

LETTER

Competitive exclusion, beta diversity, and deterministic vs. stochastic drivers of community assembly

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Abstract

Species diversity has two components – number of species and spatial turnover in species composition (beta-diversity). Using a field experiment focusing on a system of Mediterranean grasslands, we show that interspecific competition may influence the two components in the same direction or in opposite directions, depending on whether competitive exclusions are deterministic or stochastic. Deterministic exclusions reduce both patch-scale richness and beta-diversity, thereby homogenising the community. Stochastic extinctions reduce richness at the patch scale, but increase the differences in species composition among patches. These results indicate that studies of competitive effects on beta diversity may help to distinguish between deterministic and stochastic components of competitive exclusion. Such distinction is crucial for understanding the causal relationship between competition and species diversity, one of the oldest and most fundamental questions in ecology.

Keywords

Annual plants, community ecology, functional groups, habitat productivity, Mediterranean grasslands, niche vs. neutral processes, plant competition, removal experiment, species diversity.

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INTRODUCTION

Classical competition theory assumes that interspecific competition is deterministic in the sense that species differ in their competitive ability and these differences determine the outcome of local competitive interactions (Grime 1973; Keddy & Shipley 1989). Within a spatially uniform habitat, deterministic competitive exclusion is expected to reduce the degree of spatial turnover in species composition (beta diversity), by limiting the composition of the overall community to a subset of competitively superior species (Kunstler *et al.* 2012). Nevertheless, in spite of an increasing interest in patterns and mechanisms of beta diversity (Gering & Crist 2002; Anderson *et al.* 2011; Kraft *et al.* 2011; Carvalho *et al.* 2012), almost nothing is known about the effect of competitive exclusion on beta diversity. Clearly, if competitive interactions affect beta diversity, quantifying the magnitude, patterns and scales of such effects is crucial for understanding observed patterns of species diversity and their causal mechanisms.

Moreover, in a recent article, Chase *et al.* (2011) proposed that beta diversity can be used as a yardstick for discriminating between deterministic and stochastic drivers of species diversity (see also Chase 2007, 2010; Chase & Myers 2011). This approach is based on a null model that generates random species assemblages from a set of sites representing the relevant species pool. For any pair of sites, beta diversity is calculated in five steps: (1) random assignment of species

from the relevant pool to each site until the number of species assigned to the site equals the observed number, (2) calculation of a presence-absence measure of compositional similarity between the assemblages of species assigned to the two sites, (3) repeating this procedure a large number of times to obtain a 'null' distribution of compositional similarity between the two sites, (4) determination of the fraction of null values of compositional similarity that are equal to or larger than the observed value, and (5) rescaling of the resulting value to range from -1 to 1. Importantly, step (4) converts the measure of similarity into a measure of dissimilarity and step (5) rescales this measure to have a null expectation of zero. Values significantly lower than zero are interpreted as evidence for deterministic drivers of species diversity.

In this study, we apply the approach proposed by Chase *et al.* (2011) to investigate the effect of competitive interactions on the number of species in a local community. Our study is based on the premise that competition affects the number of species in a community via two distinct mechanisms: (1) deterministic competitive exclusion at the scale at which individuals directly compete with each other (the 'competitive neighbourhood' *sensu* Stoll & Weiner 2000), and (2) reduction in differences in species composition among different neighbourhoods. The advantage of the null-model approach proposed by Chase *et al.* (2011) is that it allows one to statistically separate the two mechanisms, that is, to test the effect of competitive exclusion on beta diversity while con-

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trolling for species loss caused by direct competitive interactions. As much as we are aware, our study is the first attempt to decompose competitive effects on species diversity into these two components.

When using null models for testing hypotheses concerning the role of deterministic vs. stochastic drivers of species diversity, it is important to distinguish between species-level and individual-level stochasticity (Gotelli & Ulrich 2012). The null model proposed by Chase *et al.* (2011) generates species-level stochasticity by randomly drawing species based on their frequency of occurrence in the relevant set of sites. This approach was developed to analyse presence-absence data and therefore ignores differences in *species abundance* among species. However, species with low competitive ability are often characterised by a small population size, which makes them more prone to extinctions caused by individual-level stochasticity (Suding *et al.* 2005; Ben-Hur *et al.* 2012). Such correlation between competitive ability and population size may complicate the distinction between deterministic and stochastic drivers of extinction. A rigorous demonstration that competitive effects on beta diversity have a deterministic component must therefore show that competition reduces beta diversity to lower levels than those expected due to underlying differences in species abundance.

In this study, we analyse patterns and scales of beta diversity in a system of Mediterranean grasslands in an attempt to evaluate the degree to which competitive exclusions are driven by deterministic vs. stochastic processes. We define deterministic extinctions as extinctions caused by differences in competitive ability among species ('trait-based' extinctions *sensu* Suding *et al.* 2005) and stochastic extinctions as extinctions caused by differences in species abundance ('abundance-based' extinctions *sensu* Suding *et al.* 2005). We hypothesised that neighbourhood-scale competitive extinctions are deterministic; that such extinctions homogenise the community (i.e., reduce the magnitude of beta diversity); and that both mechanisms (neighbourhood-scale extinctions and reduction in beta diversity) are involved in determining community-level patterns of species diversity.

Our study combined two experiments: a grass removal experiment and a sowing experiment. The first experiment was based on previous observations showing that grasses are the dominant species in terms of biomass but forbs comprise most of the diversity in this system. We therefore expected that plots with the resident grass species would show lower values of beta diversity than plots from which the grasses are removed because of deterministic extinction of component species. This hypothesis was tested using the approach proposed by Chase *et al.* (2011). Sowing experiments were conducted to more directly test the role of deterministic vs. stochastic drivers of local extinctions. In these experiments, we sowed seeds representing the regional species pool in quadrates that were blocked to dispersal, monitored the loss of species for 3 years, and compared the resulting patterns of beta diversity with those predicted by null models assuming abundance-based extinctions. Values of beta diversity lower than those predicted by the null models were interpreted as evidence for deterministic extinctions.

METHODS

Study site

The study was conducted in Bet Guvrin National Park, Israel. The climate is dry-Mediterranean with an average annual precipitation of about 400 mm. There are two main types of habitats in this area: valleys, characterised by deep (> 50 cm) homogeneous alluvium soils, and slopes, characterised by shallow (< 50 cm) rendzina soil. The differences in soil depth result in considerable differences in annual productivity which is much higher in the valleys (Appendix S1 in Supporting Information). The area is subject to cattle grazing and the vegetation is dominated by annual grass species, with *Hordeum spontaneum* being the dominant species in the valleys and *Stipa capensis* dominating the slopes.

The grass removal experiment

In summer 2010, three pairs of 20 × 20 m plots were established in each type of habitat. All plots were fenced to prevent grazing by large herbivores. The two plots in each pair were randomly subdivided into two treatments: one plot (20 × 20 m) was assigned to removal of all grass species and the other was left as an experimental control. Grasses were removed using the herbicide FOCUS ULTRA (cycloxydim 10%), a selective post-emergence herbicide that does not affect broadleaf species (<http://www.chemicalize.org/structure/#!/mol=cycloxydim>). The removal treatment was applied at the end of the germination period during two successive years (2010 and 2011) and its effect on the vegetation was tested at the peak of the flowering period in the second year (April 2012). To reduce edge effects, only the 10 × 10 m area in the middle of each plot was used for data collection (Fig. 1).

Species presence-absence data were determined in 25 sampling quadrates of 20 × 20 cm (0.04 m²) within each plot. The size of the quadrates was chosen to represent the scale at which individual plants directly interact with each other (the 'competitive neighbourhood'). Field observations of shoot and root overlap indicated that neighbouring plants interact with each other at this scale. The sampling quadrates were aggregated in clusters of five units per cluster, with each cluster representing an area of 1 × 1 m² (Fig. 1). The five clusters were located at the four corners of the plot and in its center (Fig. 1). This sampling design allowed us to analyse diversity responses to grass removal at three scales – 0.04 m² (individual quadrates, hereafter the patch scale), 1 m² (the cluster scale), and 100 m² (the plot scale).

The sowing experiment

The sowing experiment was designed to test whether extinctions at the scale at which individuals interact with each other reduce beta diversity into lower levels than those predicted by abundance-based null models. A major advantage of this experiment over the grass removal experiment was the homogenisation of initial conditions among all quadrates, the blocking of the quadrates from dispersal (to prevent con-

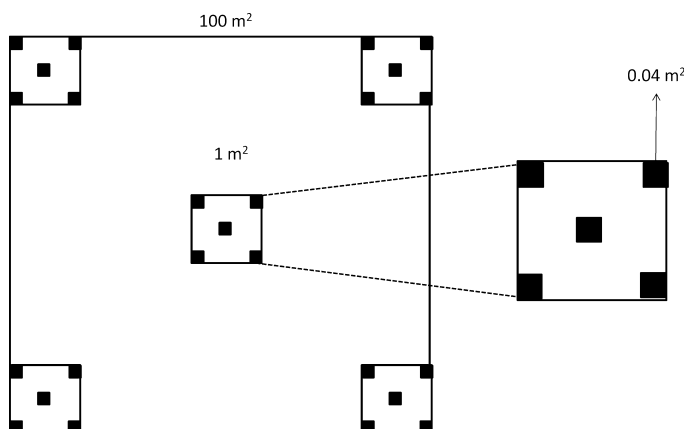


Figure 1 Schematic presentation (not to scale) of the sampling design. The basic experimental unit is a fenced area of 20×20 m treatment and all measurements were taken within the central area of 10×10 m (the 100 m^2 plot). Within each plot, five units of 1×1 m were marked (four units at the corners and one at the center of the plot), and each unit was sampled by five quadrates of 20×20 cm for presence-absence of all plant species.

founding effects by colonisation processes), and the integration of measurements of species abundance.

During summer 2010, we collected samples of seeds representing the regional species pool by scraping the top layer of soil (about 1 cm) in 50 sampling points representing the study area. All samples were mixed together and samples of 1250 mL taken from this mixture were sown in 25×25 cm quadrates that were disposed of their original seed banks by replacing their original soil, up to a depth of 10 cm, with soil excavated from layers deeper than 15 cm in nearby sites to minimise germination from the seed bank. This sowing procedure differs from experiments in which a known number of seeds are added to experimental quadrates (e.g., Clark *et al.* 2007), but allowed us to more effectively represent the overall seed bank of the study area. The experiment had 40 replicates in the valleys and 30 replicates on the slopes. All quadrates were surrounded by 50 micron nylon meshes during the dispersal period (May–October) to block immigration of seeds from the outer area. Meshes were cylinders 80 cm high and 60 cm in diameter. Plants germinating within the nets but outside the sowing quadrates were removed. Preliminary experiments confirmed that germination from the soil used to replace the original top soil in the quadrates was negligible and the meshes were highly effective in preventing immigration of seeds from outside the quadrates.

Individuals of all species emerged within the sowing quadrates were identified following germination in the first year (2011) in order to determine the initial richness of each quadrate. This survey was repeated during both the seedling stage and adult stage of three successive years (2011–2013) in order to determine the magnitude of species loss in each quadrate. In addition to these presence-absence surveys, we counted the number of individuals of all species in each quadrate at the seedling stage of 2011–2013, and at the adult stage of 2013 (hereafter final count). Due to logistic difficulties, seedling count in 2011 was limited to four quadrates in the valleys and six quadrates on the slopes.

Data analysis: grass removal experiment

Species richness

The effect of grass removal on species richness was determined at three hierarchical scales: individual quadrates (0.04 m^2), clusters of quadrates (1 m^2), and plots (100 m^2). Richness of clusters and plots was determined by aggregating the data from the relevant quadrates. At a first step we tested the effect of grass removal, habitat type, and their interaction on richness at the quadrate scale using a linear regression model. The results showed that residuals of quadrates within the same cluster were strongly and significantly correlated (Moran's $I = 0.228$, $P < 0.001$), those of quadrates located at different clusters within the same plot were weakly, though still significantly correlated (Moran's $I = 0.044$, $P < 0.001$), and those of quadrates located at different plots were uncorrelated. In order to account for the spatial dependency between quadrates within the same cluster, the quadrate scale (0.04 m^2) richness was averaged for each cluster and the analysis was repeated using simultaneous autoregressive regression (SAR) model (Dormann *et al.* 2007) with clusters as the basic unit of the analysis ($n = 60$, see Appendix S2 for details). For the cluster scale (1 m^2), a similar SAR model was used, but without averaging. For the plot scale (100 m^2), a linear regression without spatial correction was used because no spatial autocorrelation was detected at that scale (Appendix S2).

Beta-diversity

Beta diversity was calculated using the Beta Raup-Crick (β_{RC}) measure as proposed by Chase *et al.* (2011). This measure ranges from -1 to $+1$ with negative values indicating communities sharing more species than expected at random, positive values indicating communities sharing fewer species than expected at random, and zero indicating the null expectation (see Introduction). Values of β_{RC} were calculated for two spatial scales within each habitat-treatment combination: among quadrates within clusters, and among clusters within plots. Regression analyses were used to test the effect of grass removal on beta diversity at each scale within each habitat (see Appendix S2 for details).

Data analysis: sowing experiment

Species richness

For each quadrate we determined the magnitude of species loss as the difference between the number of species recorded in the initial survey (seedling stage, 2011) and last survey (adult stage, 2013). By averaging these values we were able to test for differences in extinction rates between the two habitats.

Beta-diversity

A 'null species composition' was determined for each quadrate by randomly sampling species from the list of species recorded in the first survey under two constraints: (1) the number of species sampled equalled the actual number of species observed in the relevant quadrate at the final count (adult stage in 2013); and (2) the probability of each species to be

sampled was proportional to its abundance during the seedling stage of 2012. We used data from 2012 and not 2011 to determine sampling probabilities because only a small subset of the quadrates was counted in 2011, resulting in a low statistical power. Null models based on relative abundance in 2011 provided similar though less significant results (Appendix S3).

The above randomisation was repeated for each quadrate, and the resulting lists of species were used to calculate a Jaccard index of dissimilarity (Legendre & Legendre 1998) between all possible pairs of quadrates within each habitat. These values were averaged to obtain a null value of beta diversity for each habitat, and the overall procedure was repeated 10,000 times to obtain a null distribution of beta diversity for each habitat. An observed value of beta diversity was calculated for each habitat based on pairwise comparisons of the actual lists of species recorded at the final count. The proportion of null values of beta diversity that were equal to or lower than the observed value was used as a measure of the probability that extinctions at the quadrate level were caused by purely stochastic (abundance-based) processes. Since values of species richness in the null expectations were fixed to the observed values, no correction was needed to be applied to the data. In order to compare the reduction in beta diversity between the two habitats we also calculated a measure of effect size as $\beta_{ES} = \text{Log}(\beta_N/\beta_O)$ where β_N = mean beta diversity predicted by the null model and β_O = observed beta diversity.

In further analyses we repeated the procedure described above using a quantitative measure of dissimilarity (Bray & Curtis dissimilarity index, Legendre & Legendre 1998). The randomisation approach was similar to that of the original analysis – random assignment of species to each quadrate based on initial species abundance until the number of species reached the observed number. However, in contrast to the analysis of the Jaccard index, here we also recorded the number of times each species was sampled when assigning the species to the relevant quadrate, and used this information to construct a null distribution of relative species abundance. These distributions were used to determine null values of the Bray & Curtis index of dissimilarity.

RESULTS

The grass-removal experiment

Species richness

Forb richness was significantly influenced by both grass removal and habitat type (Table 1). In the valleys, grass removal significantly increased forb richness at all scales (Fig. 2). However, the magnitude of this effect decreased with increasing scale (0.04 m²: 240%; 1 m²: 186%, 100 m²: 108%). On the slopes the effect was much weaker and only at the smaller scales it was statistically significant (Fig. 2). The interaction between the effects of grass removal and habitat type was statistically significant at the two smaller scales (Table 1). Corresponding analyses testing the effects of grass removal and habitat type on total richness revealed qualitatively similar results (Fig. 2, Table 1). These findings indicate that competitive interactions are important in limiting the number of forb species in the study system, that this limitation causes a drastic reduction in overall species richness, and that the magnitude of this reduction is both habitat-dependent and scale-dependent.

Beta diversity

In the valleys, grass removal had a significant negative effect on beta diversity of forb species at both spatial scales (Fig. 3). When all species were included in the analysis, the effect was highly significant at the neighbourhood scale (0.04 m²) but insignificant at the larger scale (1 m²). On the slopes the effect was insignificant at all cases (Fig. 3). Importantly, the effect of grass removal on beta diversity in the valleys was opposite to our expectations, indicating that competitive interactions increased, rather than decreased beta diversity in this habitat.

The sowing experiment

Species richness

The sowing quadrates showed extremely high values of species richness following germination in the first year of the experiment (Mean \pm 1 SE = 51.0 \pm 0.8 and 49.2 \pm 1.4 species per quadrate in the valley and slope habitats, respectively, Fig. 4). However, during the two subsequent years a drastic and highly

Table 1 Effect of grass removal, habitat type and their interaction on forb richness and total richness at three spatial scales

Group	Parameter	0.04 m ²		1 m ²		100 m ²	
		Z	P	Z	P	t ₈	P
Forbs	Grass-removal	10.18	< 0.001	9.23	< 0.001	3.72	0.006
	Habitat	6.57	< 0.001	8.73	< 0.001	5.53	0.007
	Grass-removal \times Habitat	-3.69	< 0.001	-3.20	0.013	-1.73	0.120
	Lambda*	LR = 4.83	0.028	LR = 1.68	0.194		
Total	Grass-removal	8.32	< 0.001	7.74	< 0.001	3.09	0.015
	Habitat	7.92	< 0.001	9.79	< 0.001	5.59	< 0.001
	Grass-removal \times Habitat	-4.76	< 0.001	-3.85	0.013	-1.82	0.106
	Lambda*	LR = 3.76	0.052	LR = 1.15	0.282		

*The simultaneous autoregressive error coefficient Lambda is reported for SAR models with significance level based on a Likelihood Ratio (LR) test for spatial autocorrelation.

The two smaller scales (0.04 and 1 m²) were analysed using simultaneous autoregressive regression (SAR) model and the largest Scale (100 m²) was analysed using linear regression model (see Appendix S2 for statistical details). Significant results are shown in bold.

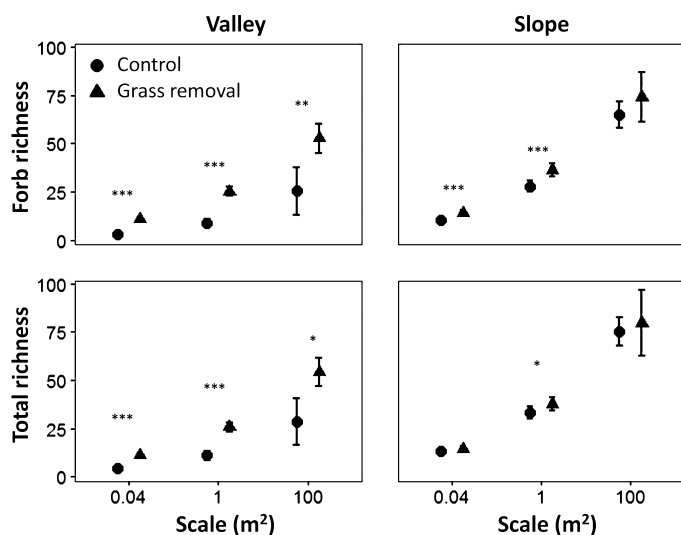


Figure 2 Effect of grass removal on forb richness and total richness in two types of habitats (valleys and slopes) and at three spatial scales (0.04 m², 1 m², and 100 m²). Bars represent 95% confidence levels, significance levels are marked by asterisk (* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$). A separate analysis was performed for each scale in each habitat.

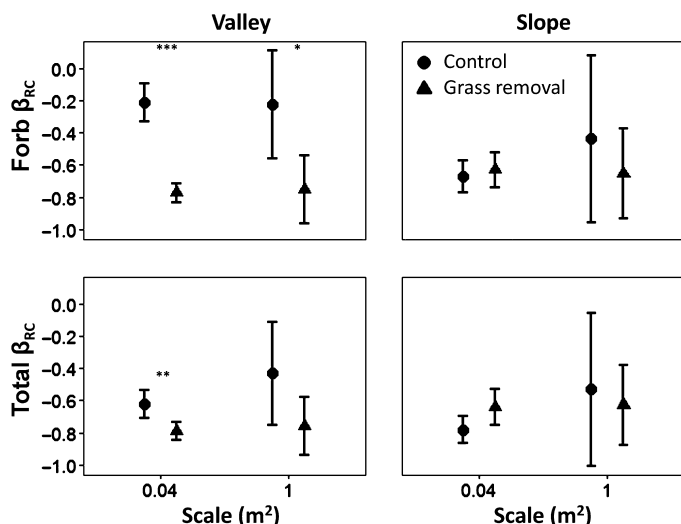


Figure 3 Effect of grass removal on beta-diversity (β_{RC}) of forbs and all species in two types of habitats (valleys and slopes) and at two spatial scales (0.04 m² – among the five quadrates within a cluster, 1 m² – among the five clusters within a plot). Bars represent 95% confidence levels, significance levels are marked by asterisks (* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$). A separate analysis was performed for each scale in each habitat.

significant ($P < 0.0001$) loss of species was documented in both habitats (Fig. 4). Final richness was 3.7 ± 0.4 species per quadrate in the valleys (a reduction of 92.7%) and 11.1 ± 1.1 species per quadrate on the slopes (a reduction of 77.4%). The difference in the magnitude of species loss between the two habitats was highly significant ($t = 4.87$, d.f. = 44.9, $P < 0.0001$, t -value corrected for unequal variance).

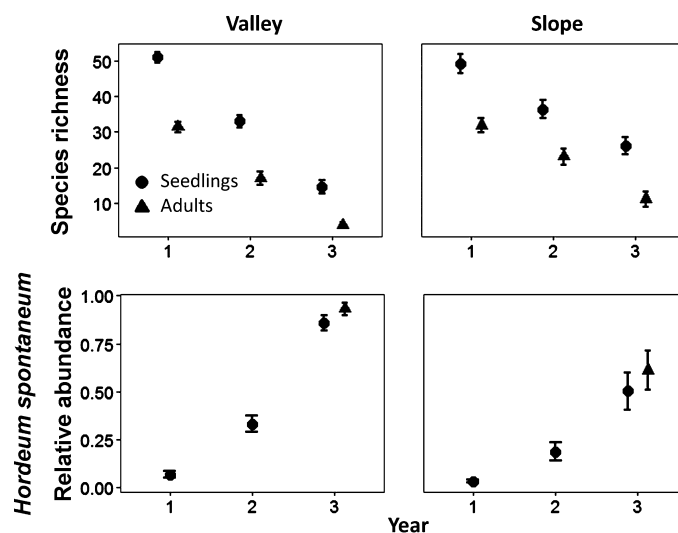


Figure 4 Analysis of the sowing experiment. The upper panels show the average (\pm CIs of 95%) number of species per quadrate in the valleys (left) and on the slopes (right) during the 3 years of the study. For each year, we determined richness at the seedling stage and at the adult (flowering) stage. The bottom panels show the corresponding changes in the relative abundance of *Hordeum spontaneum* during the 3 years of the study.

Abundance of *Hordeum spontaneum*

A striking pattern observed in the valley habitat was a convergence of all sowing quadrates into assemblages dominated by the annual grass *Hordeum spontaneum* (Fig. 4). This species comprised only a small fraction of the individuals in the first count (mean \pm 1 SE relative abundance = 0.068 ± 0.01), but became the most dominant species in the last count (mean \pm 1 SE relative abundance = 0.93 ± 0.02). This increase was associated with a significant increase in absolute abundance (from 19.5 ± 2.2 to 168.14 ± 9.4 individuals per quadrate). We do not have comparable abundance data for the grass removal experiment, but in terms of frequency of occurrence, *Hordeum spontaneum* was the most dominant species in the valleys (present in 100% of the 75 quadrates) and comprised most of the biomass in this habitat. Slope quadrates showed a similar though weaker convergence (Fig. 4).

Beta diversity

In both habitats, values of beta diversity measured at the end of the experiment were significantly lower than those predicted by the null models ($P < 0.0001$, Fig. 5). This result was consistent for both the compositional based (Jaccard) and abundance-based (Bray & Curtis) measures of dissimilarity, indicating that changes in both species composition and relative species abundance had a significant deterministic component.

While all measures of beta diversity were significantly lower than the null expectations, quadrates located in the valleys showed larger deviations from the null expectation (i.e., a higher effect size) than quadrates located on the slopes (Fig. 5). Thus, although the two habitats started from similar species assemblages, quadrates located in the valleys showed higher rates of extinction and a stronger evidence for deter-

ministic effects, than quadrates located on the slopes. It can also be seen that for both habitats, effect sizes based on the Bray & Curtis index of dissimilarity were larger than those based on the Jaccard index (Fig. 5). These results indicate that patterns of species abundance were more sensitive to deterministic effects than patterns of species composition.

DISCUSSION

Our study provides the first experimental evidence that inter-specific competition affects species diversity by influencing both the number of species (species richness) and the magnitude of spatial turnover in species composition (beta diversity). The results further indicate that the latter effect might be negative or positive, and that both effects might be influenced by habitat conditions and the scale at which the patterns are examined. Below, we elaborate on each of these effects and the manner by which the combination of both effects determines the overall number of species at the level of the community.

Effect of competition on species richness

The results of the grass removal experiment confirm the hypothesis that competitive interactions reduce the number of species in the study communities. However, the magnitude of this effect was habitat-dependent, with valley communities showing higher rates of competitive exclusions than slope communities (Fig. 2). The sowing experiment revealed similar patterns: quadrates located in the valleys lost a significantly higher portion of their initial species richness than quadrates located on the slopes (Fig. 4). Moreover, in the valleys, species loss was associated with a ten-fold increase in both the absolute and relative abundance of a single grass species

(*Hordeum spontaneum*), which was the dominant species in the control quadrates of the grass removal experiment (Fig. 4). In the final count of the sowing experiment, this species accounted for 94% of the total number of individuals survived in quadrates of the valley habitat (6735 out of 7163 individuals). We therefore conclude that, at least in the valleys, species loss was driven predominantly by competitive exclusions, with *Hordeum spontaneum* being the most successful competitor.

We relate the differences in the magnitude of competitive exclusions between the two habitats to underlying differences in habitat productivity. Measurements of above-ground biomass in the study area showed that the valleys are much more productive than the slopes (Appendix S1). Such differences are a general characteristic of Mediterranean grasslands, and are attributed to differences in soil depth between the two habitats (Zeligman & van Keulen 1989; Osem *et al.* 2002). Although the manner by which habitat productivity affects the intensity and mode of competition in grassland communities is subject to a long-standing debate (Kadmon & Shmida 1990; Rajaniemi 2002, 2003), it is widely accepted that increasing productivity increases the intensity of competition for light, that light competition is strongly asymmetric, and that such asymmetric competition accelerates competitive exclusions (Goldberg & Miller 1990; Huston & DeAngelis 1994; Rajaniemi 2003).

Within each habitat, the rate of competitive exclusion was highest at the patch scale and lowest at the plot scale. We attribute this difference to two factors. First, increasing spatial scale (in our experiment – aggregating quadrates into larger units) increases the number of individuals per species, thereby increasing the likelihood that at least some individuals would escape from competition with the dominant species. Second, increasing scale facilitates opportunities for spatial mechanisms of coexistence such as niche partitioning (Davies *et al.* 2005), competition-colonisation trade-off (Tilman 1994), source-sink dynamics (Kadmon & Tielborger 1999), and mass effect (Shmida & Wilson 1985), which may partially compensate for competitive exclusions (Amarasekare 2003).

Effect of competition on beta diversity

The effect of competition on beta diversity was also habitat-dependent. In the valleys, where competitive interactions were more intense, the negative effect of competition on forb richness was associated with a significant increase in beta diversity (Fig. 3). This increase was documented for both the quadrate and the cluster scales, and was observed also at the level of the total community (Fig. 3). On the slopes, where the effect of competition on forb richness was much weaker, beta diversity was not significantly influenced by competition (Fig. 3). The finding that the presence of grasses reduced richness but increased beta diversity in the valleys suggests that competitive exclusions were stochastic in this habitat (different species were excluded in different patches of the vegetation).

In contrast to these results, values of beta diversity obtained for the sowing experiment were all significantly lower than the null expectations, indicating that extinctions within the sowing quadrates had a significant deterministic component (Fig. 5).

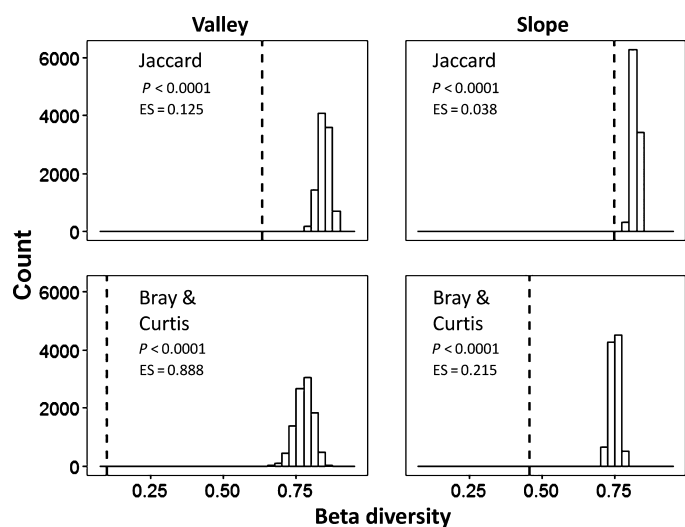


Figure 5 Results of null model analysis of beta diversity in quadrates of the sowing experiment. For each type of habitat, beta diversity was determined using two indices, a presence-absence index (Jaccard index of dissimilarity) and an abundance-based index (Bray & Curtis measure of dissimilarity). Histograms represent the distribution of the relevant index under the null hypothesis and vertical dashed lines indicate the observed values. ES = Effect Size calculated as $\text{Log}(\beta_N/\beta_O)$ where β_N = mean beta diversity predicted by the null model and β_O = observed beta diversity.

This result was consistent for both types of habitats and both measures of dissimilarity, but the magnitude of the deviation from the null expectation (effect size) was larger in the valleys, indicating that deterministic effects on both species abundance and species composition were stronger in this habitat.

Thus, the patterns of beta diversity obtained in the grass removal experiment suggest that neighbourhood-scale extinctions are stochastic, while the patterns obtained in the sowing experiment reveal a significant deterministic component. How can these differences be explained? We propose that these apparently conflicting patterns can be reconciled by a coupling between three elements: (1) a low level of beta diversity at the absence of competitive exclusions, (2) a strong asymmetry in competitive ability of the study species where one species is a dominant competitor and all other species have a much lower competitive ability, and (3) a larger magnitude of competitive exclusions in the sowing experiment than in the grass removal experiment. If initial levels of beta diversity are low and all species except the strongest competitor are relatively equivalent in their competitive ability, a moderate level of competitive exclusion should increase beta diversity since different species go extinct at different patches, resulting in large differences in species composition among patches. This scenario fits the results of the grass removal experiment. However, if most species are competitively excluded from the community, the remaining assemblages should show a low value of beta diversity since the dominant species is present in all patches and the overall number of species per patch is very small. This scenario fits the pattern obtained for the sowing experiment.

The first element (a relatively low level of beta diversity before competitive exclusions take place) is demonstrated by the grass removal quadrates of the valley habitat (Fig. 3). Values of the Raup-Crick index of dissimilarity in these quadrates were much smaller than zero, indicating that similarity in species composition at the absence of grasses was much higher than that expected by chance. The second element (a strong dominance by a single species) is reflected by the strong dominance of *Hordeum spontaneum* in terms of both biomass and frequency of occurrence in the valley habitat, and its dominance in terms of relative abundance in the final count of the sowing quadrates. The third element (higher rates of competitive exclusion in the sowing experiment) is reflected by the fact that quadrates of the sowing experiment suffered a higher degree of competitive exclusion than those of the grass removal experiment. This pattern was particularly strong in the valleys (92.7% vs. 56%, respectively). We relate the latter difference to the fact that the grass removal experiment has started from communities that have already been influenced by competition, while the sowing experiment has started from artificial communities representing the overall species pool of the study area. The fact that richness in control quadrates of the grass removal experiment was much smaller than initial richness of the sowing quadrates supports this conclusion.

Integrating the effect of competition on species richness and beta diversity

Our results demonstrate that inter-specific competition affects the number of species in the study communities by two dis-

tinct mechanisms: direct competitive exclusion at the scale of small vegetation patches (the competitive neighbourhood); and reduction or enhancement of differences in species composition among local patches. The use of the Raup-Crick index of dissimilarity as a measure of beta diversity verifies that the latter effect is not a statistical artifact of the former effect, and that the two mechanisms are statistically independent.

An important conclusion emerging from this finding is that a given level of competitive exclusion at the scale of the competitive neighbourhood may lead to very different impacts on species richness at the level of the community, depending on whether extinction processes are deterministic or stochastic. If neighbourhood-scale extinctions are deterministic, species loss at the community level should be larger than that observed at the patch scale since both alpha (patch-scale) diversity and beta diversity respond in the same direction, thus intensifying each other. However, if such extinctions are stochastic, species loss at the community level should be smaller than that observed at the patch scale, since the positive effect on beta diversity partially compensates for the negative effect on alpha diversity. Clearly, any prediction of the effect of competitive exclusion on species diversity at the community level must take into account both responses.

Our finding that competitive interactions affect beta diversity has important implications for the interpretation of removal experiments. Such experiments have been used repeatedly to evaluate responses of species richness to competition (Smith *et al.* 1999; Suding *et al.* 2006; Munson & Lauenroth 2009; McLaren & Turkington 2011), but have always focused on a single spatial scale. If competition affects beta diversity, such responses are scale-dependent, and estimates obtained for one scale cannot be extrapolated to other scales. According to our results, even small differences in the scale at which such responses are examined may result in large differences in estimates of competitive exclusion.

A note about null models

In this study we used a null model approach to evaluate the role of deterministic vs. stochastic drivers of community assembly. Null models have been used extensively in research of community assembly rules (Gotelli & Graves 1996; Gotelli & McCabe 2002; Gotzenberger *et al.* 2012; Munkemüller *et al.* 2012), but most of these studies have focused on natural species assemblages (though see Sanders *et al.* 2007; Englund *et al.* 2009; Larsen & Ormerod 2014). A major limitation of such observational studies is that different mechanisms are capable of generating similar patterns of species assemblages. For example, significant negative association between species can be generated by either competitive exclusion or environmental filtering (Gotzenberger *et al.* 2012). Significant spatial association among species can be generated by patchiness in habitat conditions or limited dispersal, even if the underlying processes are purely stochastic (Bell 2005). Thus, a significant deviation of an observed pattern from the prediction of a random null model does not necessarily imply a particular alternative mechanism. Actually, many of the indices that have traditionally been used to discriminate between deterministic

and random drivers of community assembly may show significant deviations from randomness under purely stochastic demography (Ulrich 2004). Moreover, analyses of simulated data demonstrate that different null models may provide contradicting results when applied to the same data (e.g., Gotelli & Ulrich 2012). Spatial autocorrelation poses further complexity to the interpretation of null models (Gotelli & Ulrich 2012). These overall findings indicate that the interpretation of null model analyses is far from being trivial.

In this study we attempted to minimise such problems by integrating null models in conjunction with manipulation experiments, performing separate analyses at different spatial scales, and integrating the analysis of spatial patterns with an independent analysis of temporal patterns. Yet, even such application should be interpreted with caution due to the complexity of the mechanisms affecting community dynamics and possible interactions between different deterministic and stochastic processes. Benchmark tests (*sensu* Gotelli & Ulrich 2012) provide an efficient tool for better understanding the statistical properties and limitations of null models in general and the null models employed in this study in particular but so far, such tests have not been applied for the kind of null models used in this study. Until such tests are performed, our conclusions should be taken with some caution.

SUMMARY

One of the most fundamental notions in ecology is that inter-specific competition reduces the number of species in local communities. Here, we highlight one aspect of competition that has been overlooked in previous studies – the effect of competitive interactions on beta diversity. Our results indicate that this effect might be important in determining community-level responses to competition, and that analysis of this effect may help to distinguish between deterministic and stochastic drivers of species diversity, a major challenge in community ecology (Chase & Myers 2011; Caruso *et al.* 2012; Shipley *et al.* 2012). We conclude that ecologists should pay more attention to competitive effects on beta diversity and present simple experimental and analytical methodologies by which such effects can be quantified and interpreted. Future studies should extend these methods and develop new methods for empirical tests of more complex aspects of competitive interactions, such as the relative importance of environmental vs. demographic stochasticity (Melbourne & Hastings 2008), the role of chaotic vs. ‘true’ stochastic drivers of extinctions (Ellner & Turchin 1995), and the consequences of hierarchical vs. cyclic competitive relationships and competitive intransitivity (Durrett & Levin 1998; Ulrich *et al.* 2014).

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AUTHORSHIP

HS, RR, ZH and RK designed the study; HS, NDM and RR conducted the various parts of the field work; MM designed and supervised the statistical analysis; HS and RR analysed the data; and all authors collaborated in discussing the results and writing the manuscript.

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