



Annual plant community assembly in edaphically heterogeneous environments

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Keywords

Annual plant community; Assembly rules; Calcareous soils; Community-weighted mean (CWM); Edaphic endemism; Functional diversity; Gypsum soils; Mediterranean; Regional species pool; Restrictive soils; Semi-arid; Soil affinity; Spain; *Stipa tenacissima*

Nomenclature

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Introduction

Restrictive soils usually support outstanding floras, contributing to some of the most remarkable biodiversity hotspots in terrestrial ecosystems (Harrison & Inouye 2002; Mota et al. 2011) and constituting ideal models for testing important questions of ecology and evolutionary biology, such as adaptation, speciation and endemisms (Harrison & Rajakaruna 2011; Escudero et al. 2015). Although soil specificity has long intrigued ecologists and botanists (Macnair & Gardner 1998 and references therein), not until recently has our knowledge on critical aspects of edaphic endemisms, such as the physiological mechanisms involved in coping with soil limitations (Palacio et al. 2007) and their evolutionary origins (Moore & Jansen 2007; Kay et al. 2011), been improved.

Although the plant communities on special soils have been described and classified (Rivas-Martínez & Costa

Abstract

Questions: Does edaphic heterogeneity (i.e. switches between gypsum and calcareous soils) affect annual plant community assembly in highly restrictive soils? Our main hypothesis is that soil filtering is the main determinant of species assembly, subsequently modulated by climate and lastly by biotic interactions, such as *Stipa tenacissima* and the biological soil crust (BSC) at fine spatial scales. Our study system is highly suitable to test the importance of edaphic heterogeneity to the assembly of annual plant communities, since calcareous and gypsum soils are in close contact and freely receive propagules.

Location: Annual plant communities of semi-arid steppes in central Spain.

Methods: We built a soil affinity index (SAI) for each species to measure mean soil affinity (MSA; analogous to the community-weighted mean – CWM) in each local assemblage.

Results: Most species were able to establish in both substrates, but gypsum soils clearly exerted a stronger filtering effect. *Stipa* favoured an expansion of the niche space in calcareous soils but not in gypsum, and BSCs not only reduced annual species richness, diversity and cover, but also the range of SAI values of local assemblages.

Conclusions: This study highlights the importance of the probabilistic filtering (*sensu From plant traits to vegetation structure*, 2010, Cambridge University Press, Cambridge, UK) of soil characteristics to the assembly of annual plant communities, as opposed to an ‘all-or-nothing’ filter.

1970; Meyer & García-Moya 1989 for gypsum soils; Brooks 1987 for serpentine soils), almost no information is available on the processes involved in their community assembly; but see Anacker (2011) and Schechter & Bruns (2012) for serpentines. Lack of knowledge is especially noteworthy, since one of the core topics in plant ecology is to understand processes governing community assembly and plant co-existence (Vellend 2010; Götzenberger et al. 2012; HilleRisLambers et al. 2012). In this sense, ecological assembly rules (*sensu* Götzenberger et al. 2012) are mediated through hierarchically structured ecological filters such as dispersal, the abiotic environment and biotic interactions (Callaway 2007; Stokes & Archer 2010; Michalet et al. 2015). Shipley (2010) introduced the term ‘stochastic filter’ to explain the mechanism that drives species assembly when different functional traits have different probabilities to pass through the environmental filter and establish in

the final community, as opposed to an 'all-or-nothing' filter.

The substrate can be the strongest abiotic filter selecting which plants from the species pool are able to establish in a specific site under edaphically restrictive conditions (Grace et al. 2000; Weiher et al. 2004). However, soil specificity is not an all-or-nothing plant response, since it shows a gradient from exclusive specialists to rather generalist species (Safford et al. 2005; Palacio et al. 2007). This suggests that the filtering role of special soils can be modulated by other local factors (both abiotic and biotic) that exacerbate or mitigate soil limitations and eventually affect the formation of realized assemblages. For instance, edaphic limitations posed by serpentines can interact with climate to promote large-scale community patterns (Fernandez-Going et al. 2013). Restrictive effects of gypsum soils and specific adaptation of species to cope with these restrictions are discussed in Escudero et al. (2015).

Here, we studied annual plant communities on gypsum and calcareous outcrops under semi-arid mediterranean conditions. Our aim was to clarify the role of restrictive soils in community assembly. Our study sites are especially suitable due to their dense and homogeneously distributed soil seed banks (Caballero et al. 2008; Olano et al. 2012; A.M.L. Peralta, A.M. Sánchez, A.L. Luzuriaga & A. Escudero, unpubl.) and the co-existence of gypsum and calcareous soil patches. This means that differences in local species assemblages between these two soil types are not the result of dispersal assembly rules (Zobel 1997; Spasojevic et al. 2015). Therefore, the annual communities on these soils share not only the same climate, but also the pool of available species (Escudero et al. 2015). Furthermore, the short life cycle of these annual species allowed us to cover entire ontogenetic plant development, avoiding misleading results due to changes in the magnitude and direction of interactions throughout the life stages of the co-occurring plants (Holzapfel & Mahall 1999; Luzuriaga & Escudero 2008).

Water pulses can also largely determine plant assemblages in semi-arid environments (Chesson et al. 2004; Miranda et al. 2011), particularly in those dominated by annuals (Venable et al. 1993; Pake & Venable 1995; Rivas-Arancibia et al. 2006). Some perennial neighbours act as biotic filters in annual plant assemblages (Facelli & Temby 2002; Armas & Pugnaire 2011). In a previous study, we found that *Stipa tenacissima* (Poaceae) exerted a contrasting effect on annual plant species assemblages, reducing species richness and diversity under extremely dry conditions, while increasing them under milder conditions (Luzuriaga et al. 2012). Well-developed biological soil crusts (BSCs; Belnap & Lange 2003) are also recognized as key components of drylands, not only due to their effect on ecosystem function (Maestre & Cortina 2003; Castillo-Monroy et al.

2010) but also because they contribute to small-scale heterogeneity that finally determines annual plant community structure and composition (Luzuriaga et al. 2012).

A recently developed method that quantifies plant trait distributions and their variations within and among communities under different environmental conditions allows for assessing the relative importance of climate and local filters on the formation of annual plant assemblages (Freschet et al. 2011; Bernard-Verdier et al. 2012; Violle et al. 2012). Here, we use a similar approach and propose a soil affinity index (SAI) that quantifies soil specificity (gypsum vs calcareous soil preferences) and can be scaled up to the community level. Soil affinity clearly represents a species-specific property that is crucial for species establishment (including survival, growth and reproduction) and, if quantified in the same way as a functional trait, it can help understand community assembly in restrictive substrates. We combined SAI and other tools originally developed to describe trait diversity patterns among communities to identify filters (i.e. assembly rules) operating on annual plant assemblages under contrasting environmental conditions ruled by the variable climate (three sampling years), the presence of *Stipa* and two substrate types (gypsum vs calcareous).

We hypothesized that soil filtering would have a crucial effect on species assembly, and that soil filtering would be modulated by climate, biotic interactions with *Stipa tenacissima* and with BSCs. The combined effect of these filters would be reflected in the distribution of SAIs at each local assemblage. Overall, we expected the range of the weighted community SAIs in each assemblage to be lower under stressful conditions of low water availability (dry years) and in open areas (away from *Stipa* canopies), as abiotic filtering is expected to increase species similarity (Weiher & Keddy 1999; Wilson 1999). We also expected *Stipa* to influence soil filtering by shifting the limits of SAI distribution relative to open areas or by expanding the range of SAI values ('range shift' and 'range expansion', respectively, sensu Schöb et al. 2012). Furthermore, the presence of *Stipa* tussocks may also improve niche differentiation and reduce competition (Lundholm 2009) without altering soil filtering. At the same time, BSCs together with mosses and loose stones may affect small-scale heterogeneity and, eventually, annual community assembly.

Methods

Study site

This study was conducted at two locations in central Spain (Titulcia: 40°8'N, 3°34'W, 513 m a.s.l. and Ontígola 39°58'N, 3°40'W, 607 m a.s.l.). Two nearby plots of 30 × 30 m were established at each location on two contrasting substrate types: soils derived from gypsum out-

crops and soils derived from limestone or calcareous marls on mild slopes (around 15°). Since the two geologic layers are in contact, soils occur very close and transitions are very sharp. This area has a semi-arid mediterranean climate with a mean annual rainfall of 400 mm·m⁻²·yr⁻¹ and a mean annual temperature of 14.5 °C (from the nearest weather station at Aranjuez 40°02'N, 3°37'W, 590 m a.s.l.). Above-ground vegetation in the four study plots (independent of the soil type) was a steppe dominated by *Stipa tenacissima*, a tussock-forming grass, scattered in bare ground area. Gypsum soils showed a well-developed BSC dominated by lichens (e.g. *Diploschistes diacapsis* (Ach.) Lumbsch, *Squamarina lentigera* (G.H. Weber) Poelt, *Fulgensia subbracteata* (Nyl.) Poelt and *Psora decipiens* (Hedw.) Hoffm), whereas calcareous substrates were not as lichen-rich (e.g. *Cladonia convoluta* (Lam) Cout.). Both soil types showed a rich annual plant community of up to 38 species 0.25 m⁻² (e.g. *Chaenorrhinum reyesii* – Scrophulariaceae, *Ctenopsis gypsicola* – Poaceae, *Campanula fastigiata* – Campanulaceae, *Omphalodes linifolia* – Boraginaceae, *Cleonia lusitanica* – Lamiaceae, *Arenaria leptoclados* – Caryophyllaceae; App. S1).

Experimental design and monitoring

Ten 50 × 50 cm quadrats were randomly established in each of the four plots. Five quadrats were established adjacent to mature *Stipa* plants on the upper slope of tussocks and five quadrats in open areas devoid of perennial vegetation (located at least 1 m apart from the nearest *Stipa* tussock). Each 50 × 50 cm quadrat was divided into 100 cells of 5 × 5 cm, which were our sampling units (2 locations × 2 substrate types × 10 quadrats × 100 cells = 4000 sampled cells·yr⁻¹). This grid cell size reflected the average height of the studied annuals to ensure that co-occurring species in a cell are interacting (Luzuriaga et al. 2012).

Surveys were carried out in the spring 2006, 2008 and 2009. These years differed strongly in temperature and precipitation pattern (App. S2). The year 2008 was exceptionally dry, with nearly 40% less precipitation than the mean annual precipitation of the previous 30 yr. In 2008, only 11 out of the 40 quadrats had more than three species, and their frequencies were very low in all cases. Furthermore, none of the species occurred in more than five quadrats. Consequently, data from 2008 were only used to model overall species richness, species diversity and plant cover, but were dropped from the comparison between the plots. Each quadrat was a realized combination of the regional species pool, which was defined as all the species observed in the 75 quadrats in 2006 and 2009 (five quadrats were altered by human or rabbit activity in 2009 and could not be used in the study).

The percentage cover of each annual plant species was visually estimated for each cell. Total moss and lichen cover were also visually estimated for each cell at the beginning of the experiment in 2006.

Diversity index

In order to estimate plant community diversity, we calculated the inverse Simpson index using species cover percentage per quadrat for the three sampling years as an abundance measure (Jost 2006):

$$\text{Inverse Simpson} = \frac{1}{\sum p_i^2}$$

where p_i is proportion of species i . This index has also been called the 'effective number of species' (MacArthur 1965), and represents the number of species that a community would have if species were distributed equally. This diversity index was calculated for each quadrat with PRIMER v 6.1.11 software.

Soil affinity index of each species

To evaluate the affinity of each species to gypsum or calcareous soil, we proposed a soil affinity index (SAI) for each species that appeared in more than five quadrats (out of the 75). This index was considered as analogous to a species attribute and was calculated as follows:

$$\text{SAI} = \frac{Gy - Ca}{Gy + Ca}$$

where, Gy is the number of cells on gypsum substrate occupied by species i and Ca is the number of cells on limestone (calcareous) substrate occupied by species i . The final SAI for each species was the mean of 2006 and 2009 weighted by species abundance measured at the cell level. This index varied between -1 and 1 (species that appeared exclusively on calcareous and gypsum substrate, respectively). Following this index, species were classified as gypsophytes (SAI > 0.6), calcophytes (SAI < -0.6) or indifferent to substrate type (-0.6 < SAI < 0.6; App. S1).

Community-level measures of soil affinity

The SAI distribution in each local realized assemblage was described using three parameters: range, abundance-weighted mean and diversity of SAI values. Mason et al. (2005) defined functional richness as the amount of niche space filled by species. Based on this definition, we computed the soil affinity range (SAR) as analogous to func-

tional richness in order to quantify the amount of space used in the gypsophily–calcophily gradient by each assemblage. We calculated the range of soil affinity values in each assemblage as follows:

$$\text{SAR} = \max(\text{SAI}) - \min(\text{SAI})$$

The SAR values can range between 0 (all species in the assemblage have the same SAI) and 2 (at least two species in the assemblage have extreme SAI values).

The mean soil affinity index (MSA) is analogous to community-weighted mean (Garnier et al. 2004). It weights the SAI by species relative abundance and sums overall species, providing a single community trait value. It quantifies mean gypsophily or calcophily for each quadrat, thus scaling the degree of soil affinity at the community level. It was calculated as follows:

$$\text{MSA} = \frac{\sum_{i=1}^n (\text{SAI}_i \times \text{Cov}_i)}{\sum_{i=1}^n \text{Cov}_i}$$

where SAI_i is the soil affinity index for species i and Cov_i is the cover of species i in the quadrat. MSA values can range between -1 (only calcophytes in the quadrat) and 1 (only gypsophytes).

The soil affinity diversity (SAD) describes the divergence of plant species cover along the soil affinity gradient. It was computed as the Rao (1982) quadratic diversity (Pavoine & Dolédec 2005; Lepš et al. 2006):

$$\text{SAD} = \sum_{i,j}^S d_{ij} \times \text{Cov}_i \times \text{Cov}_j$$

where S is species richness, and d_{ij} is the difference in SAI values between species i and j , calculated as:

$$d_{i,j} = (\text{SAI}_i - \text{SAI}_j)^2$$

where SAD values range between 0 and 1 (minimum and maximum dispersion in SAI values, respectively).

These three community-level parameters were computed using the package FD for R (R Foundation for Statistical Computing, Vienna, AT).

Null model approach to test abiotic filtering

Null models were constructed to test the hypothesis that plant composition is controlled by abiotic filtering of soil type, climatic conditions and/or biotic determinants, such as the sharp variation between *Stipa* neighbourhood and open areas. We generated 10 000 null assemblages, assuming a random distribution across quadrats and

species, to obtain 10 000 null values of SAR, SAD and MSA for each random assemblage. If our hypothesis was true, we would expect that the amount of space occupied along the gypsophily–calcophily gradient would be lower in real assemblages than in null ones (Mouchet et al. 2010), leading to lower SAR values in real assemblages. Likewise, SAD would be lower in real assemblages because plant abundance for each species would be concentrated in some areas along the gypsophily–calcophily gradient. Following the same reasoning, MSAs calculated from null assemblages would be closer to 0 than those calculated from real assemblages.

The null assemblages were constructed by permuting the contents of the species \times cover matrix of all the quadrats using R (R Core Team 2013).

Differences were considered to be significant when observed SAR and SAD values and observed absolute MSA values were lower than the 0.05 percentile of simulated values for these parameters.

Statistical analyses

We performed repeated measures generalized linear mixed models (rm-GLMM) to model six community attributes of the realized annual plant assemblages: richness, diversity (inverse Simpson), total cover of annual plants, mean soil affinity index (MSA), SAR and SAD. We built a fully factorial model for each variable with year, microenvironment, substrate and location as fixed factors. Although the climate, exposure and slope of the two locations were very similar, location was included in the models as a fixed factor to control for idiosyncratic differences. Quadrat was included in the models as a random variable to account for the repeated measures undertaken in each quadrat in 2006 and 2009. Total lichen cover was considered as a covariable. We checked the correlation between variables to avoid multicollinearity problems. The error distribution and link function that best fitted our data were used for each rm-GLMM (Table 1).

Results

We found 72 species in the two locations in the 3 yr of study. Species richness varied greatly among years with 47, 28 and 64 species in 2006, 2008 and 2009, respectively. Of these 72 species, 14 appeared exclusively on gypsum soils, 20 on calcareous soils and 38 species on both. The SAI was calculated for the 42 species that appeared in more than five quadrats (6.6%). According to this index, 19 species were classified as gypsophytes ($\text{SAI} > 0.6$), ten as calcophytes and the rest (23) as indifferent (App. S1). Most of the regional species pool occurred on both calcareous

Table 1. Wald's Chi-square of repeated measures GLMMs with six community attributes for 2006 and 2009. Year 2008 was not included in these models because few quadrats had more than three species. Quadrat was considered a random variable to account for the repeated measures in the 2 yr of study. The diversity index was calculated as the inverse Simpson's dominance index.

	Richness	Diversity Index	Total Cover	MSA	SAR	SAD
Error Distribution	Poisson	N	N	N	N	N
Link	Log	Log	Log	Id	Id	Id
Micro-environment	0.2	0.003	2.2	0.2	0.1	0.05
Substrate	21.4***	5.9*	4.8*	34.7***	2.3	1.6
Year	2.1	0.4	269.0***	0.6	12.7***	3.1
Microenv × Substrate	5.0*	1.7	1.0	0.1	8.4**	0.4
Microenv × Year	0.01	1.6	4.3*	2.6	3.9*	0.1
Substrate × Year	0.1	1.6	3.3	4.4*	3.0	0.1
Location	14.9***	1.7	5.3*	1.3	14.6***	11.9***
COVAR.						
Lichen Cover	(-) 14.3***	(-) 3.9*	(-) 4.2*	0.4	(-) 14.3***	2.9

MSA, mean soil affinity; SAR, soil affinity range; SAD, soil affinity diversity.

Error distributions and link functions assumed in the GLMMs are as follows. N: normal. Id., identity link function; Log, logarithmic link function; COVAR, covariates. (-), negative coefficient; (+), positive coefficient.

*0.01 < P < 0.05; **0.001 < P < 0.01; ***P < 0.001.

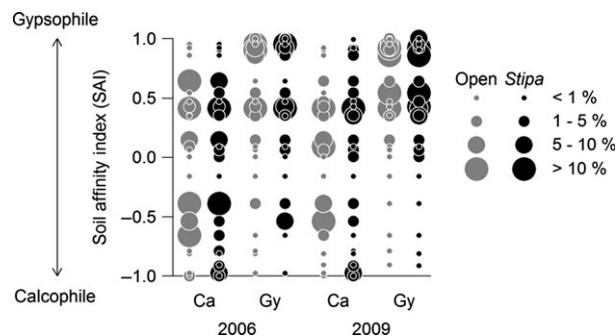


Fig. 1. Distribution of annual species and their percentage covers along the calcophile-gypsophile gradient (in terms of the SAI) for each experimental scenario (ten local assemblages pooled for each scenario) for 2006 and 2009. Ca, calcareous substrate; Gy, gypsum substrate.

and gypsum soils and mainly differed in their relative abundance (Fig. 1).

Although gypsum soils had a slightly lower number of species from the accumulated species pool than calcareous soils (52 vs 58 species, respectively), average species richness and diversity per quadrat were significantly higher on gypsum soils (Table 1, Fig. 2). *Stipa* tussocks had a positive effect on species richness, and this marked effect of *Stipa* was enhanced on calcareous soils. No significant interaction between *Stipa* and year was observed when considering the three study years (Wald's Chi-square = 4.8, $P > 0.05$). Plant cover was mainly dependent on year, and the highest cover was obtained in 2006. The cover of above-ground annuals was higher on gypsum soils and increased in the vicinity of *Stipa*, especially in 2006. Lichen cover negatively affected richness, diversity and total cover of annual species.

The MSA values revealed that assemblages on gypsum soils had a larger share of soil specialists (Table 1, Fig. 3a). Variability of MSA values of local assemblages was higher on calcareous soils than on gypsum soils. Differences in MSA values between gypsum and calcareous soils were higher in 2006 than in 2009 (substrate × year interaction). Furthermore, *Stipa* had an opposing effect on the variability of MSA values in calcareous soils, restricting MSA variability in 2006, but increasing it in 2009. However, on gypsum soils, *Stipa* increased the range of MSA values in 2006, but had nearly no effect in 2009.

The SAR, which quantifies the amount of space along the gypsophily-calcophily gradient occupied by the species that form each local assemblage, was higher in 2006 than in 2009 (Table 1, Fig. 3b). *Stipa* increased SAR on calcareous soils but not on gypsum soils. Lichen cover significantly reduced SAR. None of the predictors had a significant effect on SAD, which always remained low (average SAD = 0.13 ± 0.1).

The null models showed that MSA values of the local assemblages were significantly different from random in 40% to 60% of the quadrats on gypsum soils, especially in open areas in 2006 (Fig. 4). However, MSAs of most calcareous assemblages were similar to random simulations. We detected lower SAD values than expected at random in gypsum soils (>60% of the quadrats).

Discussion

This study provides solid evidence of probabilistic soil filtering of annual plant assemblages (*sensu* Shipley 2010). This implies that soil filtering does not produce an all-or-nothing response, since most species were able to establish in both soil types. When the SAIs of

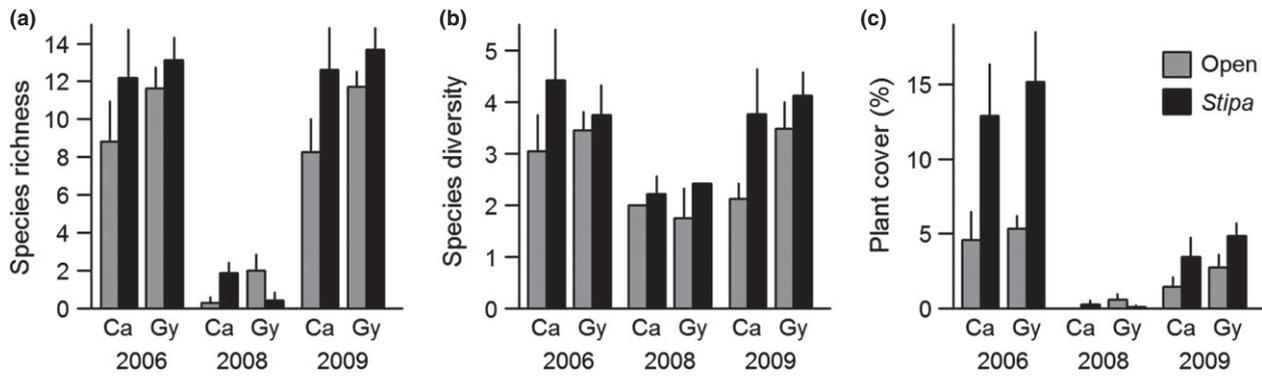


Fig. 2. (a) Mean species richness, (b) mean species diversity (inverse Simpson) and (c) mean percentage cover of each experimental scenario. Vertical lines represent SE. Ca, calcareous substrate; Gy, gypsum substrate.

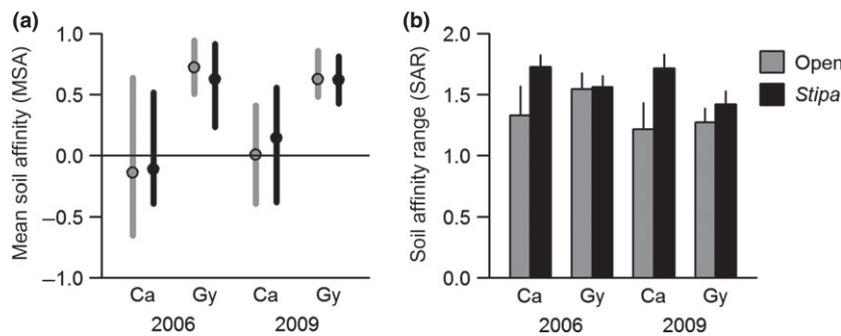


Fig. 3. (a) Average (circles) and range (vertical bars) of MSA values for the ten quadrats of each experimental scenario. (b) Mean SAR values of experimental assemblages for 2006 and 2009. Vertical lines represent SE. Ca, calcareous substrate; Gy, gypsum substrate.

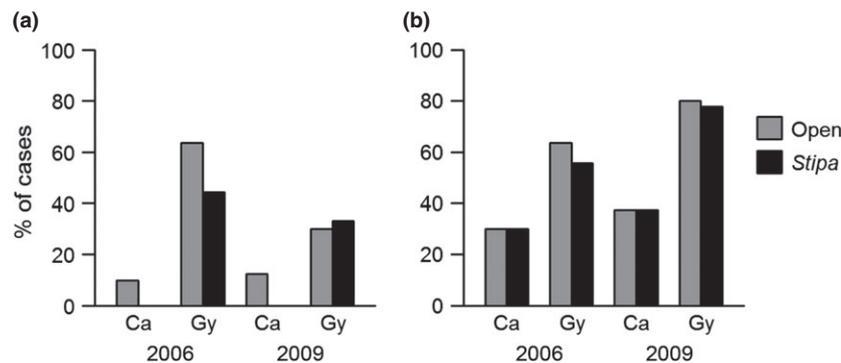


Fig. 4. (a) Percentage of local assemblages (quadrats) that showed observed MSA values significantly different from the simulated MSA values of the 10 000 null assemblages. (b) Percentage of local assemblages (quadrats) that showed observed SAD values significantly lower than simulated SAD values of the 10 000 null assemblages for 2006 and 2009. Ca, calcareous substrate; Gy, gypsum substrate.

constitutive species were weighted by their relative abundance at the community level, the effect of soil filtering on realized assemblages was greatly highlighted. These two geologic substrates are well known for their restrictive nature (see Escudero et al. 2015), yet soil filtering was stronger in gypsum assemblages

(larger departures of MSA values from zero) than in calcareous assemblages, suggesting higher soil specialization in the former. These results agree with the previous findings that gypsum endemics are the main components of gypsum communities (Palacio et al. 2007; Mota et al. 2011).

Other studies have used the variability of CWM of some plant functional traits among local assemblages as an indicator of the intensity of an environmental filter (see Spasojevic & Suding 2012). In our study, variability of MSA values (analogous to CWM) among local assemblages was lower in gypsum soil, which may indicate the occurrence of a strong filter constraining MSA values in these soils. Furthermore, the role of gypsum soils as crucial abiotic filters during the species assembly process was highlighted by the non-random distribution of soil affinity values of local assemblages in gypsum soils.

Interestingly, the edaphic filtering observed in gypsum soils was not reflected in limited species richness and diversity. Contrary to our expectations, local species assemblages on gypsum soils had higher richness, diversity and total cover than on calcareous soils. Fernandez-Going et al. (2012) showed that serpentine assemblages were also more species-rich than neighbouring communities. They did not offer an explanation for this increased richness, but we suggest that this effect relates to the probabilistic filtering. This mechanism of filtering exerted by soils permits most species from the regional pool to occur in the realized communities, and thus can explain the high species richness and increased SAR detected in our local assemblages. Interestingly, although species composition varied greatly between the different years (data not shown), the consistent pattern of MSA values in the 3 yr of study (regardless of contrasting climate conditions) suggests that soil affinity can be a factor largely independent from other environmental conditions to conform the concept of 'azonal vegetation' sensu Ellenberg (1996). Fernandez-Going et al. (2012) suggested that 'stress-tolerant' functional traits might have limited fluctuations in community composition in their restrictive substrates.

Despite the high richness and taxonomic diversity observed in gypsum soils, very low SAD values were found, indicating that species with very similar soil affinity values co-exist at very fine spatial scales. This suggests that competition among these species can be considerable, and raises a difficult question of how these neighbouring plants can co-exist in such rich communities. Plants may avoid competition by having close to equal performance in the same environment (Hubbell 2001), by regenerating in different microsites or by resource partitioning (Chesson 2000) mediated by different rooting depths, uptake of different nitrogen compounds, light capture strategies, pollination traits or water-use patterns (Cornwell & Ackerly 2009). These possibilities are yet to be explored in restrictive soils.

Our results support our hypothesis that soil type is most probably the main abiotic filter and that other abiotic (annual weather variation) and biotic filters (*Stipa* and BSCs) only modulate the realized assemblage. The higher

richness beneath *Stipa* together with the higher SAR in calcareous soils suggest an expansion of the niche space close to *Stipa*, allowing more calciphilous species to enter the community. The facilitation exerted by *Stipa* on calcareous soils is supported by the presence of six extra species that were recorded on calcareous substrates in comparison to gypsum ones, where *Stipa* did not exert any meaningful facilitative interaction. This pattern may indicate a relaxation of the soil filter mediated by *Stipa* in calcareous soils, probably due to improved soil resources and an increase in the variety of micro-environmental conditions. The expansion of niche space is just one of several potential mechanisms by which facilitation can affect community assembly (Cavieres et al. 2014). Improved niche differentiation between co-occurring species in the available niche space could also play an important role in facilitation (Schöb et al. 2012).

Contrary to the pattern observed in calcareous soils, *Stipa* tussocks did not significantly affect species richness or SAR of gypsum assemblages. Probably under the highly restrictive conditions of gypsum substrates the above-ground amelioration of the micro-environment by *Stipa* was not able to balance the negative effects of below-ground limiting factors, such as the presence of toxic compounds, thicker BSC, higher infiltration rates of nutrients and water, etc. (Maestre et al. 2003). The biological soil crust reduced not only the annual species richness, diversity and cover, but also the SAR of local assemblages. These results suggest that the BSC may enhance the effect of soil filtering on the annual plant community by constraining the range of soil affinity values at a site. In this sense, the mechanisms of BSCs that modulate annual plant community composition and structure are probably related to the occupation of space and small-scale variability in water and nutrients below BSCs (Concostrina-Zubiri et al. 2013).

Conclusions

Our results clearly demonstrate the stochastic environmental filter (*sensu* Shipley 2010) 'in action', exerted by restrictive soils. At finer spatial scales, *Stipa* tussocks expanded niche space in calcareous but not in gypsum soils, demonstrating the intense control of soil on plant communities. Subsequently, the BSC also restricted the range of soil affinity values, suggesting crucial small-scale modulations that will additionally shape the realized assemblages.

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Supporting Information

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

Appendix S1. Plant species present in the study area during the three study years, together with their soil affinity indices.

Appendix S2. Mean daily temperature and daily precipitation during the three study years.