



Environmental conditions and biotic interactions acting together promote phylogenetic randomness in semi-arid plant communities: new methods help to avoid misleading conclusions

Santiago Soliveres, Rubén Torices & Fernando T. Maestre

Keywords

Competition; Diversity; Environmental filtering; Facilitation; Habitat differentiation; Mediterranean; Niche expansion; Phylogenetic structure; Plant–plant interactions

Abbreviations

Climate = first component of the PCA ordination conducted with eight environmental variables; COMBO = species combination index, indicator of co-occurrence among species pairs; MPD = mean phylogenetic distance; PCA = principal components analysis; SES = standardized effect size; Similarity = Chao–Jaccard abundance-based similarity index

Nomenclature

Mateo & Crespo (2001)

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Soliveres, S. (corresponding author, santiagosoliverescodina@gmail.com): Evolution and Ecology Research Centre, School of Biological, Earth and Environmental Sciences, University of New South Wales, Sydney, NSW, 2052, Australia

Soliveres, S. & Maestre, F. T. (fernando.maestre@urjc.es): Área de Biodiversidad y Conservación, Departamento de Biología y Geología, Escuela Superior de Ciencias Experimentales y Tecnología, Universidad Rey Juan Carlos, 28933, Móstoles, Spain

Torices, R. (rubentorices@gmail.com): Department of Life Sciences, Centre for Functional Ecology, University of Coimbra, P.O. Box 3046, 3001-401, Coimbra, Portugal

Abstract

Questions: Molecular phylogenies are increasingly used to better understand the mechanisms structuring natural communities. The prevalent theory is that environmental factors and biotic interactions promote the phylogenetic clustering and over-dispersion of plant communities, respectively. However, both environmental filtering and biotic interactions are very likely to interact in most natural communities, jointly affecting community phylogenetic structure. How do environmental filters and biotic interactions jointly affect the phylogenetic structure of plant communities across environmental gradients?

Location: Eleven *Stipa tenacissima* L. grasslands located along an environmental gradient from central to southeast Spain, covering the core of the distribution area of this vegetation type in Europe.

Methods: We jointly evaluated the effects of environmental conditions and plant–plant interactions on the phylogenetic structure – measured with the mean phylogenetic distance index – of the studied communities. As an indicator of environmental conditions, we used a PCA ordination including eight climatic variables. Different metrics were used to measure the following processes: (1) competition/facilitation shifts at the entire community level (species combination index), and (2) the effect of microclimatic amelioration provided by the two most important nurse plants on neighbour composition (similarity indices and comparison of the phylogenetic pattern between canopy patches and bare ground areas).

Results: Biotic interactions and, to a less extent, environmental conditions affected the phylogenetic pattern of the studied communities. While positive plant–plant interactions (both at community level and the scale of individual nurse plants) increased phylogenetic overdispersion, higher rainfall increased phylogenetic clustering. The opposing effects of environmental conditions and biotic interactions could be the main cause of the overall random phylogenetic structure found in most of these communities.

Conclusions: Our results illustrate, for the first time, how an overall random phylogenetic pattern may not only be promoted by the lack of influence of either environmental filtering or biotic interactions, but rather by their joint and opposing effects. They caution about making inferences on the underlying mechanisms shaping plant communities from the sole use of their phylogenetic pattern. We also provide a comprehensive set of easy-to-measure tools to avoid misleading conclusions when interpreting phylogenetic structure data obtained from observational studies.

Introduction

The recent development of molecular phylogenies has provided ecologists with a powerful tool to better understand the mechanisms shaping plant communities (Webb et al. 2002). The phylogenetic structure of a given community has been extensively used to assess the relative importance of environmental conditions (environmental filtering) or competition as drivers of community structure (reviewed in Webb et al. 2002; Cavender-Bares et al. 2009; Vamosi et al. 2009). However, although biotic interactions and environmental conditions are known to interactively affect plant community structure and dynamics (e.g. Lortie et al. 2004), the relative importance of both factors as drivers of the phylogenetic structure of ecological communities is still poorly understood (Cavender-Bares et al. 2004; Helmus et al. 2007; Elias et al. 2008; Verdú et al. 2009). Furthermore, the phylogenetic structure of a given community may be strongly affected by other factors, including herbivore or pollinator preference for closely related taxa (Webb et al. 2006; Sargent & Ackerly 2008), the spatial scale considered (Cavender-Bares et al. 2006; Silvertown et al. 2006; Kraft et al. 2007), historical or local constraints on species arrival to a given habitat type or location (Prinzing et al. 2008), or differences in niche and competitive ability among co-occurring species (Mayfield & Levine 2010). This complex array of factors makes the use of phylogenetic structure alone insufficient to correctly infer the mechanisms shaping natural communities (Helmus et al. 2007; Cavender-Bares et al. 2009; Mayfield & Levine 2010). Thus, more comprehensive approaches, including the study of environmental factors and co-occurrence patterns, have been recommended to further refine conclusions drawn from phylogenetic analyses (Helmus et al. 2007; Elias et al. 2008; Pausas & Verdú 2010).

Positive interactions among plants largely influence the structure and diversity of plant communities in virtually all terrestrial ecosystems (Callaway 2007; Brooker et al. 2008) and can even promote the expansion of realized species niches over evolutionary time frames (Valiente-Banuet et al. 2006; Lortie 2007). These interactions are highly dependent on the abiotic environment (Callaway 2007; Maestre et al. 2009) and on the evolutionary relationships between the interacting species (Valiente-Banuet et al. 2006; Castillo et al. 2010; but see Cahill et al. 2008). It has been hypothesized that harsh environmental conditions reduce phylogenetic diversity (Webb et al. 2002); however, the predicted prevalence of pair-wise positive interactions at the community level under harsh conditions (Bertness & Callaway 1994; but see Maestre et al. 2005) may increase phylogenetic diversity (Valiente-Banuet & Verdú 2007). The interplay between competition and facilitation, which depends on environmental conditions,

necessitates studying both environmental filtering and biotic interactions together to understand their relative importance as drivers of the phylogenetic structure of natural communities (Helmus et al. 2007; Cavender-Bares et al. 2009; Pausas & Verdú 2010).

Furthermore, in the same way that climate conditions act as environmental filters for plant communities (increasing phylogenetic clustering), the different micro-climatic conditions provided by nurse plants could promote an alternative environmental filter for their understorey species. This double environmental filtering is known to affect plant community composition at the patch scale (e.g. Pugnaire et al. 1996; Badano & Cavieres 2006) and therefore could also affect the phylogenetic pattern of entire communities. The effects of nurse plants on their understorey composition interact with those of climate; species less tolerant to the prevalent stressors are more abundant under the canopy of nurse plants than in open areas (e.g. Pugnaire et al. 1996; Tewksbury & Lloyd 2001), but the differences in composition between open/nurse patch types usually decrease under more benign environmental conditions (Callaway et al. 2000; Badano & Cavieres 2006). Thus, the interactions between climate conditions and plant–plant interactions at the patch scale may lead to counterintuitive results. Harsh environmental climate conditions may reduce phylogenetic diversity by means of environmental filtering. However, the same environmental conditions can increase the differences in plant composition between open and nurse patch types, thus increasing phylogenetic diversity.

To our knowledge, no previous study has evaluated the relative importance and joint effects of the different components of biotic interactions and environmental conditions as determinants of the phylogenetic structure of whole plant communities. We aimed to do so in semi-arid *Stipa tenacissima* L. grasslands located along an environmental gradient from central to SE Spain, taking into account the multiple components of biotic interactions likely to affect the phylogenetic pattern of these communities. In this study, we test the following hypotheses: (1) biotic interactions and environmental conditions interact and jointly define the phylogenetic pattern of the studied communities, and (2) environmental conditions affect both directly (via environmental filtering) and indirectly (via their effect on biotic interactions) the phylogenetic pattern of the studied communities. To test these hypotheses, we simultaneously measured the phylogenetic structure, climatic conditions and different components of biotic interactions (facilitation/competition shifts and the double environmental filtering promoted by nurse plants) along the environmental gradient studied.

Methods

Study area

We studied 11 *Stipa tenacissima* L. communities located along a climatic gradient spanning from the centre to the southeast of Spain (Table 1). Our sites have annual precipitation and temperature values ranging from 273 to 488 mm, and from 13 to 17 °C, respectively. To minimize the experimental noise produced by environmental factors other than climate, which could affect our conclusions, all the sites were located in limestone areas and had similarly oriented slopes. Vegetation was in all cases an open grassland dominated by *S. tenacissima*, with total cover values ranging from 35% to 68%. Sparse resprouting shrubs like *Quercus coccifera* L., *Pistacia lentiscus* L. and *Rhamnus lycioides* L. were also present in all sites.

Like any arid and semi-arid environment, vegetation at our study sites is severely constrained by scarce and unpredictable rainfall (Whitford 2002), but also by cold temperatures typical of inland Mediterranean areas (Olivera & Peñuelas 2004). Therefore, the environmental filter is assumed to be an important driver for the assemblage of species in *S. tenacissima* grasslands. Furthermore, these communities are strongly shaped by facilitation, with *S. tenacissima* or sprouting shrubs commonly acting as nurse plants (Armas & Pugnaire 2005; Maestre & Cortina 2005; Navarro et al. 2008). Furthermore, plant–plant interactions in this ecosystem depend on environmental conditions; different studies have shown how their direction or intensity shifts along environmental gradients smaller than that studied here

(Maestre et al. 2003; Gasque & García-Fayos 2004; Maestre & Cortina 2004; Soliveres et al. 2010). Thus, we would expect that both plant–plant interactions and the environment jointly affect assemblage of the communities studied and their phylogenetic pattern (Lortie et al. 2004; Helmus et al. 2007). On the other hand, important ecophysiological traits, such as dispersal or drought resistance, are extremely well conserved through evolutionary time in the Mediterranean flora (Herrera 1992; Ackerly 2004; Valiente-Banuet et al. 2006). This evolutionary conservatism in important ecological traits is needed to avoid confusion when inferring ecological processes from a given phylogenetic structure (Webb et al. 2002). In other words, to infer a higher importance of either facilitation/competition or environmental filters as drivers of community assemblage, evolutionary conservatism of most ecological traits is assumed or should be measured (Webb et al. 2002; Cavender-Bares et al. 2004; Silvertown et al. 2006). The well-known evolutionary conservatism of important ecological traits, together with the existence of strong relationships between plant–plant interactions and abiotic conditions, make *S. tenacissima* grasslands a well-suited ecosystem to address the role of plant–plant interactions, climatic conditions and their interaction, as drivers of community assembly and phylogenetic pattern.

Vegetation survey

The vegetation survey assessed two different spatial scales: the community level, including the vegetation

Table 1. Characteristics (environmental conditions, species richness, plant–plant interactions, phylogenetic pattern and coordinates) of each study site used in this paper. Highlighted in bold are the significant aggregation (positive species combination indices) or segregation (negative species combination indices) in species co-occurrences, and the significant over-dispersion [positive mean phylogenetic distance (MPD)] or clustering (negative MPD) in the phylogenetic pattern of the communities studied. Bold text with an asterisk indicates significant differences ($P < 0.05$), while the absence of the asterisk in the bold text indicates marginally significant differences ($0.1 < P < 0.05$).

Site	Climate	Species richness	COMBO	Similarity		MPD	MPD _{FAC} – MPD	Latitude	Longitude
				Stipa	Quercus				
Crevillente	–160.9	36	0.85	0.92	0.77	1.56	–2.61	38°14'15" N	0°55'49" W
El Ventós	–134.7	35	–1.83	0.79	0.72	0.38	0.70	38°28'14" N	0°37'03" W
Carrascoy	–121.6	38	–4.62*	0.75	0.55	–0.09	–1.06	37°48'02" N	1°18'32" W
Sierra Espuña	–14.4	32	1.31	0.93	0.86	–1.50*	0.73	37°49'27" N	1°40'41" W
Yecla	–10.8	47	0.37	0.89	0.56	0.55	–0.99	38°35'40" N	1°12'15" W
Zorita	43.4	38	–1.36	0.68	0.50	1.58	0.12	40°21'30" N	2°52'62" W
Barrax	49.0	24	–2.06*	0.81	0.86	–0.91	1.82	39°02'91" N	2°13'82" W
Titulcia	55.5	21	–4.40*	0.96	0.69	–0.82	1.84	40°11'28" N	3°30'13" W
Camporreal	62.2	9	–1.69	0.83	0.67	–0.79	–	40°19'72" N	3°25'36" W
Villarrobledo	63.7	18	–5.94*	0.65	0.66	–0.86	0.64	39°12'64" N	2°30'77" W
Morata	73.0	22	–3.10*	0.78	0.84	–0.99	1.75	40°27'62" N	3°05'31" W

Climate, values of the first component from a PCA performed with eight climate variables; COMBO, Standardized effect size (SES) value for the species combination index used; Similarity, Chao–Jaccard individual-based similarity index between Open microsites and the nurse studied (*Stipa tenacissima* or *Quercus coccifera*); MPD, SES for the mean phylogenetic distance; and MPD_{FAC} – MPD, phylogenetic pattern for the facilitated species assemblage in comparison with the phylogenetic pattern of the whole community.

composition at each study site, and the patch level (nested within the community level), including differences in composition among different patch types (i.e. open areas vs different nurses). At each site, we established a 30 m × 30 m plot representative of the surrounding vegetation. This plot size allowed the inclusion of a number of grass and shrub patches large enough to conduct the survey described below. In every plot, we located four 30-m long transects across the slope for the survey of vegetation at the community level, each 8-m apart. Along each transect, we placed 20 contiguous 1.5 m × 1.5 m quadrats and recorded the presence/absence of each perennial plant species within each quadrat. To evaluate the interactions at the patch level (i.e. the degree of microhabitat amelioration provided by the dominant nurses in the studied ecosystem – *Q. coccifera* sprouting shrubs and *S. tenacissima* tussocks, hereafter *Quercus* and *Stipa* patches, respectively), we established a different sampling design. We randomly selected ten *S. tenacissima* tussocks at each site, and sampled the area under their canopy using 0.5 m × 0.5 m quadrats (~30 quadrats per site). Ten paired open areas (areas located at least 1 m away from any *S. tenacissima* tussock or resprouting shrub, hereafter ‘Open patch’) were randomly selected adjacent to these tussocks. The same number of 0.5 m × 0.5 m quadrats sampled at each *Stipa* patch was sampled at each Open patch selected, to balance the sampling effort. Finally, the same area was also sampled under the canopies of five *Q. coccifera* individuals. The abundance (number of individuals) of all perennial plant species was recorded within each sampled quadrat. Annual plant composition in arid and semi-arid areas may substantially change through the year and among different years (Whitford 2002). Thus, we did not include annual species in our observational design to avoid confounding effects in the phylogenetic patterns or in the differences among study sites derived from sampling ‘incomplete’ communities depending on the time of the year that each site was sampled. The null modelling approach used (see below) allowed us to assess the degree of competition or facilitation among all the species in the community. Moreover, *S. tenacissima* and sprouting shrubs such as *Q. coccifera* have been shown as the main species having facilitative effects on their understoreys in these ecosystems (e.g. Pugnaire et al. 1996; Maestre et al. 2003; Maestre & Cortina 2005; Navarro et al. 2008). Hence, since these species are the only ones to likely have an important effect on their neighbours, by assessing their impacts we can assume that we have a good surrogate of the effect of plant–plant interactions at the whole community level (Cavieres & Badano 2009).

Data gathering and reduction

Synthesizing climate conditions

Eight climate variables (annual radiation, minimum, maximum and mean temperature, annual rainfall, temperature range (maximum–minimum) and minimum and maximum temperatures for the coldest and warmest month, respectively) were collected for each site using available climate models (Ninyerola et al. 2005). We reduced these to a single synthetic variable using PCA to obtain a more general assessment of their influence. We used the first component of this PCA (referred in the main text to as *Climate*) as our surrogate of the climate gradient present at our sites. This component explained 88.6% (eigenvalue = $8.08 \cdot 10^3$) of the variance in the climate data, and was highly correlated with both rainfall and radiation (eigenvector coefficients = 0.864 and –0.502 for rainfall and radiation, respectively, the rest of the coefficients in the eigenvector were <0.03 in all cases). PCA was carried out using the Primer v. 6 statistical package for Windows (PRIMER-E Ltd., Plymouth Marine Laboratory, Devon, UK).

Assessment of phylogenetic structure

We assembled a phylogenetic tree for the 80 species included in this study using Phylomatic2 (Webb et al. 2008). All the families in our data set matched the family names of the angiosperm megatree used in Phylomatic (R20091110.new), which was based on the APG III phylogenetic classification of flowering plant orders and families (Angiosperm Phylogeny Group 2009). Within-family phylogenetic relationships were further resolved based on data from various published molecular phylogenies (Asteraceae: Funk et al. 2005; Susanna et al. 2006; Cistaceae: Guzmán & Vargas 2009; Guzmán et al. 2009; Fabaceae: Allan & Porter 2000; Allan et al. 2004; Wojciechowski et al. 2004; Poaceae: Bouchenak-Khelladi et al. 2008, 2010; Rubiaceae: Bremer & Eriksson 2009). After assembling the phylogenetic tree, we adjusted its branch lengths with the help of the Phylocom BLADJ algorithm, which fixes the age of internal nodes based on clade age estimates, whereas undated internal nodes in the phylogeny are evenly spaced (Webb et al. 2008). We used TimeTree (Hedges et al. 2006) to fix as many nodes in the tree as possible, or with other published sources when this database did not provide any data (Cistaceae: Guzmán & Vargas 2009; Guzmán et al. 2009; Asteraceae: Kim et al. 2005; Torices 2010; Poaceae: Bouchenak-Khelladi et al. 2010; Fabaceae: Lavin et al. 2005; Bello et al. 2009; Brassicaceae: Franzke et al. 2009; Caryophyllaceae: Valente et al. 2010). This procedure resulted in the fixation of 45 nodes (representing almost 70% of internal nodes of our tree).

Apart from the prevailing ecological processes driving assemblage of the studied communities, both the selected species pool, the local community size/total species ratio and the spatial scale strongly influence the results obtained for a given phylogenetic pattern (reviewed in Cavender-Bares et al. 2006; Kraft et al. 2007; Kraft & Ackerly 2010). To avoid misleading conclusions, we constrained our species pool to those species occurring in the studied community, and not to species present in other ecosystems throughout the whole studied region. The use of regional floras to infer our species pool would include species that never occur in *S. tenacissima* grasslands, and therefore would affect our results and conclusions. Furthermore, spatial scales too large or too small may overestimate the influence of environmental filtering or biotic interactions, respectively (e.g. Cavender-Bares et al. 2006). The spatial scale selected (30 m × 30 m) was of a reasonable size to include both of these processes, if they are important to determine community assemblage (e.g. Rajaniemi et al. 2006), and community size included ~33% of the total species pool, as recommended in previous studies (30–60% of the total species pool; Kraft et al. 2007). Thus, we believe that the species pool, the community size to species pool relationship and the spatial scale used are appropriate to test our hypotheses.

Once we assembled the phylogenetic tree for all the species surveyed, we measured the mean phylogenetic distance (hereafter MPD) as an indicator of phylogenetic pattern (Webb et al. 2002; Kraft et al. 2007). MPD is related to the number of species for each community (Webb et al. 2008); to avoid this confounding factor when interpreting our results, we calculated the standardized effect size (SES) of MPD with the Picante package (Kembel et al. 2010) for R version 2.10.1 (R Development Core Team, R Foundation for Statistical Computing, Vienna, Austria). The SES was calculated as $(MPD_{obs} - MPD_{sim}) / sdMPD_{sim}$, where MPD_{obs} was the observed value of the MPD for each community and MPD_{sim} and $sdMPD_{sim}$ were the mean and standard deviation, respectively, of the MPD obtained from the 5000 simulations performed under the null model. Two different null models were used to do these calculations. The first (phylogeny.pool), randomizes species identity across the entire phylogeny; the second (taxa.label) also randomizes species identity, but maintains species richness in each sample (each of the 11 plots in our case; Webb et al. 2008). Since results for both null models were highly correlated (Pearson's correlation $r > 0.95$), we only present here the results obtained with the phylogeny.pool null model. Positive SES having an associated P -value > 0.95 indicates significant phylogenetic over-dispersion in the sampled community, while negative SES with associated P -values < 0.05 indicates phylogenetic clustering.

Evaluating plant–plant interactions

We estimated plant–plant interactions at the community level using null models based on the patterns of species co-occurrence found within the 80 1.5 m × 1.5 m quadrats (Gotelli & Graves 1996). We estimated species co-occurrence with the species-combination index (hereafter COMBO, *sensu* Gotelli 2000), which examines the number of possible species pairs that are actually observed in the community (Gotelli 2000). The logic underlying COMBO is that competitive exclusion (or facilitation) should result in fewer (or more) species pairs co-occurring than expected by chance. This index depends on the number of species (and therefore possible species pairs) in this community. To avoid this artefact, we obtained a standardized effect size for COMBO as $(I_{obs} - I_{sim}) / S_{sim}$, where I_{obs} is the observed value of COMBO, and I_{sim} and S_{sim} are the mean and standard deviation, respectively, of this index obtained from the n simulations performed (Gotelli & Entsminger 2006). Standardized effect size (SES) values of COMBO less than or greater than zero indicate prevailing spatial segregation (competition) and aggregation (facilitation; Tirado & Pugnaire 2005) among the species within a community, respectively. We used 'fixed rows–equiprobable columns' null models and 5000 simulations. With this approach, each species conserved its own abundance (rare species remained rare and common species remained common) and each quadrat was assumed to have the same probability of being colonized as the remaining quadrats (Gotelli 2000). We decided to choose this index instead of the more widely used C-score (Stone & Roberts 1990; Gotelli 2000). This was chosen because of the sensitivity of the C-score to the existence of two different species guilds (i.e. facilitated vs non-facilitated species) in which species within each guild co-occur with each other, but co-occur much less than would be expected by chance with species from the other guild (Stone & Roberts 1992). This would render a high C-score index, indicating that the community is mainly driven by competition when, in fact, facilitation would be prevalent (see detailed discussion in Stone & Roberts 1992). COMBO is more robust to this situation, and thus we decided to use it in our study. We calculated both indices and found that they were correlated ($r = -0.59$; $P = 0.054$; $n = 11$) and produced similar patterns; thus, only COMBO results are presented here.

The environmental conditions beneath the canopy of the nurse plants can profoundly differ from those in bare ground areas (Franco & Nobel 1989; Callaway 1995). Hence, in the same way that different local environmental conditions act as an environmental filter (Webb et al. 2002), we would expect that this microhabitat differentiation promoted by nurse plants would act as a 'double environmental filter' (Badano & Cavieres 2006). To assess the

degree of this double environmental filter promoted by *Stipa* and *Quercus* patch types, we used the Chao–Jaccard abundance-based similarity index (hereafter *Similarity*; Chao et al. 2005). *Similarity* is based on the probability that two randomly chosen individuals, one from each of two selected patch types (Open, *Stipa* or *Quercus*), belong to species shared by both patch types. A lower *Similarity* among *Stipa/Quercus* patches and open areas will indicate a higher influence of the double environmental filter provided by nurse canopies. We calculated *Similarity* by summing over the number of individuals and species recorded in all of the 0.5 m × 0.5 m quadrats per patch type and site ($n = 30$) using EstimateS 8.2.0 for Windows (Colwell 2000).

As a secondary assessment of this double environmental filter, we calculated the difference between the MPD for the whole set of species in a given community (described in *Assessment of phylogenetic structure* above) and the MPD for only the facilitated species guilds (hereafter MPD_{FAC}). If the double environmental filter proposed has a significant effect, the facilitated species guilds should be more phylogenetically clumped than the whole species assemblage of each community, i.e. $MPD > MPD_{FAC}$, because of their shared adaptations to the same environmental conditions.

Statistical analyses

To test our hypotheses we used regression analyses, with MPD as the response variable and with either COMBO or *Similarity* between Open–*Stipa* and Open–*Quercus* microsites (our surrogates of biotic interactions at the community and patch scales, respectively), as independent variables (see Table 2 for a summary of our analytical approach). Considering biotic interactions at both spatial scales (community and patch) separately is important because their interactions with climate may lead to different results (see below). Thus, two regression models, one for each scale considered, were fitted. In the community-scale model, we included as independent variables: *Climate* (first PCA component), COMBO (representing biotic interactions at the community scale) and their interaction. In the patch-scale model, we used as independent variables: *Climate*, *Similarity* between Open and *Stipa* patch types, *Similarity* between Open and *Quercus* patch types, and their interaction terms. In this second model, the interactions '*Similarity* Open–*Stipa* × *Climate*' and '*Similarity* Open–*Quercus* × *Climate*' were correlated ($r = 0.56$, $P = 0.038$). To avoid multicollinearity, we introduced just one of these interaction terms in our model. Since *Similarity* between Open–*Quercus* patch types, but not *Similarity* between Open–*Stipa* patch types, was a significant predictor of the MPD, we used the *Similarity* Open–*Stipa* × *Climate* interaction. The interaction terms were built by multiplying the Z-scores (obtained by subtracting the mean and dividing

by the SD) of both *Climate* and the surrogate of the biotic used (either COMBO or *Similarity*). To aid confidence in these results, we also tested our hypotheses using mmodel selection based on information theory and OLS regression (Burnham & Anderson 2002). These analyses produced very similar results, and thus are not presented in the text (see details in Appendix S1).

Regarding the interpretation of these models, if both climate conditions and biotic interactions (at the community and patch scales) are important drivers of the phylogenetic pattern, we would expect them to be significant predictors of the MPD in both regression models, being the most important predictor explaining a higher amount of the variance in MPD (Table 2). If only biotic interactions at the community or at the patch scale are important drivers of the phylogenetic patterns observed, we would expect this predictor to be significant only in one of the two regression models performed. If the interaction between climate and biotic interactions is important to define the phylogenetic pattern of the studied communities, we would expect the interaction term introduced in the models to be significant. The latter result would support our second hypothesis (i.e. the existence of direct and indirect effect of environmental conditions on phylo-diversity). To aid with interpretation of these models, separate linear regressions were performed to evaluate pair-wise relationships between the variables involved [*Climate* vs MPD (Fig. 1a); *Climate* vs COMBO, *Similarity* and MPD_{FAC} – MPD (Appendix S2; Fig. 1c); COMBO and *Similarity* vs MPD (Fig. 1b,d)]. The different '*Climate* × biotic interactions' interaction terms were not included in these analyses since they were not significant in any of the models tested (see below).

In the regression models described above, we applied a step-wise procedure to assess significance of the different introduced predictors. Type I (or α) error is highly dependent on the sample size (Quinn & Keough 2002); thus, we relaxed the level of statistical significance to $\alpha < 0.10$, to account for our low sample size. We hereafter refer to those results with P -values < 0.05 as significant, and those with $0.10 < P < 0.05$ as marginally significant. Apart from giving the commonly used type I error in our results, we also provide the type II (or β) error in the pair-wise regressions performed (Appendices S2–S4). This error informs us about the probability of accepting our null hypothesis (no relationship between the studied variables) when this hypothesis does not hold true. The possibility of this error increases with lower sample sizes, such as those used in this study. We calculated this error using an online calculator (Soper 2011) for those analyses that were not significant or marginally significant.

Our data met the requirements of regression and correlation analyses, and thus were not transformed. Model

Table 2. Summary of the different metrics used in this paper, showing the factor, response variable, spatial scale (patch or community, the former nested within the latter) and mechanism to which they are related. The results corresponding to each analysis are also detailed in the table. Predictions based on current literature are summarized. MPD_{FAC} , phylogenetic pattern for the facilitated species assemblage in comparison with the phylogenetic pattern of the whole community. Other abbreviations as in Table 1.

Mechanism	Factor	Response	Scale	Metric	Prediction
Effect of environmental filtering on phylogenetic pattern	Environmental conditions	Phylogenetic pattern (Appendix S1)	Community	Climate vs MPD	Drier conditions increase phylogenetic clustering
Facilitation/competition shift depending on environmental conditions		Plant–plant interactions (Appendix S2)	Community	COMBO vs Climate	Drier conditions increase facilitation (positive COMBO scores, low <i>Similarity</i> between patch types, high phylogenetic clustering among facilitated species)
The degree of microhabitat amelioration changes depending on the environmental conditions			Patch	<i>Similarity</i> vs Climate $MPD_{FAC} - MPD$ vs Climate	
Facilitation/competition at community level	Plant–plant interactions	Phylogenetic pattern (Figures 2b and 2d)	Community	COMBO vs MPD	Dominance of either facilitation or competition (significant COMBO scores) increases phylogenetic over-dispersion. Lower <i>Similarity</i> between patch types also leads to phylogenetic over-dispersion
Microhabitat amelioration (double habitat filtering)			Patch	<i>Similarity</i> vs MPD	
Environmental filtering affects plant–plant interactions at the community level, which indirectly modify the MPD	Plant–plant interactions × Environmental conditions	Phylogenetic pattern (Table 3)	Community	Climate × COMBO vs MPD	Biotic interactions and environmental filters jointly influence the phylogenetic pattern
Environmental filtering affects microhabitat amelioration, which indirectly modify the MPD			Patch	Climate × <i>Similarity</i> vs MPD	

selection was conducted using SAM v. 4.0 (Rangel et al. 2010). The rest of analyses were carried out using SPSS 13.0 for Windows (Chicago, IL, USA).

Results

Do biotic interactions and environmental conditions interact and jointly define the phylogenetic pattern of the studied communities?

Most of the studied sites showed a random phylogenetic structure (Table 1). Despite this lack of phylogenetic pattern, multiple regression models at both the community and patch scales identified biotic interactions as the main driver of phylogenetic diversity along the environmental gradient studied. Their importance was higher than that of climate conditions and the *Climate* × biotic interactions interaction terms introduced in the models (Table 3). These results were also confirmed by the model selection using information theory (Appendix S1). A higher co-occurrence among species pairs or a lower similarity between patch types (more specifically between Open–*Quercus* patches) promoted an increase in the phylogenetic diversity of the studied communities (Fig. 1b,d). Interest-

ingly, the significance of climate conditions as a predictor of the phylogenetic pattern varied between the two regression models. In the model including COMBO (community scale; Table 3), only biotic interactions were selected as a significant predictor, explaining the 45% of the variance in MPD. It is important to note that we found an outlier when analysing MPD vs COMBO [Cook's distance ~1 (0.92); important change in the studied relationship: $R^2 = 0.11$, $P = 0.314$ with outlier vs $R^2 = 0.45$, $P = 0.035$ without outlier]. Therefore, we removed this outlier from the regression analyses performed, although it is shown in Fig. 1b. In the model including *Similarity* indices (patch scale; Table 3, Appendix S1), *Climate* was a significant predictor of secondary importance after *Similarity* between Open and *Quercus* patches. *Climate* explained over ~20% of the variance in MPD, with wetter sites showing a reduced phylogenetic diversity (Fig. 1a).

Overall, our results, and specifically those relating *Climate* and *Similarity* between Open–*Quercus* patch types, partially support the idea that the phylogenetic over-dispersion promoted by biotic interactions and the phylogenetic clustering observed in wetter climates could cancel each other out. This might be the most plausible

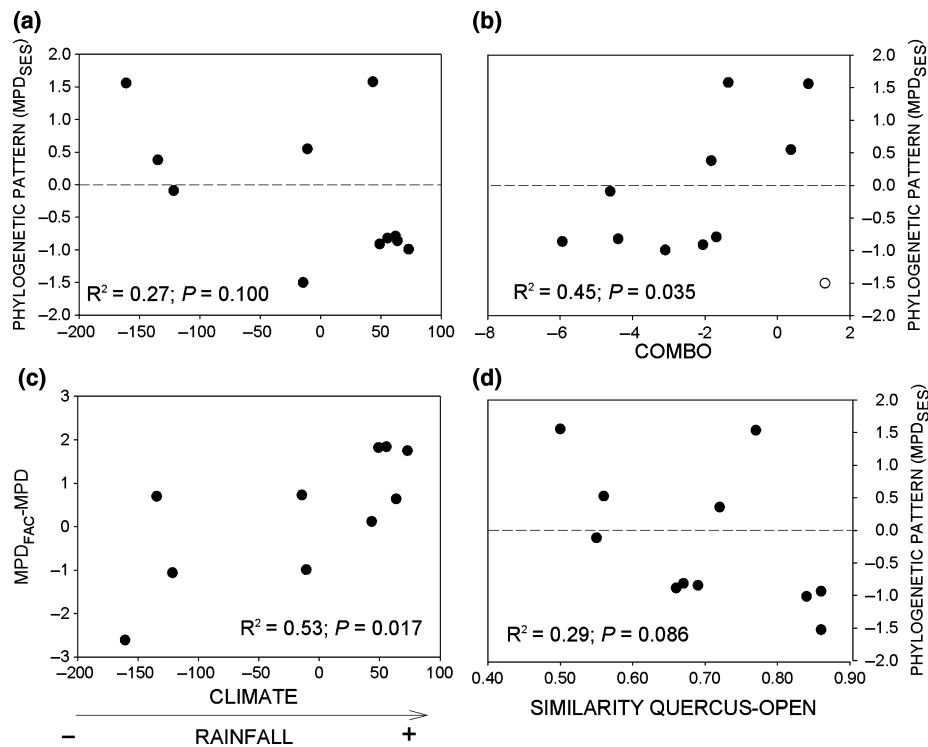


Fig. 1. Pair-wise relationships between the phylogenetic pattern [standardized effect size of the mean phylogenetic distance (MPD_{SES})] of the studied communities and the most important variables tested (*Climate*, COMBO, and *Similarity* between Open and *Quercus*; panels **a**, **b** and **d**, respectively). Figure also includes the relationship between *Climate* and the MPD_{FAC} – MPD coefficient (panel **c**). Values above 1.5 or below –1.5 indicate a significant departure from randomness in the phylogenetic pattern. Results of the linear regression are given in the figure. The outlier removed in the relationship between COMBO and MPD_{SES} (panel **b**, see main text for details) is marked with an open dot.

explanation for the overall random phylogenetic structure found in most of the studied communities (Table 1). To fully support this idea, sites with a random phylogenetic pattern under high rainfall availabilities should also show either positive COMBO scores or low *Similarity* indices; and *vice versa* (low rainfall associated with either negative COMBO scores or high *Similarity* indices). Communities

with random phylogenetic patterns having relatively high rainfall availabilities (PCA scores > 40; see Appendix S1) also had relatively low Open–*Quercus Similarity* indices (Titulcia, Camporreal and Villarrobledo). Conversely, those sites with low rainfall (PCA scores < –100; see Appendix S1) and with a random phylogenetic pattern showed either a significantly negative COMBO score or high

Table 3. Summary of the multiple regression models performed with the phylogenetic pattern [standardized effect size of the mean phylogenetic distance (MPD_{SES})] of the studied communities as a response variable. Predictors introduced in the model at the community level were COMBO, *Climate* and *Climate* × COMBO interaction. The step-wise procedure used only selected COMBO as a significant predictor, thus only this variable is included. Predictors introduced in the model at the patch scale were *Similarity* between Open and *Stipa*, *Similarity* between Open and *Quercus* ('*Similarity*' in this table), *Climate* and *Climate* × *similarity* Open–*Quercus* interaction. The total amount of variance explained by each model (R²), its P-value and the standardized coefficient (β) for each predictor are given. At the patch scale, three models with an increasing number of predictors were chosen. Since the increase in the amount of variance explained was marginally significant (P = 0.08) between consecutive models, the three are summarized in the figure. Last column in the table (effect) summarizes the effect of each significant variable on the phylogenetic pattern of the studied communities.

Scale	Model	Introduced variables	R ²	P-value	β	Effect
Community	1	COMBO	0.45	0.035	0.668	Facilitation increases phylodiversity
Patch	1	<i>Similarity</i>	0.29	0.086	–0.541	Wetter conditions or higher similarity
	2	<i>Similarity</i>	0.53	0.049	–0.507	between microsites reduce phylodiversity
	3	<i>Climate</i>			–0.487	
		<i>Similarity</i>	0.70	0.031	–0.439	
		<i>Climate</i>			–0.454	
		<i>Climate</i> × <i>Similarity</i>			–0.419	

Similarity values. It must be noted, however, that results found in four of the 11 sites studied contradicted this idea.

Do environmental conditions affect both directly and indirectly the phylogenetic pattern of the studied communities?

Although our type II error rates were high ($\beta > 0.25$), and thus we cannot be sure of these particular results, none of the surrogates of biotic interactions employed were related to *Climate* ($R^2 < 0.15$ and $P > 0.3$ in all cases; Appendix S2). This lack of dependence of biotic interactions on climate conditions would explain the lack of significance of the interaction terms as predictors of MPD. However, one important exception was found regarding this pattern; while *Similarity* between patches was not significantly affected by *Climate*, we found a significant and positive effect of *Climate* on the $MPD_{FAC} - MPD$ difference (Fig. 1c). This latter result suggests that decreasing rainfall availability increased the degree of double environmental filtering provided by the nurses, with a higher degree of phylogenetic clumping among the facilitated species under drier conditions.

Discussion

Unlike most previous studies, which assume rather than measure the possible mechanisms behind a phylogenetic pattern (reviewed in Pausas & Verdú 2010), in this study we jointly considered information on abiotic conditions, state-of-the-art phylogenetic tools and different aspects of biotic non-trophic interactions (competition/facilitation shifts and double environmental filter). With this approach we were able to explore the joint effects and tease apart the relative importance of plant–plant interactions and the environment as drivers of the phylogenetic structure of *S. tenacissima* grasslands. We are confident that the experimental approach followed allowed us to correctly assess the influence of both environmental conditions and biotic interactions on the phylogenetic patterns of the studied communities (Cavender-Bares et al. 2006; Kraft et al. 2007; see *Methods* above). However, our results need to be interpreted with caution, given our low sample size and the lack of measurements of important ecological traits (we assumed that they are evolutionary preserved in the studied species based on previous studies; Herrera 1992; Ackerly 2004; Valiente-Banuet et al. 2006). Despite these limitations, our results suggest that biotic interactions are more important than environmental conditions in determining the phylogenetic structure of *S. tenacissima* grasslands, although both factors seemed important drivers of such structure (Helmus et al. 2007; Pausas & Verdú 2010). Caution is increasingly being recommended when inter-

preting a given phylogenetic pattern because of the existence of different processes leading to the same result (Silvertown et al. 2006; Prinzing et al. 2008; Cavender-Bares et al. 2009; Mayfield & Levine 2010). Our results highlight the necessity of taking into account environmental conditions and different components of the biotic non-trophic interactions when interpreting such patterns, and provide a comprehensive set of easy-to-measure tools to avoid misleading conclusions when interpreting phylogenetic structure data obtained from observational studies.

Biotic interactions and environmental conditions jointly define the phylogenetic pattern of the studied communities

We found partial support for the patterns found in previous studies, with facilitative interactions (positive COMBO scores or low *Similarity* indices) increasing the phylogenetic diversity of plant communities (Valiente-Banuet & Verdú 2007). However, contrary to our expectations and in sharp contrast with most current literature, wetter climate conditions slightly reduced (rather than increased) phylodiversity. Biotic interactions at both community and patch scales were more important than *Climate* as predictors of the phylogenetic pattern of the studied communities (Table 3). Several possibilities arise to explain the relatively weak effect of climate conditions on the phylogenetic patterns observed: (1) climate conditions were not sufficiently harsh to act as environmental filters for the studied communities, which is unlikely since we found a counterintuitive increase in phylogenetic clustering under the most mesic, rather than under the most xeric, conditions; (2) we only used data from a climate atlas, ignoring other important environmental features such as herbivory pressure (Cavender-Bares et al. 2009) or soil fertility (Fine & Kembel 2011), hence, we could be underestimating the influence of other important environmental filters as drivers of the assemblage of the studied communities; and (3) the presence of nurse plants reduced the strength of environmental filters by providing microclimatic amelioration to their neighbours, and therefore reducing their influence on community assemblage (Lortie et al. 2004; Valiente-Banuet et al. 2006). This would explain the high importance of biotic interactions as drivers of the phylogenetic patterns found, and the counterintuitive increase in phylogenetic clustering under mesic conditions.

Our low statistical power and the contradictory results found do not allow us to be confident about the existence of interactions between climatic conditions and biotic interactions. On one hand, the *Climate* × biotic

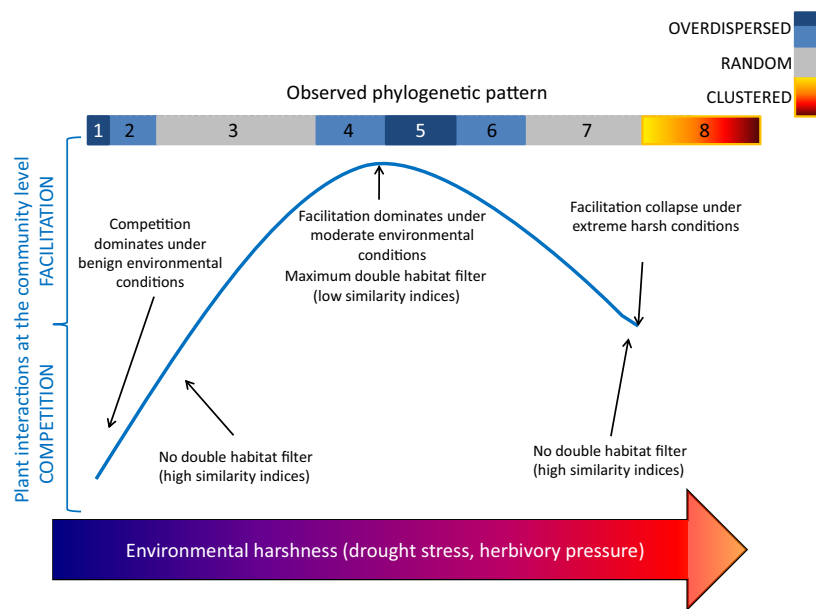


Fig. 2. Theoretical framework predicting the joint effect of plant–plant interactions and the environment on the phylogenetic pattern of plant communities. This model proposes eight different scenarios, and is based on changes in the relative importance of plant interactions and environmental filters in the assemblage of the studied communities along environmental gradients. From left to right: (i) competition dominates under benign climate conditions, with no importance of environmental factors (scenarios 1–2); (ii) as we move towards less benign climate conditions, competition is reduced and its importance for community assemblage equilibrates with the importance of environmental factors, producing a random phylogenetic pattern (scenario 3); (iii) the dominance of facilitation in the assemblage of plant communities under moderate environmental conditions leads to over-dispersed phylogenetic patterns (scenarios 4–6); (iv) under harsher conditions, facilitation starts to collapse and so does its importance for community assemblage, therefore a random phylogenetic pattern is expected (scenario 7); and (v) only environmental filters are important under extremely harsh conditions. Thus only species sharing traits adapted to live under such conditions will survive and a clustered phylogenetic pattern is expected (scenario 8).

interactions interaction terms did not show any significant relationship with the phylogenetic pattern in most cases (Table 3, Appendix S1): the non-significant relationships between *Climate* and the different surrogates of biotic interactions also point in the same direction (Appendix S2; see Soliveres et al. 2011 for a detailed discussion of this topic). On the other hand, wetter conditions significantly reduced the phylogenetic clustering among the facilitated species guild (i.e. $MPD_{fac} - MPD$ coefficient; Fig. 1c). This suggests that the negative relationship between *Climate* and MPD could be in part mediated by the effect of climate conditions on species co-occurrence. The contrasting effects of *Climate* found for the *Similarity* indices (no influence; Appendix S2) and for the $MPD_{fac} - MPD$ coefficient (an increase in phylogenetic clustering among facilitated species with drier conditions; Fig. 1c) suggest that although climatic conditions did not affect the microclimatic amelioration of each nurse type separately (*Similarity* indices), they affected the phylogenetic pattern of the community by altering the degree of phylogenetic clustering among the facilitated species. Moreover, it is clear that wetter environmental conditions counterintuitively worked as an environmental filter and increased phylogenetic clustering. The only plausible explanation for these results is an

indirect effect of environmental conditions on community assemblage mediated by their effect on plant–plant interactions, either through a reduction in the importance of positive plant–plant interactions or through an increase in competitive exclusion (Bertness & Callaway 1994; Lortie et al. 2004; see also Fig. 2).

Regardless of which process was more important, our study suggests that both climate conditions and biotic interactions affected the phylogenetic pattern of the studied communities (Table 3, Appendix S1). Similar results have previously been found in fish (Helmus et al. 2007) and insect (Elias et al. 2008) communities. The phylogenetic over-dispersion promoted by biotic interactions and the phylogenetic clustering observed in wetter climates could cancel out each other, and seem to be the most plausible explanation for the overall random phylogenetic structure found in most of the studied communities (Table 1). This explanation was partially supported by results found in seven out of the 11 study sites (see Results), where random phylogenetic patterns were found in sites with high rainfall availabilities associated with low *Open–Quercus Similarity* indices, and in sites with low rainfall associated with negative COMBO scores or high *Open–Quercus Similarity* values. Although the

dominance of dispersal limitations and stochastic processes may also lead to a random phylogenetic pattern (Kembel & Hubbel 2006; Kraft et al. 2007), our study suggests that the joint and contrary effects of both environmental filters and biotic interactions (especially at the patch scale), and not these stochastic processes, promoted a random phylogenetic pattern, at least in most of the studied communities.

Theoretical and methodological implications

The use of manipulative experiments including different communities under contrasting environmental conditions and measurement of the direct and indirect effects of biotic interactions have been recommended to overcome current limitations associated with the interpretation of phylogenetic structure data alone (Cavender-Bares et al. 2009; Vamosi et al. 2009; Pausas & Verdú 2010). However, such experiments are often logistically prohibitive. The observational and analytical approach employed here may serve as an alternative to experimentation, and can help to avoid misleading conclusions when inferring the several possible mechanisms underlying the assemblage of natural communities.

Considering our own results and those of previous research, we propose a theoretical framework aiming to predict the joint effects of biotic interactions and environmental conditions on the phylogenetic structure of plant communities (Fig. 2). The predictions of this model only hold for those spatial scales in which both biotic interactions and environmental filtering are important determinants of community assemblage. Changes in the interpretation of a given phylogenetic pattern with scale have been addressed elsewhere (Cavender-Bares et al. 2006, 2009; Silvertown et al. 2006; Kraft et al. 2007). We assume evolutionary conservatism in important eco-physiological traits of most plant lineages (e.g. Herrera 1992; Prinzing et al. 2001; Valiente-Banuet et al. 2006). A second assumption in our model is the prevalent role of plant interactions as drivers of the phylogenetic structure of the studied communities (Valiente-Banuet et al. 2006; Elias et al. 2008; Table 3). Current theoretical models regarding the behaviour of plant interactions at the community level along environmental gradients agree in the prevalence of positive interactions at moderate levels of environmental stress (e.g. Maestre & Cortina 2004; Holmgren & Scheffer 2010; scenarios 4–6 in Fig. 2). These positive interactions, both at the community and patch scale, will either disappear under extremely harsh conditions because nurse plants will not be able to improve microclimatic conditions sufficiently to allow recruitment of most species under such conditions (e.g. Kitzberger et al. 2000; Smit et al. 2007; scenario 8), or

shift to competition under more benign conditions (Bertness & Callaway 1994; scenarios 1–2 in Fig. 2). The third assumption of this model is that the prevalence of either facilitation or competition will overcome any environmental filtering (i.e. via microclimate amelioration or because of high availability of resources) and therefore will lead to phylogenetic over-dispersion, as does a high degree of double environmental filtering (Webb et al. 2002; Valiente-Banuet & Verdú 2007; scenarios 1–2 and 4–6 in Fig. 2). This phylogenetic over-dispersion will increase together with the relative importance of biotic interactions for community assemblage.

We do not specifically discuss here the processes occurring at the community or the patch scale because they are tightly related. Facilitative interactions among plant species at the community level are only explained by the microenvironmental amelioration provided by the different nurses present in such communities (i.e. the degree of double habitat filtering). The reason for measuring these two different surrogates of plant–plant interactions (COMBO, at the community scale, and *Similarity* and $MPD_{\text{fac}} - MPD$ coefficient, at the patch scale) are: (1) the degree of spatial co-occurrence among plants can be caused by mechanisms other than the interactions among these plant species, such as soil resource heterogeneity. These confounding factors are reduced with the spatial scale of the sampling and thus measuring plant–plant interactions at different spatial scales add confidence to the results. (2) Although it is beyond the scope of this paper, we include predictions at both community and patch scales because studying plant–plant interactions at different scales may help to better understand the implications of their effect on important ecosystem attributes related to phylogenetic diversity. While positive plant interactions increase phylogenetic diversity at the community scale, they reduce it at the patch scale (as suggested by the $MPD_{\text{fac}} - MPD$ results). Hence, plant interactions may reduce phylodiversity and its related processes at this patch scale. For example, more phylodiverse communities have been shown to provide more ecosystem services and functions (e.g. Forest et al. 2007; Constán-Nava et al. unpubl. data). Thus, facilitative interactions could increase those functions or processes working at the community-scale (i.e. abundance and diversity of medicinal plants, Forest et al. 2007; higher resilience to disturbances, Zavaleta et al. 2010), but reduce those processes occurring at the patch scale (i.e. nutrient cycling, Constán-Nava et al. unpubl. data; avoidance of phytophagy, Yguel et al. 2011). Therefore, simultaneously studying plant–plant interactions and their effect on phylodiversity at different scales may help to better understand the relative importance of biotic interactions on the assemblage of – and processes related to – plant communities.

Examples of both competition-dominated (scenarios 1–2 in Fig. 2) and facilitation-dominated (scenarios 4–6 in Fig. 2) communities that show an over-dispersed phylogenetic pattern are abundant in the literature (e.g. Webb et al. 2002; Cavender-Bares et al. 2004; Valiente-Banuet & Verdú 2007). However, a lower importance of plant–plant interactions for community assemblage will equilibrate their importance with environmental conditions as drivers of community assemblage and therefore lead to a phylogenetic random pattern (scenarios 3 and 7 in Fig. 2; which correspond with most of our own plots). Conversely, when the influence of plant interactions on community assemblage is minimum relative to environmental filters, we will expect phylogenetic clustering in the community. This clustering will be more pronounced when the importance of the environmental factors for community assemblage is higher (scenario 8 in Fig. 2). This would be the case for those ecological communities measured at scales where positive interactions are not important (Cavender-Bares et al. 2006; Kraft et al. 2007), or those strongly dominated by environmental factors such as fire, generalist herbivores, climate conditions or soil type (Verdú & Pausas 2007; Cavender-Bares et al. 2009; Fine & Kembel 2011; Machac et al. 2011). An increase in the importance of positive plant–plant interactions in the latter examples, either during secondary succession after fire (Verdú et al. 2009), by protecting grazing-sensitive species from herbivory (Callaway et al. 2000; Smit et al. 2007) or by improving soil or environmental conditions (Callaway 2007; Espeland & Rice 2007; our own results), is likely to increase phylogenetic diversity and therefore lead to a random phylogenetic pattern (scenario 7 in Fig. 2). It must be noted, however, that our predictions need to be considered with caution since some of them are speculative, as they have not been tested yet, and are beyond our own results. These predictions can be tested and further refined through the application of the analytical techniques provided here on the large data sets from observational assessments of plant composition that have become increasingly available in the literature.

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Supporting Information

Additional supporting information may be found in the online version of this article:

Appendix S1. Alternative analysis using model selection.

Appendix S2. Relationships between *Climate* and biotic interactions.

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