (14.8 ± 6.7 species/m²). We use vegetation surveys at two different grain sizes (0.06 m² and 1 m²) nested within 15 m × 15 m plots. A previous study has found evidence for both trait convergence and divergence when these communities are compared to regional species pools of ca. 6 km × 4 km land units (May et al., 2013a). At the same time, regional processes, i.e. propagule exchange between habitat patches, are negligible in this area (Gemeinholzer et al., 2012; May et al., 2013b). Therefore, it is especially relevant to investigate coexistence mechanisms at the plot-scale.

We address the following questions:

- Does environmental heterogeneity affect species assembly within plots, indicated by trait convergence in microsites?
- Does the phylogenetic approach point to the same species assembly pattern as the functional approach does?
- How does environmental heterogeneity, measured at the plot-scale, affect the diversity within microsites (alpha), turnover between microsites (beta) and the diversity of the plot (gamma diversity)?
- Is the heterogeneity's effect on diversity consistent between species, functional and phylogenetic diversity and along a steep precipitation gradient?

2. Methods

2.1. Study area

The study area is situated in the Southern Judean Lowlands, Israel (31°24'00"–31°40'50"N, 34°48'30"–34°50'30"E), at the transition zone between Mediterranean and desert ecosystems. Rainfall in this area is restricted to winter (October–April) with decreasing annual amounts from north (430 mm) to south (291 mm) along a distance of 30 km (May et al., 2013a). The fragmented landscape contains patches of semi-natural vegetation, set within a matrix of intensive agricultural land. The semi-natural vegetation has resulted from heavy grazing since the Bronze Age and can be referred to as semi-steppe batha and grassland (see Giladi et al., 2011 for further details). These vegetation types feature a high diversity of annual plant species. Woody vegetation is dominated by small shrubs (mostly *Sarcopoterium spinosum*) and some larger bushes. The common tussock grass *Hyparrhenia hirta* is frequently found in grasslands, where it builds dense populations. Previous studies showed that the species composition changes drastically along the precipitation gradient, including a decrease of species richness and density towards aridity (Giladi et al., 2011) accompanied by a decrease of community weighted mean traits of specific

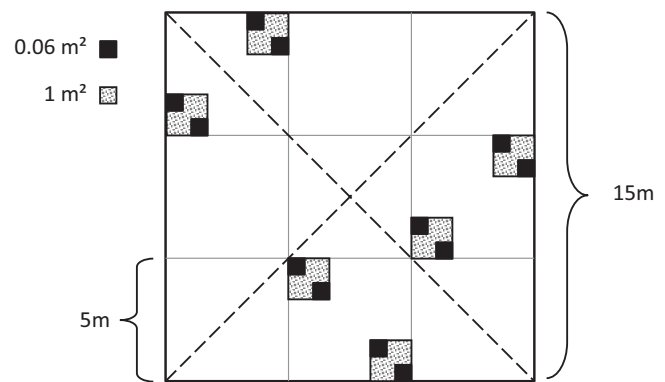


Fig. 1. Sampling design of the study. Vegetation surveys were done at two different scales: 0.25 m × 0.25 m and 1 m × 1 m within a plot of 15 m × 15 m. The environmental heterogeneity was assessed along two transects that represent the diagonals of the plot (dashed lines). Along these transects the diversity of microhabitats was quantified within the 15 m × 15 m plot.

leaf area, plant height and seed mass (May et al., 2013a). These shifts indicate a stress-productivity gradient from north (productive) to south (stressful).

2.2. Vegetation sampling & environmental heterogeneity measurements

The vegetation sampling was conducted in three land units (6 km × 4 km each), which were placed from north to south along the precipitation gradient (see Giladi et al., 2011 for details of the vegetation sampling). In each land unit, we established 15 m × 15 m plots (south n=25, mid n=28, north n=28) in different patches of semi-natural vegetation. Each of these plots contained 12 small quadrats 0.0625 m² in size (0.25 m × 0.25 m, henceforth 0.06 m²), nested in six larger quadrats of 1 m² (1 m × 1 m) (Fig. 1). These quadrats define our 'microsites' at two different grain sizes. In spring 2009, all plant species were recorded for each quadrat and the number of individuals was counted in the finer quadrats (0.06 m²).

In order to estimate environmental heterogeneity, we determined the diversity of microhabitats within the plots. Along two transects that form the diagonals of the plots, we placed at each half meter a 0.06 m² quadrat left and right of the transect (Fig. 1). We visually assessed the most common microhabitat within each of the resulting 84 quadrats per plot and assigned each to one of six microhabitat types: 'large bush', '*Sarcopoterium spinosum*', 'small shrub' (other than *S. spinosum*), '*Hyparrhenia hirta*', 'exposed rock' and 'herbaceous patch'. Shrubs and perennial grasses are key structures that modulate the light and water availability for annual plants, which has a strong impact on the annual species composition (Luzuriaga et al., 2012; Segoli et al., 2012). Similarly, differences in soil depth and micro-topography, indicated by exposed rocks, influences the species composition in Mediterranean ecosystems (Bernard-Verdier et al., 2012). The proportions of the different microhabitat types within the plots were used to calculate the Shannon index, which defines our environmental heterogeneity (Giladi et al., 2011). We are aware that our index quantifies the environmental heterogeneity of the whole 15 m × 15 m plot and that the scale at which environmental heterogeneity is measured may influence the effect on species richness (Tammé et al., 2010). However, previous analyses have shown that this index is also highly correlated ($r=0.87$) with small-scale heterogeneity at 1 m² (Giladi et al., 2011).

2.3. Trait sampling & construction of the phylogenetic tree

Following standard protocols (Cornelissen et al., 2003), we measured species mean traits of specific leaf area [mm^2/mg], seed mass after removing appendages [mg] and canopy height [cm] for 129 of the 237 observed annual species in the study area. For specific leaf area and seed mass, we measured ten individuals; for canopy height 25 individuals of one healthy population within the whole study area (see May et al., 2013a for details of trait measurements). Since mostly abundant species were measured, we covered 89% and 85% of the annual species occurrences at the 0.06 m^2 and 1 m^2 grain size, respectively. The three measured traits constitute the principle axes of the Leaf-Height-Seed (LHS) plant ecological strategy scheme by Westoby (1998), which is a simple, generic way to characterize the ecological strategy of plants.

We constructed a phylogenetic tree of all annuals present in the study area. At first, we built a tree of the respective plant families based on the proposed phylogeny of The Angiosperm Phylogeny Group (2009). Nodes and branch lengths of this tree were adjusted to divergence times estimated by molecular data, which were calibrated to known fossil ages (Bell et al., 2010). The relationships between species within the families were resolved with 39 further publications (see supplementary material A1 for details).

2.4. Analyses

2.4.1. Phylogenetic trait conservatism

First, we revealed whether the investigated traits are phylogenetically conserved by using K-statistics (Blomberg et al., 2003), implemented in the R-package 'picante'. K quantifies the degree of trait conservatism in comparison to a Brownian motion model of trait evolution. $K < 1$ signifies that traits are more divergent than predicted by the model, whereas $K > 1$ indicates a high degree of trait conservatism. The observed K values were compared to expected K values, under the consideration of no relationship between traits and phylogeny, derived from 999 random trait-tree associations.

2.4.2. Calculation of diversity indices

We used the mathematical framework of Rao's quadratic entropy (RaoQ) to estimate the mean diversity of microsites (alpha), turnover between microsites (beta) and plot-scale diversity (gamma). RaoQ is known to reflect community assembly processes well (Mouchet et al., 2010) and allows a comparison of species (often referred as taxonomic), functional and phylogenetic diversities using the same index. Here, we followed the approach of de Bello et al. (2010). Alpha diversities were calculated for each microsite (i.e. 0.06 m^2 and 1 m^2) as follows:

$$\alpha_{\text{Rao}} = \sum_{i=1}^s \sum_{j=1}^s d_{ij} p_i p_j$$

with d_{ij} the dissimilarity between species i and j where p is their relative abundance in the microsite. For species diversity, d_{ij} between species is always 1. Functional dissimilarities between species were gathered from the Euclidean distance of the three log-transformed and standardized traits (seed mass, canopy height, specific leaf area). Phylogenetic dissimilarities were derived from the phylogenetic tree with the *cophenetic* function of the R-package 'picante'. The relative abundance of the species was gathered from the number of individuals, which was counted within the 0.06 m^2 microsites. For 1 m^2 microsites, no relative abundances were available and presence-absence data were used. The alpha diversities of all microsites for a given grain size (either 0.06 m^2 or 1 m^2) within a $15 \text{ m} \times 15 \text{ m}$ plot were averaged to estimate the mean

alpha diversity. Gamma diversity was calculated in the same way as alpha diversity, but with the addition of pooling all microsites (either 0.06 m^2 or 1 m^2) of the plot into one sample. Beta diversity can finally be calculated as the proportional ($\beta_{\text{prop}} = (\gamma - \bar{\alpha}) / \gamma$) or additive difference ($\beta_{\text{add}} = \gamma - \bar{\alpha}$) between gamma and mean alpha diversity (de Bello et al., 2010). We report in the manuscript only findings of the proportional beta diversity, since both indices showed very similar results. Pearson's correlation coefficient was used to assess the correlation between species, functional and phylogenetic diversity indices.

2.4.3. Null model analyses

We used two different null models in order to reveal species assembly processes. The first null model assessed how species assembled from the plot-scale species pool ($15 \text{ m} \times 15 \text{ m}$) and was conducted for both grain sizes considered (0.06 m^2 and 1 m^2). For this approach, observed mean alpha functional and phylogenetic diversities were compared to expected mean alpha diversities under the consideration of random species assembly within the plots. The null model shuffled species occurrences (presence-absence) among microsites of the same plot by keeping the frequency of species within the plot and the number of species in the microsites constant. We used the *trialswap* algorithm implemented in the R-package 'picante' with 999 repetitions and 10 000 permutations. The second null model assessed how species abundances at the very fine scale (0.06 m^2) are related to traits and phylogenetic relationships, respectively. If the particular environmental conditions of a microsite favor a specific ecological strategy, species with high abundances should have similar traits, leading to trait convergence. Otherwise, if niche differentiation prevails, species with high abundances should have dissimilar traits, which would cause trait divergence (Bernard-Verdier et al., 2012). We used the abundance-weighted RaoQ to quantify the (alpha) functional and phylogenetic diversity within the 0.06 m^2 microsites. The observed values were compared with expected values derived from a null model that shuffled abundances among the species within the plots (999 repetitions). This analysis was only conducted for microsites ($n = 712$) that contained more than two annual species whose traits were available. Since assembly processes may act contrastingly on different traits (Spasojevic and Suding, 2012), we performed both null model analyses for each trait separately as well as jointly in a multidimensional analysis. In both null model approaches, we calculated the standardized effect size, in order to assess the deviation of the observed diversities (D) from the expected diversities, $\text{SES} = (D_{\text{obs}} - \bar{D}_{\text{exp}}) / \text{sd}(D_{\text{exp}})$. For each plot, we calculated a mean SES for both null models. Significance across $15 \text{ m} \times 15 \text{ m}$ plots was evaluated with a two-tailed Wilcoxon test.

2.4.4. Heterogeneity & precipitation effect on diversity

In order to reveal whether heterogeneity and precipitation gradient affect the diversity indices as well as the assembly pattern of species, we fitted a series of linear models. As response variables, we used observed mean alpha, beta (log-transformed) and gamma diversity indices (species, phylogenetic and functional) and the standardized effect size (SES) of both null models. As predictors we used the linear and quadratic term of the environmental heterogeneity index, land unit as categorical effect and the interaction between both heterogeneity terms and land unit. Since beta diversity indices often are dependent on the size of the species pool (Kraft et al., 2011), the number of species of each plot was incorporated as covariate in these models. Models that had SES as response variable included additionally the number of species and the observed functional diversity included in the null model, since both variables have a strong impact on the magnitude of SES (de Bello, 2012). Following Crawley (2007), we did a stepwise backwards selection and removed non-significant terms ($p < 0.05$) with a single-term dele-

tion F-test to obtain the minimal adequate model. If the quadratic term of heterogeneity was significant (three out of 27 models), we additionally fitted models that did not include the quadratic term, in order to test the significance of the linear term of heterogeneity. The analyses were conducted with presence-absence data for both grain sizes and including abundances on the finer grain size (0.06 m²).

2.4.5. Spatial autocorrelation of CWM traits

Finally, we investigated whether the environment selects upon traits at a specific scale, i.e. whether closely-situated microsites share more species with similar traits than do distantly-situated microsites. For this purpose, we analyzed the spatial autocorrelation of community weighted mean (CWM) traits. For each plot, we calculated Moran's I correlograms for the CWM traits of the 0.06 m² microsites for seven distance classes with 'correlog' (R-package 'ncf'). All statistics were carried out in R version 3.1.1 (R Core Team 2012).

3. Results

Our three investigated traits were moderately conserved, although they were less conserved than a Brownian motion model of trait evolution would predict (seed mass $K=0.35$, $p < 0.001$; specific leaf area $K=0.29$, $p < 0.001$; canopy height $K=0.24$, $p < 0.001$), indicating that closely-related species tended to share similar traits. Community weighted mean traits showed no apparent spatial autocorrelation within our plots (15 m × 15 m) (supplementary material A2).

Species assembly was assessed with a null model that assumes random species assembly within the plots. The comparison between observed and expected functional diversities revealed strong support for non-random assembly processes (Table 1). Functional diversity of the multidimensional leaf-height-seed approach was lower than expected, indicating trait convergence at both grain sizes considered (0.06 m² and 1 m²). Similar results were obtained when functional diversity was calculated solely for seed mass as well as for canopy height (Table 1). Specific leaf area showed no deviation from the null model. The phylogenetic approach revealed that at the 1 m² grain size closely-related species tended to co-occur (phylogenetic underdispersion). At the finer grain size (0.06 m²), species appeared to assemble randomly with respect to their phylogeny (Table 1).

The second null model analyzed how species abundances within fine microsites (0.06 m²) are related to the species' traits and phylogeny. This null model detected trait convergence for all traits considered, indicating that species with high frequencies share similar traits (Table 1). In contrast, species abundances were more evenly distributed across the phylogeny than expected by chance (phylogenetic overdispersion). We found no indication that the results of both null models changed along the precipitation gradient or with plot-scale heterogeneity (one exception: null model 2, specific leaf area, interaction between heterogeneity and land unit $p=0.049$; supplementary material A3).

The effect of environmental heterogeneity and precipitation gradient (represented by three land units) on diversity within microsites (alpha diversity, 0.06 m² and 1 m²), turnover between microsites (beta) and plot-scale diversity (gamma) was analyzed for species (SD), functional (FD) and phylogenetic (PD) diversity. Observed SD, FD and PD indices were highly correlated with each other, though the relationships were less strong with increasing grain size (supplementary material A4). Both heterogeneity and land unit affected the diversity indices, but we found no evidence for significant heterogeneity by land unit interaction (Table 2, analyses of presence-absence data; Fig. 2, analyses includ-

ing species abundances). Beta diversity (SD, FD and PD) consistently increased with heterogeneity, particularly at the finer grain size (0.06 m²), indicating that environmental heterogeneity increases the turnover among microsites (Fig. 2). Along the precipitation gradient, beta diversity showed no differences among the three land units if the analyses included species abundances (Fig. 2) and decreased with precipitation, if presence-absence data were used (Table 2, supplementary material A5). The analyses and comparisons of alpha and gamma diversities revealed some remarkable differences between SD, FD and PD in relation to heterogeneity and precipitation gradient. Heterogeneity had no significant effect on alpha SD and positively influenced gamma SD (Table 2). In contrast, heterogeneity had a stronger effect on FD compared to SD and positively affected both alpha and gamma FD. Furthermore, FD showed in some models an unexpected U-shape pattern, if quadratic terms were included in the maximal models (Table 2, supplementary material A5). Alpha and gamma PD appeared to be independent of heterogeneity (one exception gamma PD, 0.06 m² including species abundances). With respect to the precipitation gradient, species diversity increased with annual precipitation amount at all grain sizes. In contrast, alpha and gamma FD was highest in the intermediate land unit (particularly at the 1 m² grain size, supplementary material A5). Alpha and gamma PD increased with precipitation at the fine spatial grain sizes (0.06 m²) and showed a similar pattern like FD diversity at the 1 m² grain size.

4. Discussion

Environmental heterogeneity is a key factor in promoting species coexistence and diversity, although the underlying mechanisms are still poorly understood (Chesson, 2000; HilleRisLambers et al., 2012; Stein et al., 2014). In particular, it remains unclear, whether environmental heterogeneity has the potential to facilitate coexistence at fine grain sizes (Chase, 2014; Gazol et al., 2013; Tamme et al., 2010). In this study, we found evidence that within 15 m × 15 m plots species assembly of annual plants is strictly non-random and further environmental heterogeneity positively affected functional and species diversity at different spatial scales.

Null model 1 revealed that annual species are non-randomly distributed within our 15 m × 15 m plots. Species with similar ecological strategies, as quantified by the LHS concept (Westoby, 1998), or solely by seed mass and canopy height, tended to co-occur at both grain sizes considered (0.06 m² and 1 m²). This trait convergence pattern can be attributed to environmental differences among microsites, as other processes that may cause trait convergence, e.g. herbivory and pollination (Cavender-Bares et al., 2009), are unlikely to affect the investigated traits at the considered scale. The detection of trait convergence shows that environmental heterogeneity has an impact on the assembly and co-occurrence of species. In order to reveal whether the environment selects upon traits at a particular scale, we additionally assessed the spatial autocorrelation of community weighted mean traits. Since community weighted mean traits showed no apparent autocorrelation, it becomes evident that the trait (and species) composition changes considerably even between nearby microsites (1.1 m distance), which is likely to be a result of small-scale heterogeneity; potentially associated with shrubs, perennial grasses and variation of soil depth that modulate the light and water availability for annual plants (Bernard-Verdier et al., 2012; Luzuriaga et al., 2012; Segoli et al., 2012). In congruence with the null model approach, environmental heterogeneity positively influenced beta diversity, particularly at the finer grain size (0.06 m²). Hence, both analyses – the null model approach and the effect of environmental heterogeneity on beta diversity – provide compelling evidence that local

Table 1

Results of both null model approaches that analyzed species assembly within 15 m × 15 m plots (null model 1) and the trait abundances within 0.06 m² quadrats (null model 2). Observed functional and phylogenetic diversities were compared with the expected diversities generated by the null models. The deviation between observed and expected diversities was quantified with the Standard Effect Size (SES). + and – indicate whether the mean SES is positive (obs > exp) or negative (obs < exp). The table shows significant deviations of the SES from zero across all 81 plots, with the respective p-values revealed by a two-tailed Wilcoxon test. LHS stands for the Leaf-Height-Seed strategy by Westoby (1998), which is a multidimensional analysis of the three log-transformed traits; seed mass (SM), canopy height (CH) and specific leaf area (SLA).

Null model	Grain size [m ²]	LHS	SM	CH	SLA	Phylogeny
1	0.06	–	0.0007	–	0.0025	0.31
	1	–	0.003	–	0.0002	0.58
2	0.06	–	<0.0001	–	0.038	<0.0001

Table 2

Effect of environmental heterogeneity (Het) and land unit on mean alpha, beta, gamma species (SD), functional (FD) and phylogenetic (PD) diversity for both grain sizes (0.06 m², 1 m²) and presence-absence data (see supplementary material A5 for graphical illustration). The maximal models included heterogeneity as linear and quadratic term, land unit and the interaction between heterogeneity and land unit. The table reports the minimal adequate models with marginally significant (p < 0.1) terms, which were revealed with single-term deletion F-test. The interaction between land unit and heterogeneity was not significant in any model. F-values marked with “#” base on models that did not include the quadratic term of the heterogeneity index (see methods for details). Statistical models of beta diversities also included the species richness of the 15 m × 15 m plot, since beta diversity indices are often influenced by the number of species. **** < 0.0001, *** p < 0.001, ** p < 0.01, * p < 0.05, . p < 0.1.

Scale	facet	Grain size [m ²]	Het F	Het ² F	Land unit F	
mean Alpha	SD	0.06			84.17	
		1	2.8	.	40.03	
	FD	0.06	4.94	*	54.4	
		1	#14.45	***	5.11	13.55
	PD	0.06	0.015		*	63.31
		1	0.029			8.26
log Beta	SD	0.06	12.38	***	14.86	
		1	4.95	*	5.61	
	FD	0.06	8.8	**	14.47	
		1	2.41		10.75	
	PD	0.06	15.55	***	13.62	
		1	7.41	**	5.18	
Gamma	SD	0.06	3.59	.	43.44	
		1	7.35	**	35.05	
	FD	0.06	#10.92	**	6.8	24.03
		1	#18.34	****	6.89	11.34
	PD	0.06	2.06		*	22.31
		1	0.04			4.65

environmental heterogeneity may act as stabilizing factor for coexistence among species by the provision of different microhabitats.

The second null model analyzed whether species abundances are related to traits within microsites (0.06 m²). Irrespective of which trait was considered, species with high abundances shared similar traits, as indicated by trait convergence. Hence, at the grain size where individuals interact and compete for resources, the environmental conditions favor species with similar strategies.

The consistent detection of trait convergence at fine scales contrasts the expectation and findings of other studies arguing that at very fine spatial grain sizes species assembly appears randomly or that competition creates trait divergence (Weiher et al., 2011). For instance, de Bello et al. (2013) found trait divergence for temperate grasslands at 1 m²; the same was detected by Bernard-Verdier et al. (2012) in Mediterranean grasslands at 54 m². The contradiction between our and other studies may have multiple reasons. While we analyzed annual communities, the other studies focused on perennial-dominated systems. Annual plants are on average smaller compared to perennials and thus the influence of small-scale heterogeneity should have a larger effect on the assembly of annuals compared to perennials. Moreover, competitive intensity is assumed to be lower between annuals compared to perennials (see Emery et al., 2009 for a summary of differences between annuals and perennials), especially in less productive system like ours (e.g. Schifffers and Tielbörger, 2006). At the same time, a large body of literature highlight differences in regeneration strategies, like dormancy and germination timing, as important coexistence mechanism in annual communities (Pake and Venable, 1996; Siewert and Tielbörger, 2010; Venable and Brown, 1988),

while differences in regenerative strategies between perennials seem to be less important (Emery et al., 2009). Hence, annual communities may show trait divergence particularly in complex regenerative traits (see below phylogenetic analyses), since low competitive intensities do not drive trait divergence in ‘key functional traits’. However, Adler et al. (2013) showed that patterns of trait divergence observed at a larger scale can actually result from small-scale environmental filtering within microhabitats. Under this consideration, the trait divergence observed by other studies may need to be re-evaluated. For instance, the trait divergence findings by May et al. (2013a), who analyzed the same annual communities as in the current study but from a regional perspective, may be the result of small-scale ‘environmental filtering’. Our approach, therefore, underlines the need for a better understanding of how small-scale heterogeneity affects the trait-based assembly of species (Adler et al., 2013).

Environmental heterogeneity may affect species richness positively by widening the available niche space and negatively by reducing suitable area and increasing micro-fragmentation for species (Kadmon and Allouche, 2007; Laanisto et al., 2012). We found no indication for the unimodal species richness-heterogeneity pattern predicted by Kadmon and Allouche (2007). In our study, heterogeneity positively influenced species diversity at the plot-scale. As the null model analyses suggest, microhabitats favor species with different traits and thus plots with a higher diversity in microhabitats may contain a higher overall species diversity. Additionally, we observed that heterogeneity had an even larger positive effect on functional diversity compared to species diversity. This pattern indicates that heterogeneity indeed affects the

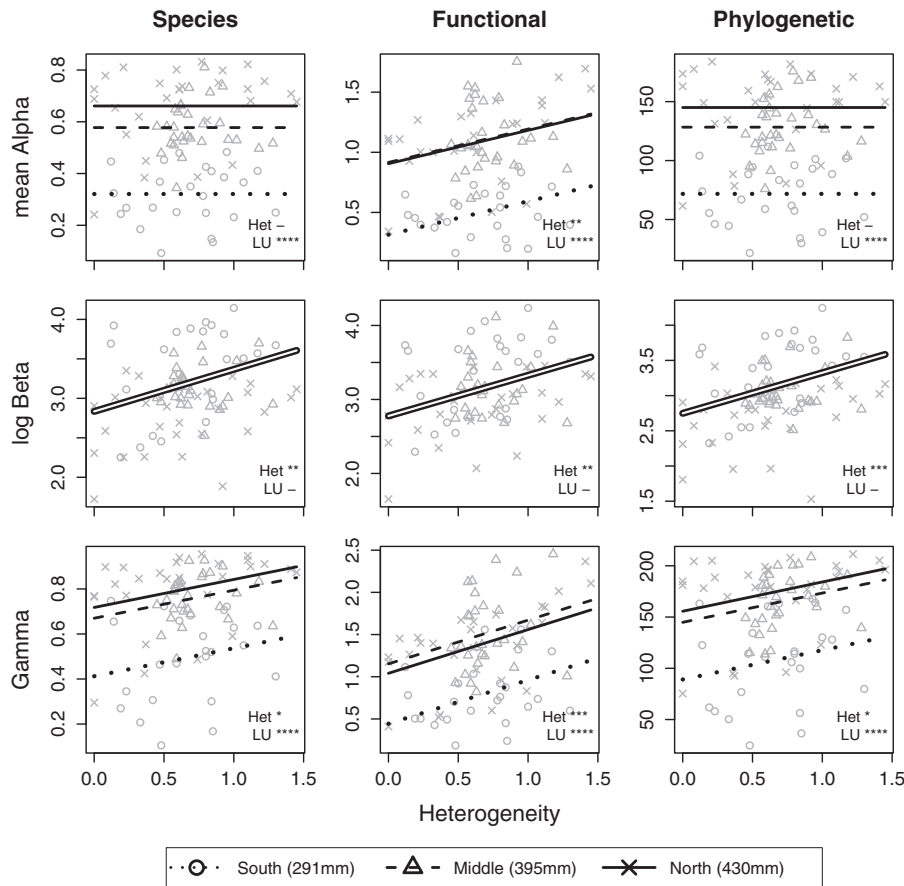


Fig. 2. Effect of environmental heterogeneity (Het) and land unit (LU) on mean alpha, beta and gamma species, functional and phylogenetic diversity. The figure shows data of the finer grain size (0.06 m^2) and considered species abundances (Table 2 shows results of presence-absence data). Lines indicate predictions of the minimal adequate models. Significance of both predictors is shown at the right bottom of the figure. Please note that the maximal models also included the interaction between land unit and heterogeneity, which was not significant in any model. Beta diversity models included additionally the number of species as covariate. For the graphical illustration, number of species was set to the median. The legend includes mean annual precipitation amounts at the three land units. **** < 0.0001 , *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$, '-' indicates not significant ($p > 0.05$).

available niche space, since it increases the diversity of ecological strategies of the species. Species may have very similar ecological strategies and traits (functional redundancy) as indicated by the weak correlation between taxonomic and functional diversity at larger spatial extents. As a result, heterogeneity should primarily affect the functional diversity rather than the species diversity *per se*, as our analyses indicate. Moreover, heterogeneity, which was measured at the plot-scale ($15 \text{ m} \times 15 \text{ m}$), positively influenced the functional diversity within microsites (0.06 m^2 and 1 m^2). The higher functional diversity in microsites may be the result of small-scale heterogeneity within the microsite, since plots with a high heterogeneity at the plot-scale also feature a higher heterogeneity within microhabitats (see Methods). Spatial mass effects, i.e. the inflow of species from neighboring sites, may also increase the functional diversity of microhabitats. However, such mechanisms seem to be ineffective to increase the species diversity in microsites, which may be due to very limited dispersal distances of annuals in our study system (Siewert and Tielbörger, 2010) and small-scale 'environmental filtering' even between closely-situated microsites (see above). The strong relationship between heterogeneity and functional diversity across different grain sizes highlights the role of heterogeneity on niche-based processes and shows that analyses that solely rely on species diversity may miss important insights. Moreover, we found an unexpected, although weak, non-linear increase of functional diversity with heterogeneity in some models indicating that not only the strength, but also the shape of heterogeneity may affect species and functional diversity differently.

Along the precipitation gradient, we observed contrasting trends of species and functional diversity. Alpha and gamma species diversity increased with precipitation amount, which is consistent with numerous studies along similar precipitation gradients (e.g. Giladi et al., 2011). Noteworthy, the corresponding alpha and gamma functional diversity showed an idiosyncratic pattern towards precipitation amount, with a peak in the intermediate land unit. Our study region is located at the transition zone between desert and Mediterranean ecosystems with a substantial species turnover between the three land units (only half of the species occur in all three land units, Giladi et al., 2011). Hence, the intermediate land unit contains possibly the largest overlap of species from these two ecosystems and features therefore the highest diversity in functional traits. While beta diversity did not differ between land units if species abundances were included in the analyses, beta diversity decreases with precipitation, if the analyses based on presence-absence data. The latter pattern is quite surprising, since beta diversity indices generally increase with the size of the species pool (Kraft et al., 2011). However, the observed differences in beta diversity between land units are no indication for changing assembly processes along the precipitation gradient. If the size of the species pool varies much between land units, as in our study, observed differences in beta diversity may be a mathematical artefact (Kraft et al., 2011). In this context, the effect of heterogeneity on diversity and on species assembly (i.e. SES of null models) appeared to be consistent along the precipitation gradient. Further, we found no indication that species assembly was affected by the hetero-

geneity of the plot. It should be noted that also 'environmental homogenous' plots in terms of microhabitat diversity, may contain some degree of environmental variation across microsites, as for instance differences in soil properties were not assessed with our heterogeneity index. Therefore, it seems likely that the heterogeneity gradient in our study was not sufficiently large to reveal differences in species assembly.

We used phylogenetic relationships in order to extend our functional approach, which relies on three key functional traits (de Bello et al., 2015). Corresponding to the observed trait convergence pattern, we expected to detect phylogenetic underdispersion, since closely related species tended to share similar traits. As predicted, phylogenetic underdispersion was found within larger microsites (1 m²), but at the finer grain size (0.06 m²) species appeared randomly assembled with respect to the phylogeny (null model 1). The combination of a lower chance of detecting assembly processes with decreasing species numbers at finer scales (Weiher et al., 2011) and a lower sensitivity of phylogenetic approaches (Kraft and Ackerly, 2010) may explain the deviation between the trait and phylogenetic approaches at 0.06 m². However, more striking is the phylogenetic overdispersion of the second null model. This pattern indicates that species' abundances are more evenly distributed across the phylogenetic tree than expected by chance, and thus species with high abundances tend to be distantly related. This finding has two alternative explanations. One is that environmental conditions favor species with similar traits, but closely-related species actually have different ecological strategies. This scenario would lead to the detection of phylogenetic overdispersion, but it is unlikely because trait conservatism is in general high, if the investigated community comprises different phylogenetic clades (Cavender-Bares et al., 2009). More likely, competition might create divergence in traits that are phylogenetically conserved, but which were not measured in this study. As mentioned above, niche differentiation in generative traits is important in annual plant communities and generative traits show phylogenetic conservatism (e.g. Hoyle et al., 2015). The contrasting pattern between trait-based and phylogenetic approaches indicate that species assembly is affected contrastingly by traits (Spasojevic and Suding, 2012). Therefore, rather than considering the disadvantages of phylogenetic studies, we think that observed phylogenetic patterns build an excellent starting point for further research to reveal the underlying mechanisms and traits.

In conclusion, our analyses provide compelling evidence that environmental heterogeneity facilitates coexistence among annual plants through the provision of microhabitats and species sorting among these microhabitats. The combination of null models and analyses of heterogeneity-diversity relationships at different grain sizes and diversity facets allowed us to highlight the importance of heterogeneity on niche-based processes. This study, therefore, highlights the need for trait-based approaches that are conducted at small spatial extents in order to analyze coexistence mechanisms at local scales, which remain overlooked or even misinterpreted when a more regional perspective is followed.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.ppees.2017.01.001>.

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