



Co-existence in a species-rich grassland: competition, facilitation and niche structure over a soil depth gradient

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Keywords

Community structure; Environmental gradient; Hydrological niche; Niche breadth; Niche overlap; Null model; Resource enrichment model; Semi-arid grassland; Species richness; Stress-gradient hypothesis

Abbreviations

SGH = stress-gradient hypothesis; CA = correspondence analysis; *B* = Levin's niche breadth index; *C* = crowding; *D* = niche position; *L* = Hurlbert's niche overlap index.

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Abstract

Question: Niche differentiation may promote species co-existence because it precludes competitive exclusion. However, in stressful environments, facilitation may predominate, and large niche overlaps may result from niche widening and positive spatial associations. We analysed the niche structure of a species-rich system over a soil depth gradient (a niche axis positively correlated with water availability) and tested for various patterns expected from competition or facilitation.

Location: Semi-arid grassland, Oaxaca, Mexico.

Methods: We recorded species abundance and soil depth in 1200 0.1 × 0.1 m quadrats from four sites. Community structure was described through correspondence analysis and correlated with soil depth. We measured niche breadth (Levine's index), position (mean depth) and overlap (Hurlbert's index). We used a null model to estimate the expected overlap if interactions play no role in determining community structure. We tested whether overlap changed along the depth gradient. We also analysed if niches become narrow with higher competition.

Results: Data supported three predictions derived from competition: most species' niches were relatively narrow and differed in their position along the gradient, a pattern reflected in a changing community structure; realized niches became narrower where competition was stronger; and niche overlap was smaller than expected by chance. Facilitation had no support: large niche overlaps expected from stress amelioration were as frequent as predicted by chance. Overlap increased in the most stressful (shallow) soils, as expected if facilitation predominates there, but also in the deepest ones where evidence for competition was strong, suggesting an artifact at the extremes of the gradient.

Conclusions: In this grassland, competition seems to restrict species distribution, abating richness in the deepest soils and relegating poor competitors (succulent and poikilohydric species) to the shallow soils. There, drought tolerance rather than facilitation determined community composition and richness. Our results support the idea that hydrological niches play an important role in maintaining plant diversity because (1) differentiation in hydrological requirements (small niche overlaps over the water-use axis) reduces competition, and (2) spatial heterogeneity and stress create competition-free patches. Our results also support the hypothesis that facilitation is rare when stress is caused by resource (in this case, water) scarcity.

Introduction

The debate on whether co-existence in species-rich plant communities is determined by the niche has gained renewed impetus over the last decade (Silvertown 2004; Leibold & McPeck 2006; Adler et al. 2007, 2010; Ricklefs 2008; Levine & HilleRisLambers 2009; HilleRisLambers et al. 2012). Plants depend on the same set of resources, and thus are expected to have similar niches (*sensu* Hutchinson 1957) and to compete intensely with each other (Silvertown 2004). Because competition is frequently asymmetrical (Freckleton & Watkinson 2001), a few species should out-compete the others, excluding them from the community (Giller 1984; Wedin & Tilman 1993; Keddy 2001). According to niche theory, differentiation over some niche axes is required for co-existence to take place (Hutchinson 1957; Pianka 1981; Giller 1984; Leibold 1995; McKane et al. 2002). The emergence of alternative models that predict high species richness even if such differentiation is lacking (Bell 2000; Hubbell 2001) makes it critical to advance our understanding on whether niche differentiation plays a role in determining the diversity of plant communities.

The recent evidence that positive plant–plant interactions also shape communities (Bruno et al. 2003; Brooker et al. 2008; Martorell & Freckleton 2014) has important implications on niche theory. Facilitation may widen niches (Higashi 1993; Bruno et al. 2003), thus increasing overlap. The positive spatial association between species arising from facilitation would lead them to share the same portions of at least the niche axis over which facilitation and associations occur. This does not necessarily mean that there are large overlaps in other niche dimensions, as even small overlaps may promote positive interactions (Kraft et al. 2008; Butterfield & Callaway 2013). However, The stress-gradient hypothesis (SGH), which states that positive interactions are more important in stressful environments (Callaway & Walker 1997; Brooker & Callaghan 1998; Brooker et al. 2008), implies that larger niche overlap is to be expected in harsh than in benign ecosystems. This may not be the case, however, if the stressor is the lack of a resource for which plants may compete (Maestre et al. 2009).

The exhaustive description of a species' niche is daunting due to its high dimensionality, but recognizing one or a few of the main axes along which differentiation takes place in a community may provide valuable insights (Tilman 1982; Silvertown 2004). Soil heterogeneity may promote plant species co-existence through niche differentiation (Wedin & Tilman 1993; Reynolds et al. 1997; Casper & Cahill 1998; Silvertown et al. 1999; Fransen et al. 2001; Hutchings et al. 2003; Wardle & Peltzer 2003;

Fargione & Tilman 2005; Wijesinghe et al. 2005). Heterogeneity also affects the development of soil biota that determine plant diversity (van Auken et al. 1994; Fitter et al. 2000; Fargione & Tilman 2005).

Soil depth is a potentially important niche axis promoting plant co-existence in rocky environments: individual species and even whole communities are restricted to specific soil depths (Oosting & Anderson 1937; Bliss & Cox 1964; Baskin & Baskin 1985; Houle & Phillips 1989; Fuhlendorf & Smeins 1998; Porembski 2007; Khumalo et al. 2008). Such zonation is the result of interspecific differences in hydrological responses and interactions. There is a growing body of evidence that niche segregation depends on hydrology (Silvertown et al. 2014). Shallow soils are considered to be stressful environments because of their low water-holding capability and low nutrient availability, so only drought-resistant species seem able to colonize them (Oosting & Anderson 1937; Sharitz & McCormick 1973; Lugo & McCormick 1981; Houle & Phillips 1989; Belcher et al. 1995). Competitive interactions also change over the gradient, precluding poor competitors from colonizing the deeper soils (Sharitz & McCormick 1973; Baskin & Baskin 1985; Houle & Phillips 1989; Baer et al. 2003). From these findings and the SGH, it follows that facilitation would be expected to dominate in the shallow, more stressful soils, as has been reported in some rock outcrop communities (Houle & Phillips 1989; Belcher et al. 1995). Nevertheless, there is evidence that the opposite occurs in some grasslands: competition may be more intense in thin soils because there is no space for the roots of different species to segregate, so resources are extracted from the same depths (Villarreal-Barajas & Martorell 2009; Dornbush & Wilsey 2010).

In this study we analyze the niche structure of a highly diverse semi-arid grassland over a soil depth gradient to test the patterns expected from negative and positive interactions. Because of the large number of species involved, it was almost impossible to conduct manipulative experiments that produce unequivocal evidence of causal relationships. Thus, to strengthen the evidence on our hypotheses, we tested several predictions derived from them. According to traditional niche theory, which is based on competition, co-existence should be possible if niche overlap over the soil depth gradient is small. From this premise (hypothesis A), three predictions may be derived: (A1) species should be segregated in space due to competition, so community structure (composition and species abundance) should change with soil depth; (A2) realized niches may become narrower if competition is strong because species may be excluded from certain portions of the environmental gradient, as suggested by Silvertown (2004). This is a potential mechanism for the

species segregation tested in A1, and also reduces niche overlap. In species-rich communities such as ours, in which species must be tightly packed against each other over the environmental gradients, narrow niches are required to reduce niche overlap. (A3) The frequency of species pairs with small niche overlap in the community should be larger than expected from a null model (Gotelli & Graves 1996; Silvertown 2004).

In contrast, if facilitation plays an important role (hypothesis B), it could be predicted that: (B1) the frequency of species pairs with large niche overlap in the community should be larger than expected by chance. This is to be expected because a facilitated species should grow in the same sites as its nurse plant, thus increasing overlap over the soil depth axis. Note that A3 and B1 are not mutually exclusive, as both the frequencies of small and large overlaps can be higher than expected by chance if intermediate overlaps are infrequent. (B2) Niche overlap would be higher in shallow than in deep soils because, according to the SGH, positive interactions would occur in the more stressful environments.

Methods

This study was conducted in Concepción Buenavista, Oaxaca, south Mexico. Very thin (usually 0–50 cm) soils occur over a 20 km² continuous pan of acidic volcanic tuff. The plant community is a very rich (>100 species) shortgrass prairie (plant formation VB3c in Mueller-Dombois & Ellenberg (1974) system) dominated by Asteraceae, Poaceae, Euphorbiaceae, Cactaceae and Convolvulaceae. Four study sites (Agua Blanca, El Cacalote, La Biznaga and Nacusenye) where livestock had been excluded for 4 yr were chosen. At El Cacalote, the parent material differed, consisting of silicified tuff, and the soil and plant community were clearly different. The altitudes of all sites varied between 2120 and 2280 m a.s.l. The annual precipitation is 530.3 mm, occurring mostly between May and September, and the mean annual temperature is 16 °C.

At the study site, water availability is known to change with soil depth. In shallow soils the water potential is lower on average than in deeper substrates: during the rainy season, the hydric potential of a 4-cm deep soil is twice that recorded in 30-cm deep soils. Moreover, humidity is lost more rapidly after a rainfall in shallow soils, which become completely dry days before their deeper counterparts (Villarreal-Barajas & Martorell 2009; Martínez-López 2014; Martorell & Martínez-López 2014).

At the studied grassland, 0.1 × 0.1 m quadrats may harbour many dozens of individuals and up to 22 species. Because of the small size of plants, this is likely to be the scale on which interactions between individuals may occur. Moreover, soil depth changes rapidly at this scale, so

larger quadrats would encompass undesired environmental variability if we are to relate depth to species abundance. Thus, we used such small quadrats as the basic unit for our study. At each site, 15 2.0 × 0.1 m non-contiguous transects were placed so as to cover the widest soil depth gradient possible. In each of the 300 0.1 × 0.1 m quadrats in each site we recorded the number of individuals of every plant species. Soil depth was measured at three points in each quadrat by driving a metallic rod into the soil until the parent material was reached. The three measurements were then averaged.

Soil properties other than depth may change over the gradient, making it difficult to impute changes in vegetation to soil depth only. To assess the effects of these soil variables, we randomly chose four quadrats in each transect. In each of these quadrats, we recorded the slope and took a soil sample. We measured the pH using indicator paper with a resolution of 1 pH unit, and estimated the organic matter and carbonate content by adding concentrated H₂O₂ and 0.1 N HCl, respectively, and recording bubbling intensity by means of FitzPatrick's (1980) scale. Finally, 10 ml of soil were vigorously mixed with 25 ml of 50 g·L⁻¹ sodium hexametaphosphate for 1 min. Sedimentation was then measured after 3 min 44 s, 1 h and 6 h 14 min to determine the sand, loam and clay content, respectively (Day 1965).

Prediction A1: community structure

Changes in species richness over the depth gradient were modelled through generalized additive models (GAMs) with a Poisson error using the mgcv package in R (R Foundation for Statistical Computing, Vienna, AT). GAMs are regression models in which no specific underlying function is assumed. Instead, the procedure looks for a function that fits the data closely, but keeps data as simple as possible. We described the community structure for each site separately using correspondence analysis (CA) of species abundance per quadrat in Statistica 6.0 (Statsoft, Tulsa, OK, US). Species occurring in less than ten quadrats were discarded (ter Braak 1995). The correlation coefficients between the quadrat scores and soil depth were calculated. The same was done for the remaining soil attributes (slope, carbonate and organic matter content, pH and fractions of sand, loam and clay). To assess the relative effect of these variables on community structure, and to check if they were correlated with soil depth, a species–environment biplot was produced (ter Braak 1995).

Prediction A2: Niche narrowing

Levins' (1968) niche breadth index (B_i) modified to consider resource abundance (Hurlbert 1978) was estimated

for each species. The calculation of this index requires discrete data, so we categorized the soil depth gradient into 5-cm intervals over the range of recorded depths (0–70 cm) and applied the following formula:

$$B_i = \frac{\left(\sum_k \frac{y_{ik}}{Y_k}\right)^2}{K \sum_k \left(\frac{y_{ik}}{Y_k}\right)^2}$$

where y_{ik} is the total number of individuals of species i in the k th soil depth category, Y_k is the total number of quadrats in the k th depth category, and K is the number of depth categories. This index is bounded between 0 and 1, and its value increases with niche breadth. A species having a B value of 1 has the widest possible niche breadth, occurring indistinctly over the whole soil depth gradient.

To assess if the realized niche becomes narrow in the presence of putative competitors, we need a measure of the strength of competition experienced by each species in each site. Any focal species would be expected to experience more competition as the number of individuals of other species in the community increases, especially if these individuals occur in close proximity to the focal species in the soil depth gradient. Thus, we first estimated the niche position (\bar{d}_i) over the gradient, as the mean soil depth in which each species occurs as

$$\bar{d}_i = \frac{\sum_j x_{ij} d_j}{X_i},$$

where X_i is the total number of individuals of species i recorded over all the transects, and x_{ij} is the number of individuals of species i occurring in the j th quadrat with soil depth d_j . With this figure, we estimated for each species the degree of crowding (C_i) it experiences as

$$C_i = \sum_{h \neq i} \frac{1}{\bar{d}_i - \bar{d}_h} X_h$$

C_i measures the density of every other species h in the community weighed by their niche proximity (the reciprocal of the difference in niche positions of species h and the focal species i). To test whether a negative relationship between crowding and niche breadth exists, we estimated B_i and C_i for each site and estimated the correlation coefficient between both variables separately for each species. For this analysis, we used only those species with 20 or more occurrences in at least three sites ($n = 15$ species). A t -test was then used to assess whether, on average, those coefficients were negative (Sokal & Rohlf 1995).

Predictions A3 and B1: Niche overlap

We used Hurlbert's (1978) niche overlap index (L) for every possible pair of species h, i

$$L_{h,i} = \frac{Y}{X_h X_i} \sum_k \frac{y_{hk} y_{ik}}{Y_k}$$

where Y is the total number of quadrats sampled. For discrete resources, the value $L_{h,i} = 1$ is expected if species are randomly and independently distributed in the environment. If $L_{h,i} < 1$ then there is less overlap than expected by chance (0 means no overlap at all), and if $L_{h,i} > 1$ then species h and i tend to occupy similar portions of the soil depth gradient (Hurlbert 1978). This index was estimated for each species pair excluding those species with less than ten individuals. Finally, we obtained the observed mean overlap \bar{L}_{obs} for each site separately.

Niche overlap is almost universally analysed assuming that resources are discrete, unordered and selected by species regardless of the use of other resources (Gotelli & Graves 1996). With resources that are not discrete in nature the assumptions do not hold: if a species' density is high in, e.g. 10-cm deep soils, it will likely also be so in soils with depths of 9.5 and 10.5 cm. Because Hurlbert's assumptions of discreteness and independence are violated, the expected niche overlap under a random scenario is not necessarily 1. The true value and its confidence interval were estimated by means of a null model. The problem posed by continuous resources can be solved using probability density functions to model the niche, but function selection may have an important effect on the estimation of niche overlap (Roughgarden 1974). We fitted normal, γ , β and log-normal functions to the distribution of individuals over the soil depth gradient for every species with >50 individuals (a large n is required to discern confidently which function produces the best fit). The β distribution was found to describe the data most accurately: the likelihood of that model was largest and, on average, the correlation between the observed and expected density of plants was 0.87. Thus, we decided to model the niche over the depth gradient using a β distribution.

To obtain the expected overlap, 'null' communities need to be randomly assembled. To do so, we used a method similar those of Case (1983) and Schoener (1988), who selected species from a pool of real taxa prone to invade a community. We lack relevant information on the hydrological/soil depth requirements of potential invaders and their identity, so we cannot use the exact same approach. Thus, we selected species from an artificial species pool through random simulation of niche parameters. Species selection was random and independent of previous draws

from the pool, thus resulting in hypothetical communities that are not structured by species interactions (Gotelli & Graves 1996).

Therefore, for each site, a null model was built through the following steps: (1) we obtained the α and β parameters of the β distribution for all species in the community with at least ten observed individuals. This allowed us to obtain the biologically feasible values for the parameters of the niche; (2) we generated the niches for new hypothetical species by randomly producing their α and β parameters. To do so, we first performed a regression between the α - and β -values of the observed species in log-log scale. There was a significant correlation between these two parameters ($R^2 > 0.35$, $P < 0.05$ at any site). Second, we observed that the logs of the observed α were approximately γ -distributed across species. Thus, we generated α -values for each artificial species from that distribution through Monte Carlo simulation. Third, from the regression of β on α obtained before, we estimated the expected β corresponding to each simulated α . A log-normal distributed error ($\mu = 0$, and σ = residual mean squares of the regression) was then added to that value to obtain the β for the new hypothetical species. The number of niches so produced was equal to the number of species with at least ten individuals in the site (i.e. the same number of species for which the observed niche overlaps were calculated). (3) We sampled the null community obtained in step 2. To do so, we performed a Monte Carlo simulation on the niche (β distribution) of each hypothetical species; each simulated datum corresponds to the soil depth in which a hypothetical individual would be found to grow. The number of individuals simulated for each artificial species was set to that observed in our real data set, so the relative abundances of the hypothetical species were kept constant and equal to those observed in nature. (4) Steps (2) and (3) were repeated 10 000 times to produce and sample as many virtual communities as possible. We then estimated the niche overlaps $L_{i,h}$ among all species in each artificial community, just as we did using the real data set.

Averaging the niche overlaps $L_{i,h}$ in each artificial community, we obtained the mean overlap \bar{L}_{null} , and estimated the 95% confidence interval. If the community was structured by competition, \bar{L}_{obs} would be expected to be significantly smaller than \bar{L}_{null} . If species were associated, we would expect the opposite pattern, suggesting that positive interactions (facilitation) prevail. We also compared the observed frequencies of $L_{i,h}$ values with those obtained from the null model. If competition and niche differentiation determine community structure, we would expect low $L_{i,h}$ values in the observed communities to be more frequent than in the null model. In contrast, if facilitation causes some species to co-occur over the gradient, we would expect the observed frequency of large overlaps to

be greater than that expected by chance. Remember that both situations can occur simultaneously in the same community if competition and facilitation act concurrently.

Prediction B2: Overlap changes over the gradient

To test whether niche overlap decreases with soil depth, we sorted species according to their niche position (\bar{d}_i), and for each one estimated the overlap $L_{i,i+1}$ with the species having the next larger \bar{d}_i value: This procedure obtains the largest overlap observed for each species without repeating any value. The overlap values $L_{i,i+1}$ were regressed on \bar{d}_i using GAMs with normal error.

Results

Prediction A1: community structure

We recorded data for 78 species (mean = 42.25 species-site⁻¹) in 28 families (Appendix 1). Richness differed among sites ($\chi^2 = 68.28$, $P < 0.001$) and changed with soil depth (Agua Blanca: $\chi^2 = 17.50$, $P = 0.010$; La Biznaga: $\chi^2 = 35.23$, $P < 0.001$; El Cacalote $\chi^2 = 13.80$, $P = 0.042$; Nacusenye: $\chi^2 = 27.94$, $P < 0.001$). Richness increased sharply from 0 to 5–10 cm in soil depth, and then decreased again from about 30 cm onwards, except at Nacusenye, where such a decrease was not observed (Fig. 1a).

There was a significant correlation between soil depth and community structure measured as the score over the first CA axis at all sites, but the fraction of the variation explained was small (Fig. 2; R^2 values: Agua Blanca = 0.361; La Biznaga = 0.307; El Cacalote = 0.032; Nacusenye = 0.255; $P < 0.001$ in all cases except El Cacalote, $P = 0.002$). Depth was the variable most correlated with species composition, with the only exception of El Cacalote, where carbonate content was as important as depth in determining community structure (Fig. 2). In our system, deeper soils generally had more organic matter and larger slopes, as shown by the large arrows in roughly the same direction as depth in Fig. 2. Soil texture showed no consistent changes with depth between sites (see variable arrow magnitudes and directions in Fig. 2). Soil pH was constant (pH = 7) among quadrats, and thus had no effect on community structure.

In accordance with the observed changes in community structure with depth, there were large differences among species in their mean soil depth (niche position \bar{d}_i). Some species only occurred in soils <5 cm and others were restricted to soils >40 cm (Fig. 3a). Nevertheless, mean depth was between 15 and 25 cm in nearly half of the species. About half of the species occurring in deep soils (i.e. with high \bar{d}_i values) were tussocks or plants with underground resistance structures (e.g. bulbs and corms; Appendix 1). Drought resistance characterized shallow soil

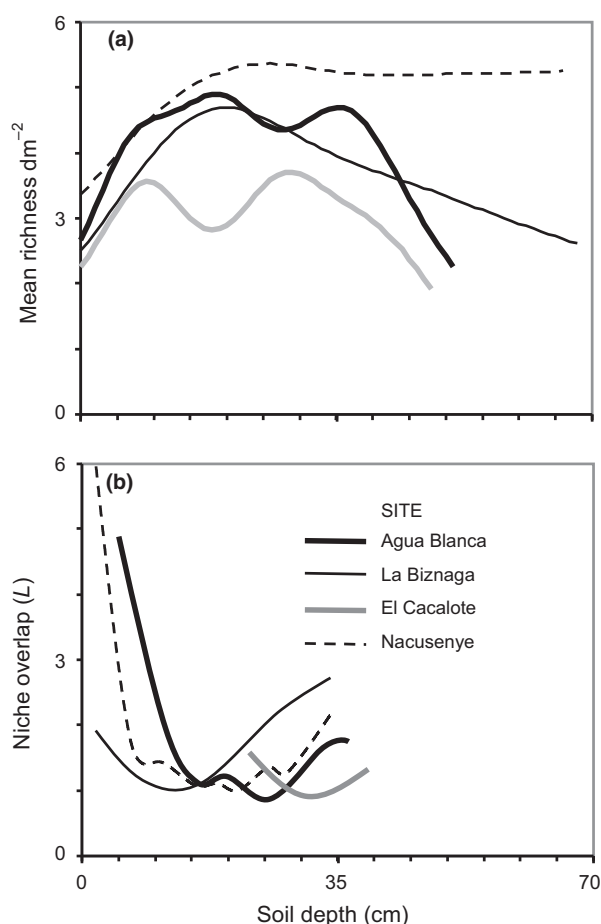


Fig. 1. Mean species richness (a) and niche overlap (b) over the soil depth gradient. Niche overlap was calculated as the Hurlbert's index for pairs of species whose niche positions (mean soil depth) are adjacent in the gradient. Regression lines were obtained using generalized additive models for each site. R^2 -values are 0.352 for panel a, and 0.589 for panel b.

specialists: 63% of the species with \bar{d}_i values <10 cm (and all species with \bar{d}_i <5 cm) were succulent plants. The poikilohydric species *Selaginella* was also found on thin soils (Appendix 1).

Prediction A2: niche narrowing

Intermediate to narrow (<0.5) niche breadths were most frequent, and few generalists occurred, except at El Cacalote where the majority of the species were generalists (Fig. 3b). To test if the bell-shaped distribution observed in Fig. 3b could be an artifact of missing species beyond the ends of the sampled gradient we conducted a randomization test (Appendix 2). The general form of the expected distribution was still bell-shaped, but we detected that the observed number of highly specialized species was higher

than expected by chance. Also, the mean niche breadth at all sites was significantly smaller than that expected from the randomization test (Appendix 2). As expected, niche breadth was reduced in sites with greater crowding indices. On average, the correlation between the niche breadth and the crowding indices was significantly negative (mean $r = -0.327$, $t = 2.619$, $P = 0.011$).

Predictions A3 and B1: Niche overlap

The mean niche overlap (\bar{L}_{obs}) was significantly smaller than that predicted with the null model (\bar{L}_{null}) at all sites (Table 1). The observed and expected distributions of L values were quite similar except for small overlaps ($L < 1$), which, in accordance to prediction A3, were more frequent than expected by chance at three of the four sites (Fig. 4). The pattern expected for facilitation, i.e. a high frequency of large overlaps (prediction B1), was not observed.

Prediction B2: changes in overlap over the gradient

Niche overlap changed with soil depth ($P < 0.001$ in all cases). As expected, there was a negative relationship between niche overlap and soil depth, but only in shallow soils. In all cases, overlap also increased in the deeper soils (Fig. 1b). In Nacusenye and Agua Blanca overlap in deep soils was much smaller than that observed in the other extreme of the gradient, but in La Biznaga the pattern was reversed.

Discussion

We found evidence for a differential distribution of species over the soil depth gradient, which is reflected in a clear zonation of the community in terms of species richness, abundance and composition. This appears to be in part the result of competition restricting species distribution, with realized niches becoming narrower in crowded communities and more differentiated than expected by chance. As predicted from the SGH, overlap was generally higher in shallow soils. However, the frequency of large overlaps was smaller than that expected by chance, casting serious doubts on whether this pattern actually arose from positive interactions.

Community structure

The observed distributions of different species and the humped form of the relationship between richness and soil depth fit Tilman's (1982) resource enrichment model. In this, resource scarcity limits richness in poor areas, and competition does so in resource-rich environments. Deep

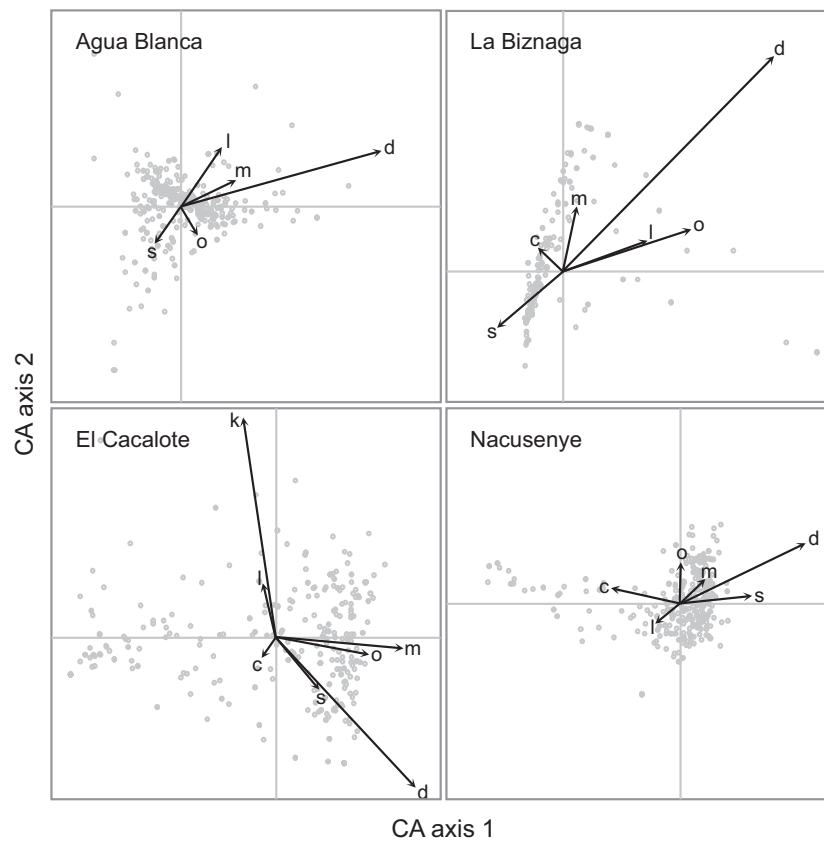


Fig. 2. Community structure–environment biplots. Points represent the position of each 0.1×0.1 m quadrat in an ordination performed through correspondence analysis (CA) on species abundance data. Arrows show the direction of change of the different environmental variables, and their magnitude corresponds to the strength of the correlation between each variable and species composition and abundance. c = clay fraction; d = soil depth; k = carbonates; l = loam fraction; m = slope; o = organic matter; s = sand fraction.

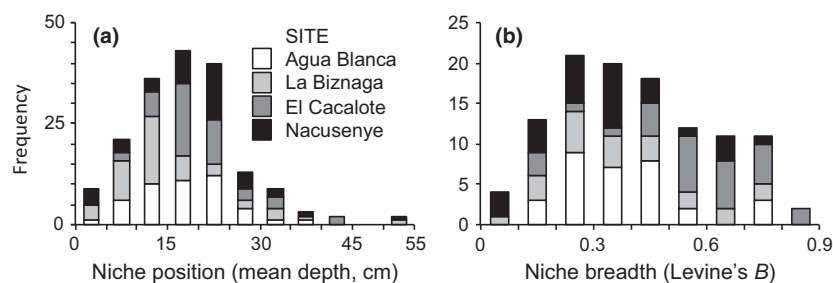


Fig. 3. Frequency of species with different niche position (mean soil depth) and niche breadth measured as the Levine's index at four different sites.

soils at the study sites retain more moisture than shallow ones (Villarreal-Barajas & Martorell 2009; Martorell & Martínez-López 2014), and may have more nutrients (as suggested by their increased organic matter contents; Fig. 2; Tate 1987), making them rich environments compared to shallow soils. According to Tilman's model, competitive species should become dominant where resources are abundant, excluding other species and reducing richness (Tilman 1982; Wedin & Tilman 1993; Hutchings et al.

2003). Competitive exclusion from deep soils has been reported in previous works dealing with depth gradients (Sharitz & McCormick 1973; Baskin & Baskin 1988; Houle & Phillips 1989; Baer et al. 2003). Exclusion from sites with deep soils may also occur at our study site because deep soil specialists were tussocks or plants with bulbs and corms, which can be thought of as strong competitors due to their large biomass (Coughenour 1985; Grime 2002). Additionally, species with underground structures develop

Table 1. Observed (\bar{L}_{obs}) and expected (\bar{L}_{null}) mean niche overlaps for the four study sites and for the pooled data set. Niche overlap was calculated using Hurlbert's index. The expected overlaps were produced with a null model in which species were randomly chosen from a virtual pool independently of each other, so no interactions occur among them. Data in parenthesis correspond to the null model's 95% confidence interval.

Site	Observed Overlap	Expected Overlap	P
Agua Blanca	0.955	1.075 (1.035–1.508)	<0.001
La Biznaga	0.999	1.277 (1.123–1.425)	0.002
El Cacalote	1.006	1.150 (1.031–1.293)	<0.001
Nacusenye	0.968	1.121 (0.995–1.339)	<0.001

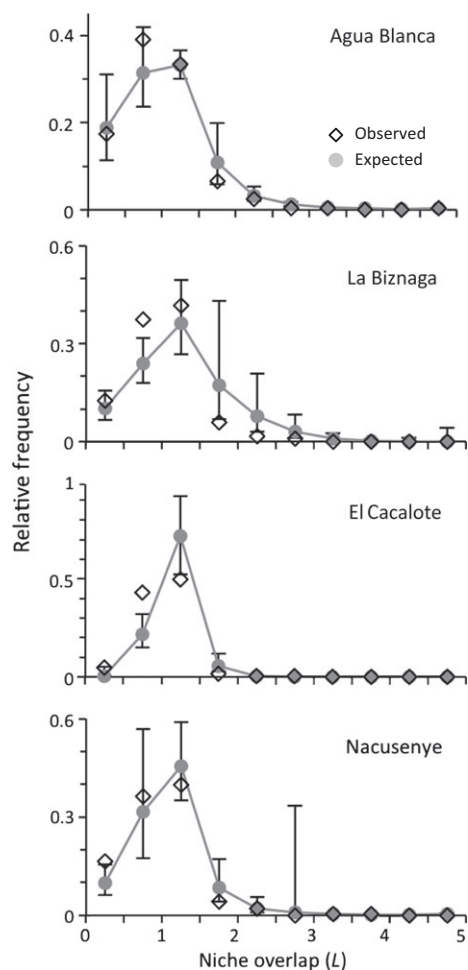


Fig. 4. Observed and expected distribution of niche overlaps at the four study sites. The expected overlaps were produced with a null model in which species were randomly chosen from a virtual pool independently of each other, so no interactions occur among them. Bars: 95% CI.

early in the rainy season, a behavior that increases the competitive advantage of plants in seasonal grasslands (Ross & Harper 1972; Verdú & Traveset 2005).

In contrast, communities developing in adverse areas are expected to be structured by the stress tolerance of

individual species (Keddy & Weiher 1999; Bruno et al. 2003; Lortie et al. 2004). According to the resource enrichment model (Tilman 1982), aridity in shallow soils may filter out those species unable to withstand stress, explaining the low diversity found there. Shallow soils also act as refuges in which drought-tolerant species avoid competition (Oosting & Anderson 1937; Day 1965; Houle & Phillips 1989). The restricted distribution and predominance of stress-tolerant succulent and poikilohydric species on thin soils, together with the evidence that cacti are poor competitors (Briones et al. 1996, 1998), support these ideas. Besides hydric stress, soil depth may also act as an environmental filter that restricts the growth of species with bulbs and long roots, which require space for developing their underground organs. The increase in richness observed at intermediate depths may result in part from the co-existence of stress-tolerant and short-rooted species with those that require more water or have long roots or bulbs.

Measuring niche overlap for continuous resources

One drawback of our null model to infer competition is that the niches of hypothetical species were based on the realized niches observed in nature. This was so because hypothetical niches were produced through Monte Carlo simulation using the observed distribution and correlation of the parameters α and β of the niches of actual species. Thus, the simulations potentially account for the observed reduction in the niche breadth due to competition, smuggling the factor we are interested in into the null model. So far, all the null models used for niche overlap suffer from this problem, be they based on rearrangement of resource-use matrices or on random selection of species from an actual pool (Case 1983; Schoener 1988; Gotelli & Graves 1996). Because data on resource use are collected under natural conditions, they reflect the realized, not the fundamental niche. This makes the test overly conservative (Gotelli & Graves 1996; Gotelli 2000), increasing the reliability of the result that niche overlap is smaller than expected by chance.

The importance of acknowledging that soil depth is a continuous resource axis becomes obvious by comparing the observed and expected values of the overlap index. At first glance it would appear that the observed niche overlap is random because its mean values were near 1, the expected value for discrete and unordered resources (Hurlbert 1978). The use of the appropriate null model is required to estimate the correct expected value for the niche overlap index (L) if resources are continuous, which in our case was >1 and significantly larger than the observed values. The same reasons underlying the mid-domain effect may cause this inflated L : given that the depth gradient is bounded, large overlaps must occur at

intermediate portions of the depth interval, particularly between species that are not specialized in tiny segments of the gradient (Colwell & Hurtt 1994; Colwell & Lees 2000). Those large overlaps would inflate the mean value of L .

Niche structure of the community

The wide range of niche position (\bar{d}_i) values observed, together with the large frequency of species with narrow niches and their smaller-than-chance mean breadths, shows that many species are specialized in small, differentiated segments of the soil depth gradient. Most species had intermediate \bar{d}_i values; this is in accordance with the resource enrichment model, as exclusion from the extremes of the gradient is expected due to competition or environmental stress and insufficient space for root development (Tilman 1982). Species with broad niches may also produce a humped distribution of \bar{d}_i values because their mean depth is necessarily found near the centre of the gradient (Colwell & Hurtt 1994; Colwell & Lees 2000). However, at our study site (with the possible exception of El Cacalote, where niches were broader), generalist species are not numerous enough to make a substantial contribution to this pattern.

Our results are consistent with the hypothesis that competition has an effect on community structure. First, there was segregation over an environmental axis. The null model and community structure analyses show that this was the case, with small niche overlaps resulting from habitat specialization of plants over the soil depth gradient. Niche segregation promotes co-existence through greater intra- than interspecific competition (Chesson 2000; Silvertown 2004), as occurs in our study site (Martorell & Freckleton 2014). Second, the removal of competitors induced niche shifts (Silvertown 2004). We did not test this experimentally, but the niche narrowing expected as a response to increased competitor density was observed when comparing the four sites. However, shared predation may reduce the overlap of the distribution ranges of species, making them narrower (Holt & Barfield 2009). If herbivores forage preferentially in sites where plant density is high, the observed reduction in niche breadth with crowding would arise without competition being involved. Third, the fact that niche breadth was smaller than expected by chance (Appendix 2) may also arise from competition, although species' habitat preferences may contribute to this pattern irrespective of whether interactions occur or not. Additionally, neighbour removal experiments have shown that competition plays a role in our grassland (Villarreal-Barajas & Martorell 2009). In contrast, there was no evidence that facilitation affects the niche structure of the community. We

expected facilitation to result in large niche overlaps, but the number of species that shared much of their niches was not higher than that expected by chance (Fig. 4). As predicted, niche overlap was large in shallow soils, but this also happened in the deeper substrates. This U-shaped relationship may be expected because species at both extremes of the soil gradient are specialists (the \bar{d}_i values for generalist species would rarely be either very large or small, as this index is an average that would be influenced by the individuals observed at the middle or even the other extreme of the gradient) and thus must share much of their niche with their neighbouring species, which are also specialized in a similar soil depth. In contrast, generalists, which are expected to have \bar{d}_i values near the middle of the gradient, would only share a small portion of their niches with intermediate depth specialists.

Yet another pattern that would be expected from facilitation theory, i.e. niche widening with crowding (Higashi 1993; Bruno et al. 2003), was only observed for two species (*Tripogon spicatus* and *Tridax coronopifolia*). From the HGS, we would expect widening to occur preferentially in shallow soils, but only one of these two species was a shallow-soil dweller ($\bar{d}_i = 8.38$ and 18.95 cm, respectively). These results are in line with evidence from neighbour removal experiments that facilitation does not take place in shallow soils at the study site (Villarreal-Barajas & Martorell 2009). Maestre et al. (2009) suggest that competition rather than facilitation may be expected in shallow soils because stress is caused by the lack of a resource, i.e. water, and because plants growing there tolerate hydric stress (they are succulent or poikilohydric) and do not require neighbours that ameliorate it.

While it is clear that niches contribute to structuring our grassland, their role seems to be relatively minor: the power of soil depth to predict community structure (as measured through R^2 -values of the models relating CA to soil depth) was low, and the distribution of niche overlaps (Fig. 4) was sometimes remarkably similar to that expected by chance (although this may allegedly be the result of incorporating some effects of competition into the null model, as discussed above). Species-specific attributes such as drought and carbonate tolerance, or requirements for deep soils in which bulbs can develop, also contributed to determining the distribution of species over the soil depth gradient. Importantly, we must also bear in mind that depth may not be the most (or the only) important axis for niche differentiation. The data from El Cacalote illustrate the point: community structure there changes more over the carbonate content than over the depth gradient. Differentiation over other axes makes it likely that niche segregation plays a more important role than may appear from our results.

Hydrological niche segregation

Studies on how hydrology determines the niche structure of plant communities are still rare, despite the strong evidence for ecophysiological trade-offs that can easily result in species segregation (Silvertown et al. 1999, 2014; Araya et al. 2011). Most of the current evidence for hydrological niche segregation comes from arid or semi-arid environments where water is a main limiting factor (Silvertown et al. 2014). Aridity gradients are not only important at geographical but also at local scales, such as soil depth. In the rainy northern England grasslands, there is only a weak niche segregation over a soil depth gradient (Mahdi et al. 1989). However, the turnover in species over a soil depth gradient was magnified by experimentally induced summer droughts. This treatment resulted in the emergence of a moisture gradient remarkably similar to that observed at our study site, with a xerophytic community occurring in the shallow soils as well, and drought-intolerant species confined to deep soils (Fridley et al. 2011).

Although many factors may determine the segregation of species over the depth gradient, some of our results suggest strongly that hydrology underlies the niche differentiation in our semi-arid grassland: (1) Drought-tolerant species (succulents, poikilohydric species) were restricted to the arid portions of the gradient. (2) Community structure (CA scores) was correlated with depth, whereas the other soil attributes played only a secondary role at three of the four sites. We did not measure nutrient content over the gradient but, as expected for volcanic soils, direct measurements show that they do not seem to be limiting at the study sites (Cruz-Cisneros & Rzedowski 1980). All this evidence, altogether with previous measurements of the strong effect of depth on soil water potential (Villarreal-Barajas & Martorell 2009; Martínez-López 2014; Martorell & Martínez-López 2014), suggests that water availability is probably one of the factors with largest impact on species distributions (3) Neighbour removal experiments show that competition increases in shallow soils, perhaps because of the impossibility to segregate roots spatially (Villarreal-Barajas & Martorell 2009), as observed in other systems in which water plays a limiting role (Nippert & Knapp 2007a,b; Silvertown et al. 2014). These findings suggest that studies in stressful environments such as ours make it possible, at least in theory, to explore the balance of facilitation and competition and the effects of these factors on the community niche structure.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Species found at the four study sites.

Appendix S2. Randomization test for expected niche breadths.