

Uncovering multiscale effects of aridity and biotic interactions on the functional structure of Mediterranean shrublands

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Summary

1. Habitat filtering (HF, trait convergence) and niche differentiation (ND, trait divergence) are known to impact upon plant community structure. Both processes integrate individual responses to the abiotic environment and biotic interactions. Thus, it is difficult to clearly identify the underlying abiotic and biotic factors that ultimately impact community structure by looking at community-level patterns of trait divergence or convergence alone.

2. We used a functional trait-based and multiscale approach to assess how biotic interactions and aridity determine the functional structure of semi-arid shrublands sampled along a large aridity gradient in Spain. At the regional scale, we investigated functional differences among species (axes of specialization) to identify important traits for community assembly. At the community scale, we evaluated the relative impact of HF and ND on community structure using a null model approach. Finally, at the plant neighbourhood scale, we evaluated the impact of biotic interactions on community structure by investigating the spatial patterns of trait aggregation.

3. The shrub species surveyed can be separated along four axes of specialization based on their above-ground architecture and leaf morphology. Our community scale analysis suggested that the functional structure of semi-arid communities was clearly non-random, HF and ND acting independently on different traits to determine community structure along the aridity gradient. At the plant neighbourhood scale, the spatial distribution of species was also clearly not random, suggesting that competition and facilitation impacted on the observed changes in the functional diversity of shrubland communities along the aridity gradient.

4. *Synthesis*: Our results demonstrated that HF and ND acted simultaneously on independent traits to jointly determine community structure. Most importantly, our multiscale approach suggested that competition and facilitation interplayed with aridity to determine this structure. Competition appeared to be constant along the aridity gradient and explained the high functional diversity observed in semi-arid shrublands. Facilitation affected subordinate and rare species and, thus, may act to enhance the biodiversity of these ecosystems. Finally, the framework employed in our study allows moving forward from the examination of patterns to the development of mechanistic trait-based approaches to study plant community assembly.

Key-words: aridity, community assembly, competition, determinants of plant community diversity and structure, facilitation, habitat filtering, Mediterranean shrubland, niche differentiation, plant functional trait, spatial analyses

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Introduction

Deterministic processes structuring natural communities, which integrate individual responses to the abiotic environment and biotic interactions, can be broadly separated into two categories: habitat filtering (HF) and niche differentiation (ND) (Keddy 1992; Weiher, Clarke & Keddy 1998; Kraft, Valencia & Ackerly 2008). At the community level, HF leads to trait convergence towards an optimum trait value in response to the local environment (Grime 2006). By contrast, ND leads to trait divergence and promotes the coexistence of species exploiting contrasted niches (Pacala & Tilman 1994; Silvertown 2004; Kraft, Valencia & Ackerly 2008).

Habitat filtering and ND are not mutually exclusive, despite their apparent opposite effects on community-level trait distributions (Cornwell & Ackerly 2009; Mason *et al.* 2011; Maire *et al.* 2012). One reason is that traits usually covary along independent axes of specialization, defining different trade-offs for plants to acquire and use local resources (Suding, Goldberg & Hartman 2003). Within communities, many independent axes have been described (Ackerly 2004; Wright *et al.* 2004; Gross, Suding & Lavorel 2007; Maire *et al.* 2009), each reflecting a different leading dimension of the species niche (Devictor *et al.* 2010). Consequently, HF can select species on a particular set of traits when ND can simultaneously occur on other independent traits (Spasojevic & Suding 2012). For instance, although competition for light may force plants to converge in height, other axes of specialization may allow competing species to coexist, for example, by exhibiting contrasting phenological niches (Fargione & Tilman 2005) or by using soil resources differently (Maire *et al.* 2012).

Examining trait convergence and divergence at the community level constitutes an important first step to study community assembly (Kraft, Valencia & Ackerly 2008). However, such an investigation does not suffice to infer the underlying mechanisms, as very different processes can lead to similar community trait distributions (Gross *et al.* 2009). Competition has been primarily hypothesized to promote trait divergence at the community level (see the 'limiting similarity theory' MacArthur & Levins 1967), but superior competitors can also have a disproportionally large effect on local resources and, thus, act as a habitat filter (e.g. in the case of competition for light, Grime 1973, 2006; Chesson 2000; Schamp, Chau & Aarssen 2008; Mayfield & Levine 2010). Facilitation has also been shown to increase trait divergence at the community level by promoting the coexistence of functionally contrasted species (Gross *et al.* 2009; Butterfield & Briggs 2011). Finally, abiotic factors are usually considered to cause community trait convergence (Grime 2006). They may also act as a disruptive force when different functional strategies exhibit equal fitness in response to similar abiotic constraints (e.g. stress avoidance vs. tolerance strategies, Freschet *et al.* 2011). As a result, when focusing only on community trait distributions, our understanding of the effects of biotic interactions and abiotic factors on community structure remains unclear and very limited (Cleland *et al.* 2011).

Disentangling the relative contributions of the abiotic environment and biotic interactions in structuring natural communities would be especially interesting for arid, semi-arid and dry subhumid ecosystems (drylands hereafter). Drylands are among the most globally significant terrestrial biomes (Reynolds *et al.* 2007). These ecosystems are currently threatened by climate change and desertification, with potentially irreversible impacts (Reynolds *et al.* 2007; Maestre *et al.* 2012). Changes in the composition of dryland vegetation in response to aridity are well documented (e.g. Alados *et al.* 2006). Nonetheless, important traits describing major axes of specialization in arid systems are not well-established compared with more mesic ecosystems (Kattge *et al.* 2011; Frenette-Dussault *et al.* 2012). In addition, the impacts of HF and ND on community structure along large aridity gradients have never been documented (Maestre *et al.* 2009a). Species from drylands generally exhibit low values of specific leaf area, suggesting a prevalent role for HF, which results in the dominance of water stress-tolerant species (Frenette-Dussault *et al.* 2012). Conversely, the high functional diversity observed within many dryland communities may indicate that ND-based processes are also important (Freschet *et al.* 2011). In this context, there is no clear understanding of how competition or facilitation interplays with aridity to determine local community structure (Tielbörger & Kadmon 2000; Maestre, Valladares & Reynolds 2005), although they have been hypothesized to play a crucial role in these systems (Fowler 1986; Kéfi *et al.* 2007; Pugnaire, Armas & Maestre 2011; Le Bagousse-Pinguet *et al.* 2012).

In this paper, we followed a functional trait-based and multiscale approach (from the regional species pool, down to the plant neighbourhood scale, Fig. 1) to evaluate the relative importance of random processes, abiotic factors and biotic interactions in determining trait distributions of semi-arid Mediterranean communities. We first aimed to identify the major axes of functional differentiation across species within semi-arid shrublands to identify the important traits for community assembly (regional scale, Fig. 1). Then, we focused on the traits related to each axes of specialization. We evaluated the relative importance of non-random community assembly processes along a large aridity gradient using null models (community scale, Fig. 1). We hypothesized that HF and ND are not mutually exclusive due to the independence among different sets of traits. However, increasing aridity may impose sufficient constraints to force species to converge in the most stressed part of the gradient, decreasing ND among species (Freschet *et al.* 2011). Therefore, we hypothesized that the most arid communities will be mainly structured by HF. Finally, we examined the spatial distribution of traits within communities to detect the impact of biotic interactions at the plant neighbourhood scale and to evaluate their consequences on community structure (Fig. 1). We hypothesized that facilitation can explain the high trait divergence observed within communities in semi-arid environments (Freschet *et al.* 2011). However, depending on the intensity of abiotic stress, the impact of facilitation on community structure may be modified, with competition prevailing at the wetter part of the

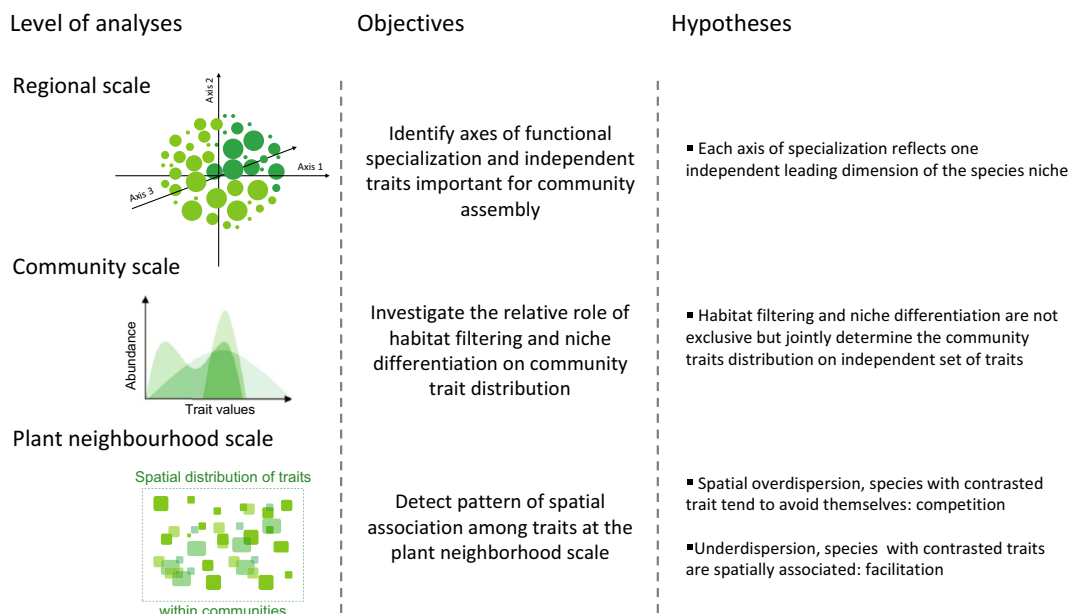


Fig. 1. Identifying the effect of abiotic factors and biotic interactions on the functional structure of plant communities using a multiscale analysis. We graphically present the three levels considered: i) the species trait pool at the regional scale, ii) the trait distributions at the community scale and iii) the patterns of spatial aggregation of traits at the plant neighbourhood scale. For each level, we present the associated objectives and hypotheses (see details in the main text).

gradient and facilitation gaining in importance with increasing aridity, as predicted by the ‘stress-gradient hypothesis’ (SGH) (Bertness & Callaway 1994).

Materials and methods

SITE SELECTION

We studied 12 experimental sites along a climatic gradient from central to south-east Spain (See Appendix S1 in Supporting Information). Site selection aimed to capture a significant range of the rainfall variability that is observed along this gradient and to reduce between-site variability associated with vegetation, slope, aspect and soil type. To achieve this goal, all the sites were located on south-facing slopes, where shrublands are dominated by the shrubs *Rosmarinum officinalis* L. and *Quercus coccifera* L. and had similar abiotic within-site heterogeneity (e.g. % bare soil, stoniness, data not shown). Soils were in all cases derived from Lithic Calciorthid (Soil Survey Staff, 1994). The sites were located along a clear aridity gradient (see Fig. S1); rainfall was negatively correlated with temperature along this gradient (Fig. S2 and Appendix S1).

SPECIES ABUNDANCE

In 2011, we assessed the composition and structure of perennial vascular plants using four 30-m-long transects at each site, parallel to the slope and situated 8 m apart from each other. In each transect, 20 consecutive quadrats (1.5 m × 1.5 m size) were placed to visually estimate the cover of each perennial species. We excluded annual plant communities from the analyses and restricted our study to perennial plants given their key role in maintaining ecosystem functioning and preventing desertification in drylands (Maestre & Escudero 2009; Maestre *et al.* 2012). Although annual plant communities constitute an important part of the diversity in arid systems, they may

have little impact on the dynamic and the functioning of arid systems within the studied shrublands due to their low plant biomass (Wiegand, Milton & Wissel 1995; Cañellas & San Miguel 2000). We used the total number and relative cover of perennial species in each of the 80 quadrats as a surrogate for species richness and species abundance, respectively.

TRAIT MEASUREMENTS

To quantify the functional structure of the sampled communities, we measured plant functional traits on species that collectively represented 90% of the total cover at each site. Measurements were conducted in spring from 20 to 25 March in order to measure traits during the growing period and to avoid late spring or summer drought. Ten individuals per species and per site were randomly selected to ensure that intraspecific trait variability (ITV) was taken into account in our sampling, a potential important factor when considering community assembly (Violle *et al.* 2012). On each individual, we measured the following above-ground traits according to standardized protocols (Cornelissen *et al.* 2003): (i) architecture and size-related traits related to competitive ability and/or plant water-use efficiency (due to allometric relationships between plant size and the architecture of the root system, Westoby *et al.* 2002), branching density (number of main stems) and ramification (number of ramifications per stem), lateral spread, reproductive and vegetative height; (ii) phenology, measured using a phenology index (1 = no reproductive stem; 2 = reproductive stem starting to grow; 3 = flowering; 4 = flower fading; 5 = fruit present; and 6 = fruit absent and senescence of the reproductive stem); (iii) foliar traits related to light interception and water stress tolerance (Westoby *et al.* 2002; Gross, Suding & Lavorel 2007), leaf area, leaf length, leaf thickness and leaf width; and (iv) specific leaf area and leaf dry matter content, which are related to the leaf economic spectrum, that is, the ability to acquire and use nutrient (Wright *et al.* 2004). These traits were selected because they reflect different plant species strategies for

acquiring, using and conserving resources (including light, nutrients and water), and for exploiting different temporal niches (Westoby *et al.* 2002; Maire *et al.* 2009). Overall, 36 of 79 perennial species found at our study sites were sampled, and a total of 994 individuals were measured (Appendix S2).

STATISTICAL ANALYSES

Regional scale: identifying major axes of functional specialization

We considered here the species pool sampled along the full aridity gradient. To identify the main axes of specialization within semi-arid Mediterranean shrublands, we performed a principal component analysis (PCA) using the 12 traits measured on all species. This approach approximates the functional niche of species, defined as their position in a multidimensional trait space (Devictor *et al.* 2010). We used a VARIMAX procedure to maximize the correlations between the PCA components and the traits considered. We selected one trait for each PCA component with eigenvalue higher than 1 as a functional marker representative of each axis of specialization. We selected these traits and used them in subsequent analyses because they are independent variables at the species level and reflect important leading dimensions of the species niche (Gross, Suding & Lavorel 2007).

Community scale: testing for HF and ND

We used a null model approach to evaluate the effects of HF and ND as drivers of community assembly (Gotelli & Graves 1996). The null assumption was that local communities should simply reflect a random distribution of individuals drawn from a regional pool, weighted by the abundance of each species present at the regional scale (Cornwell & Ackerly 2009). To generate the null assumption, we performed an individual-based randomization of species abundance across sites. We defined the community at the transect level and individuals at the quadrat level, that is, one 'individual' corresponded in our model to the sum of the cover of all individuals of a given species observed in a single quadrat. In total, we considered four community replicates (1 per transect) and 80 quadrats (20 per community) within each site.

A matrix describing the cover of each species observed at the quadrat level was randomly shuffled (9999 times) across transect and sites using the 'permatful' function in the R package *vegan* (Oksanen 2012). This procedure kept species abundance constant at the regional scale, but allowed species richness and abundance to randomly vary across quadrats within and between communities. As HF and ND may both modify the trait composition and the local species richness and density (Keddy 1992; Violle *et al.* 2011), we did not constrain the number and the local cover of species to be fixed within quadrat and communities during the randomization procedure. Our individual-based randomization had the advantage to directly reflect our sampling design by taking into account the pattern of local abundance of all sampled individuals at the quadrat level. This randomization procedure avoided any bias in the null model envelope size due to local variation in species number and cover observed at the quadrat level (Gotelli 2000). The size of the null envelope is only determined by species abundance at the regional scale, consistently with our null hypothesis.

For each of the 9999 randomizations, we used a second matrix containing the trait values of each individual species at the quadrat level, which was used to calculate the community-weighted trait

values (CWT, Violle *et al.* 2007) and the functional distance (FD, adapted from Laliberté & Legendre 2010) at the community level. The CWT estimates the 'mean trait value' of the community weighted by the relative abundance of each species present in the community:

$$CWT_j = \sum_i^n p_i T_i \quad \text{eqn 1}$$

where p_i is the abundance of the species i in the community j , and T_i is the 'mean trait value' of the species i in the community j , respectively. The FD quantifies the degree of trait divergence within a community, weighted by the relative abundance of each species within the community:

$$FD_j = \sum_i^n p_i \left(\frac{|T_i - CWT_j|}{\sum_i^n |T_i - CWT_j|} \right) \quad \text{eqn 2}$$

where p_i is the abundance of the species i in the community j , T_i is the 'mean trait value' of the species i in the community j , and CWT_j is the community-weighted traits in the community j . Abundance data (p_i) were log-transformed for all analyses. Both CWT and FD values were calculated for each selected trait from the PCA analysis.

Based on the 9999 randomizations, we calculated the 95% confidence interval and compared the observed CWT and FD indices with null predictions to infer the effects of HF and ND on community trait distributions. Observed data outside the null envelope were significantly different from random expectations, indicating that deterministic processes led to less or more divergent community trait distribution than expected by chance. Specifically, observed FD values below the null envelope indicated that traits within communities were forced to converge more than expected by chance, suggesting for HF. Habitat filtering was also inferred when significant changes in CWT occurred along the rainfall gradient. CWT indicates which trait value was selected by HF (e.g. were tall or short species favoured in a given site?). In contrast, the impact of ND was detected when communities exhibited high FD values above the null envelope, that is, coexisting species showed stronger functional differences than expected under the null hypothesis (Laliberté & Legendre 2010). Note that (i) as we used weighted abundance indices (Violle *et al.* 2007; Laliberté & Legendre 2010), our study took into account not only the effect of species turnover along the aridity gradient, but also observed changes in species abundance across sites; (ii) as multiple assembly processes can simultaneously affect community structure and influence different traits independently (Spasojevic & Suding 2012), we ran this analysis separately for each selected trait; (iii) ITV can have a non-negligible, sometimes important, impact on community structure (Violle *et al.* 2012). To take the effect of ITV into account, we calculated CWT and FD using either the mean trait value per species at the regional scale, that is, one value per species and trait along the whole gradient (without ITV), or the trait value of each species measured within each site (taking into account the observed ITV across sites).

We used linear mixed models to test for rainfall effects on community structure. We ran this analysis independently with and without ITV, that is, with data calculated at the site or at the regional level, respectively. The model had the following form:

$$CWT \text{ or } FD = f(Rain + Rain^2) \quad \text{eqn 3}$$

We introduced a quadratic term for rainfall as it has been shown that the functional response of communities to aridity is not necessarily linear (Kéfi *et al.* 2007; Cornwell & Ackerly 2009). Transect ID nested within sites was used as a random factor. We then tested

whether the slope of the relationship between rainfall and traits was affected by ITV using the same linear mixed model. When a significant interaction between rainfall and ITV was detected, we concluded that ITV modified the community response to aridity. To ensure models met the assumptions for parametric tests, we log-transformed data whenever appropriate and checked the residuals.

Within-community scale: evaluating the impact of biotic interactions

We used a similar null model approach to detect significant spatial patterns in trait distributions at the plant neighbourhood scale (i.e. quadrat level). The study of such patterns has often been used to infer the impact of facilitation or competition on community structure (e.g. Pielou 1962; Fowler 1986; Pugnaire, Armas & Maestre 2011), for example, by comparing the number of species present inside and outside nurse plant species (Cavieres & Badano 2009; Soliveres *et al.* 2010). Our trait-based analysis followed this approach by investigating the fine-scale spatial patterns of trait aggregation. Our analyses considered all sampled species in the community and were conducted for each selected trait separately. The null prediction was that the spatial distribution of species within a given community was random, that is, was not impacted by any biotic processes acting at the plant neighbourhood scale.

Using the matrix of species abundance in each site (transect level), we randomized species distribution between quadrats independently along each transect (9999 permutations). For each randomization event, we calculated for each quadrat its weighted trait value (quadrat-weighted trait value, QWT) similar to the CWT (see Eqn 1). The QWT reflects the 'mean trait value' of directly interacting species at the plant neighbourhood scale weighted by the abundance of co-occurring species at the quadrat level. Using the QWT values predicted by the null model, we calculated the sum of the absolute pairwise differences between QWT values (PwD_k) for each trait in each transect k as following:

$$PwD_k = \sum_{ij}^n |(QWT_i - QWT_j)| \quad \text{eqn 4}$$

PwD is adapted from a standard index (the nearest-neighbour distance) generally used in community assembly studies to detect niche differentiation between co-occurring species (see for instance Kraft, Valencia & Ackerly 2008). In our case, it corresponds to the degree of spatial dispersion of a trait across quadrats within a community, and we used it as a proxy of the impact of biotic interactions in structuring communities.

Based on the 9999 randomizations, we determined the mean and the 95% confidence interval of PwD_k for each transect, which reflects the null prediction of spatial trait dispersion within each community. We compared the observed PwD values obtained in each transect with the null prediction (deviation from null prediction). When PwD was significantly higher than the null prediction, it implied that species with different trait values tended to spatially avoid one another. This pattern was indicative (but not the proof) of competition between species. For instance, if spatial overdispersion was observed on plant height, it implied that shorter plants avoid taller plants because of local competition for resources (Fowler 1986; Schamp, Chau & Aarssen 2008). When PwD was lower than the null prediction, it demonstrated that species with different trait values tended to be more spatially associated than expected by chance. This pattern could be interpreted as a sign of facilitation among species, as facilitation commonly occurs in closed spatial associations of species with contrasted trait values (Cavieres & Badano 2009). Note that:

- 1 We considered ITV observed between sites in the within-community scale analyses, that is, considering one trait value per species and per site. In our model, the trait value of a species can thus vary across sites but not within. Significant spatial pattern within a given community cannot be attributed to an effect of ITV but only reflected the spatial sorting of species within communities;
- 2 The spatial dispersion of traits within a given community was statistically independent from the CWT and FD calculated at the community level, as for a given community trait distribution, we can expect different spatial patterns. However, along the aridity gradient, spurious correlations between PwD and CWT or FD can be observed if the range of trait values observed within communities changed along the gradient. To facilitate the comparison of traits across communities, we thus standardized before analysis the trait value of each species i occurring within each transect k :

$$SdTrait_{ik} = \frac{(trait_i - meantrait_k)}{(R)} \quad \text{eqn 5}$$

where $meantrait_k$ is the mean trait value of co-occurring species in a transect k , and R is the range of trait values observed in a given transect k (maximum – minimum trait value). Consequently, $SdTrait_{ik}$ is centred on zero and is independent from the range of trait value observed in a given site.

- 3 Non-random spatial patterns can also be the consequence of abiotic heterogeneity within sites (Violle *et al.* 2012). As we selected sites exhibiting similar within-site environmental heterogeneity, this further supports that the observed spatial structure within communities might be a consequence of biotic interactions between plant species.

To test how biotic interactions changed in response to aridity, we tested whether the observed deviation from the null expectation of PwD changed along the aridity gradient:

$$Deviation \text{ of } PwD = f(\text{polynomial}(\text{Rain})) \quad \text{eqn 6}$$

To ensure that our model results cannot be observed by chance alone, we ran a further round of randomizations (9999 times) and fitted the same model using randomized values and counted the number of times a significant value was obtained by chance for the polynomial relationship between rainfall and deviation of PwD detected for the observed data.

Combining effects of rainfall and biotic interactions on community structure

Our analysis using PwD can be related to the importance of biotic interactions in structuring the whole community, as spatial over- and underdispersion would denote competition or facilitation, respectively. To test how biotic interactions, quantified as above, changed along the rainfall gradient, we conducted a linear mixed model analysis that considered rainfall and PwD as the dependent variables, the transect ID as a random factor and CWT or FD indexes calculated with ITV as the variables to be explained. The model considered each trait independently and had the following form:

$$CWT \text{ or } FD = f(\text{Rain} + \text{Rain}^2 + PwD + \text{interactions}) \quad \text{eqn 7}$$

The best models were selected using Akaike information criterion (AIC) for each trait and index. We then conducted a variance decomposition analysis based on the sum of squares of the models to evaluate the relative importance of rainfall and biotic interactions (estimated with observed PwD in each community) in explaining local community structure (either CWT or the FD). Statistical analy-

ses were performed using R (R Core Development Team 2012) and JMP 7 (The SAS Institute, Cary, NC, USA).

Results

REGIONAL SCALE

We identified four independent axes of specialization within the studied shrublands, which together explained up to 82% of the total variance found in the data (Fig. 2). The first component was positively related to the plant size (VH, RH and LS, see trait abbreviations in Fig. 2) and was negatively correlated with the branching density. The second component was positively related to the leaf size (LL and LA) and negatively correlated with the number of stem ramifications and the phenology index. Note that the second component strongly contrasted grass species characterized by long leaves such as *Stipa tenacissima* L. from shrub species. The third and fourth components separated species based on their leaf

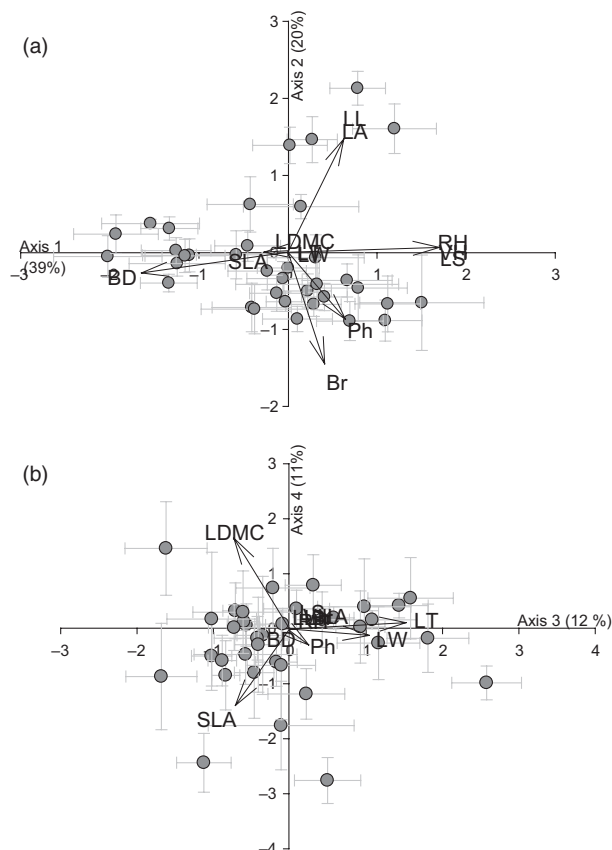


Fig. 2. Covariation of plant functional traits along four components of a principal component analysis extracted from a trait \times species matrix. Included are 36 species measured along the aridity gradient and 12 traits (A, components 1 and 2; B, components 3 and 4). Trait abbreviations are branching density (BD number of main stems), branching ramification (Br, number of ramification per stem), lateral spread (LS, m²), leaf dry matter content (LDMC, g g⁻¹), leaf area (LA, cm²), leaf length (LL, cm), leaf thickness (LT, mm), leaf width (LW, mm), phenology (Ph, index of phenology), reproductive height (RH, cm), specific leaf area (SLA, cm² g⁻¹) and vegetative height (VH, cm).

morphology, where LT was positively correlated with the third component. Specific leaf area (SLA) and leaf dry matter content (LDMC) were negatively correlated along the fourth component. Together, these results indicated that for a given SLA value, leaf morphology can vary independently across species through leaf density changes (via LDMC) and through the modification of the leaf thickness (LT). In addition, the fourth component separated exploitative species with high relative growth rate from conservative ones. We selected four traits to represent each independent component in the next analyses: vegetative height, LA, LT and SLA for the first, second, third and fourth components, respectively.

COMMUNITY SCALE

Functional differences between species translated at the community level into clear non-random community assembly patterns (Fig. 3). The values of the community-weighted traits (CWT) and FD considering all traits were in half of the cases outside the null envelope (59% and 49% for CWT and FD calculated with ITV, respectively). However, changes in CWT and FD observed in response to the rainfall gradient were trait dependent. CW-T decreased with increasing aridity, from an average of 60 cm in the wettest sites to ~50 cm height in the driest part of the gradient (Fig. 3a). At high rainfall levels, we observed FD-H values above the null prediction, indicating a high community trait divergence, while plant height became less variable in the driest part of the gradient and converged below the null envelope towards low FD-H (Fig. 3b). Quadratic relationships between rainfall and CW-LA and between rainfall and FD-LA were observed (Fig. 3c,d). We found values above the null envelope for intermediate rainfall levels and below the null envelope at the two extremes of the gradient. Conversely, CW-LT increased with rainfall with values above and below the null envelope as aridity increased (Fig. 3e). No clear pattern was observed for FD-LT along the rainfall gradient, although some communities were outside the null envelope (Fig. 3f). The CW-SLA showed a strong prevalence of significantly lower values than expected by chance (40 cm² g⁻¹), with an indication for an abrupt change (happening only for the last site) below 300 mm rainfall towards higher SLA values (up to 100 cm² g⁻¹, Fig. 3g). The FD-SLA had a negative linear relationship in response to rainfall. It exhibited underdispersed values indicating a strong trait convergence towards particularly low SLA values at the wettest part and in the middle of the aridity gradient (40 cm² g⁻¹, Fig. 3b).

Including the effect of ITV into the analysis only affected the response of community structure for some traits, that is, height and SLA. FD-H had only a significant response to aridity when taking into account ITV (Fig. 3b). The community convergence towards lower values of plant height can be then mainly attributed to an intraspecific response of dominant shrubs. Similarly, ITV decreased the response of FD-SLA to increasing aridity, leading to trait convergence at the driest part of the gradient (Fig. 3h). This result indicates that SLA convergence towards low values was partly due to ITV.

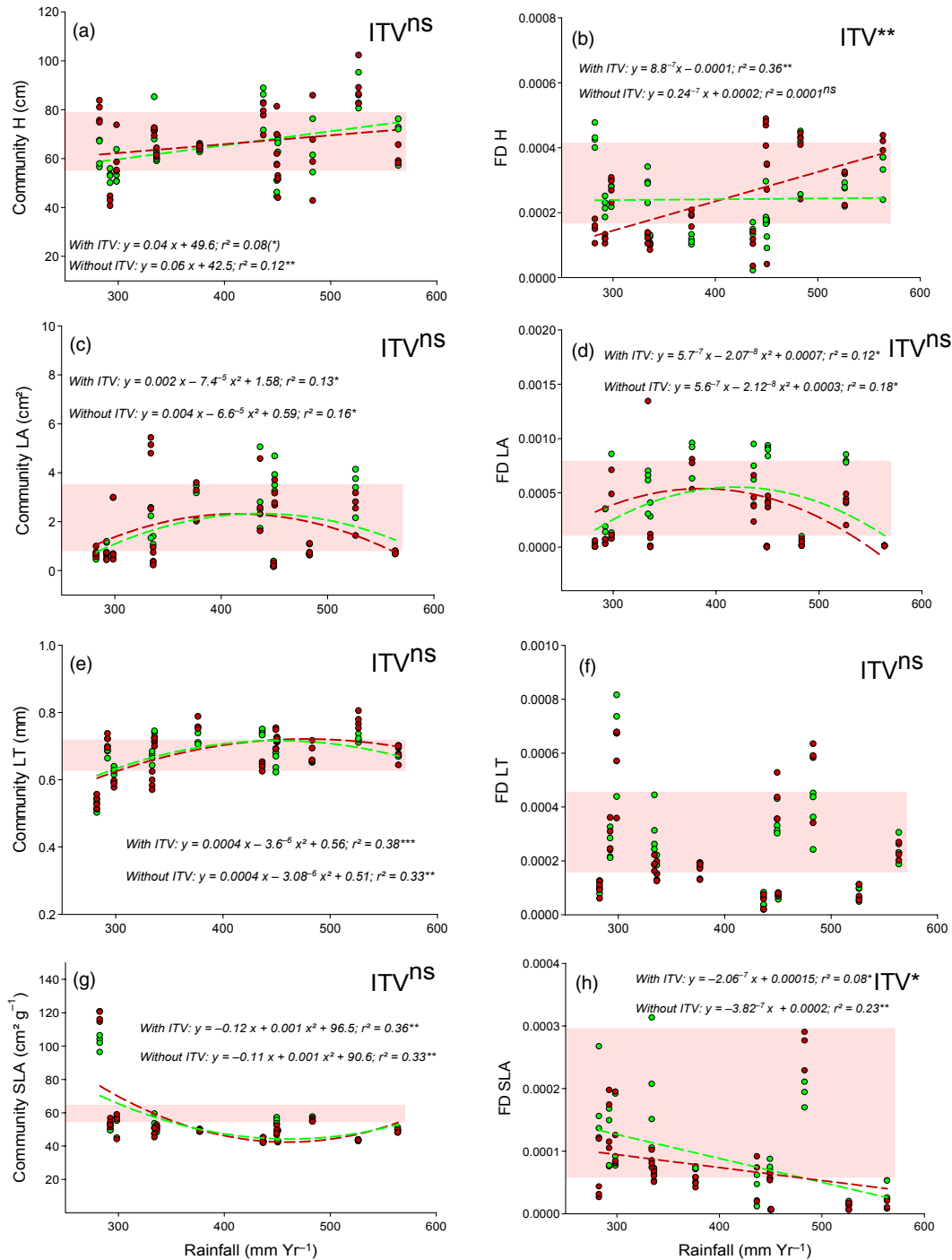


Fig. 3. Community-weighted trait (a, c, e, g) and associated functional distance (FD) (b, d, f, h) along the rainfall gradient. Red (dark grey) dots indicate the community traits and FD values taking into account for intraspecific trait variability (ITV) observed across sites. Green (light grey) dots show values without ITV (one trait value per species only). The red (shaded) zone represents the null model envelopes. Dots outside the null envelopes are significantly different from the null prediction. The equations of the relationships with and without ITV are given in each panel. We indicated when ITV significantly impacted the relationships between traits and rainfall within panels: ns, non-significant; (*) $P < 0.1$, * $P < 0.05$, ** $P < 0.001$, *** $P < 0.0001$. See Fig. 2 for trait abbreviations.

PLANT NEIGHBOURHOOD SCALE

Significant relationships between rainfall and the deviation of the sum of the pairwise distances (PwD) from the null expectation were observed for all traits with the exception of LT (Fig. 4c). The spatial dispersion of height within communities

shifted from a spatially overdispersed pattern at high levels of rainfall to a spatially underdispersed pattern under drier conditions. Species with contrasted sizes spatially avoided themselves at the wettest part of the gradient, whereas they tended to be spatially associated at the driest part (Fig. 4a). An

inverse pattern was observed along the rainfall gradient for SLA, where the spatial overdispersion of SLA peaked in the driest part of the gradient, whereas an underdispersed spatial pattern was observed in the wettest part (Fig. 4d). For LA, we found a cubic relationship with a spatial overdispersion of traits occurring at intermediate level of rainfall (Fig. 4b), while traits tended to be spatially underdispersed at the very dry end of the gradient.

The probability of observing by chance significant relationships between the deviation of *PwD* from the null expectation and rainfall was very low. Based on 9999 simulation runs, we found significant relationships in < 3% of the cases for height and SLA and < 1% for LA. These results indicate that variations of spatial distribution of traits within communities were clearly not random along the aridity gradient and provide evidence for the effect of competition and facilitation acting on the spatial structure observed within communities.

COMBINING EFFECTS OF BIOTIC INTERACTIONS AND RAINFALL ON COMMUNITY STRUCTURE

Our results suggested that the community structure is determined by the concomitant effects of rainfall and local biotic processes (estimated by *PwD*) and that these effects varied with the trait considered (see Table S2 and Fig. 5). CW-H was mainly affected by biotic interactions, while spatial overdispersion was positively correlated with taller plant types (see coefficient in Table S2, Fig. 5a). A similar pattern was observed for FD-H, where biotic interactions and higher rainfall increased the FD-H within communities (30% and 70% of model r^2 , respectively). Both CW-LA and FD-LA were impacted by the concomitant effects of rainfall and biotic interactions (80% and 71% of model r^2 , respectively), where biotic interactions tended to increase the CW- and FD-LA, respectively (Fig. 5b). CW-LT was mostly affected by rainfall (60%), while FD-LT was mainly influenced by biotic interactions (even if the total model r^2 was low in that case,

$r^2 = 0.16$; Fig. 5c). Finally, CW-SLA and FD-SLA were impacted by rainfall, with positive quadratic relationships (55% and 41% of model r^2 , respectively) indicating an increase in CW-SLA and FD-SLA at the end of the aridity gradient studied. Biotic interactions interacted positively with rainfall to increase the CW-SLA and FD-SLA (Table S2 and Fig. 5d).

Discussion

Most of the CWT and FD values found at our sites were located outside the null model envelopes, with a relatively high frequency compared with recent trait-based community analyses carried out in more mesic environments (e.g., Cornwell & Ackerly 2009; Freschet *et al.* 2011; Spasojevic & Suding 2012). This result indicated that the functional structure of the semi-arid shrublands is strongly determined by non-random processes. Consistent with our main hypothesis, we found that HF and ND act jointly to determine plant community structure along the aridity gradient. These two key community assembly processes operated together, but not necessarily in a similar way on the four axes of functional specialization identified in this study. Our results highlight the need to take multiple assembly processes into account when investigating the mechanisms that drive community structure (see also Spasojevic & Suding 2012). More importantly, our multiscale analysis helps to understand how biotic interactions interact with aridity to determine the community structure of Mediterranean shrublands.

COMMUNITY ASSEMBLY ALONG CONTRASTED AXES OF SPECIALIZATION

The first axis of specialization is related to plant size and reflects a trade-off for biophysical constraints in determining water fluxes within the plant (Enquist 2002). It corresponds to an allometric relationship, which coordinates the architecture

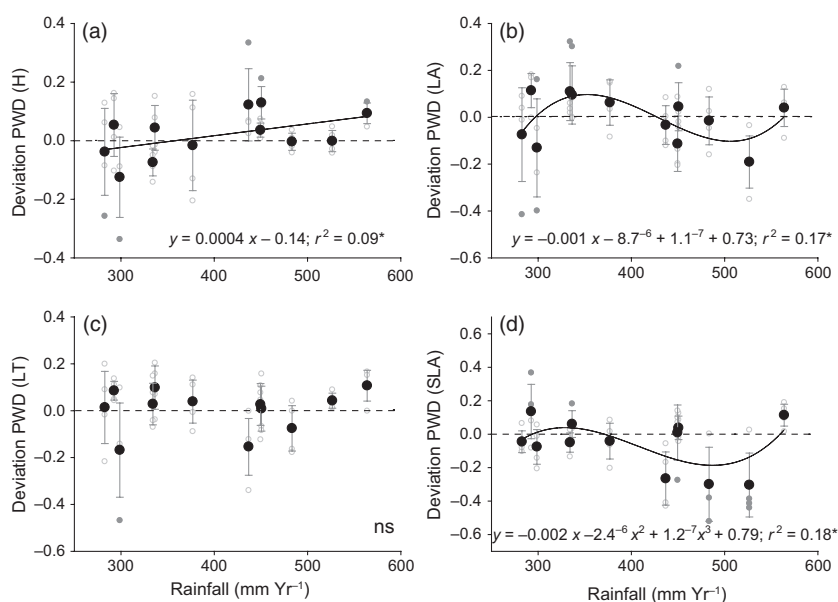


Fig. 4. Deviation of pairwise differences (PwD) from null predictions within communities for vegetative height (H, a), leaf area (LA, b), leaf thickness (LT, c) and specific leaf area (SLA, d) along the rainfall gradient. The mean deviation (black dots), associated standard deviation per site and observed data at the transect level (grey dots) are graphed. Open grey dots are located within the null envelope, and filled grey dots are significantly different from null predictions. The equations of the relationships are given for each trait in each panel; ns: $P > 0.05$; * $P < 0.05$.

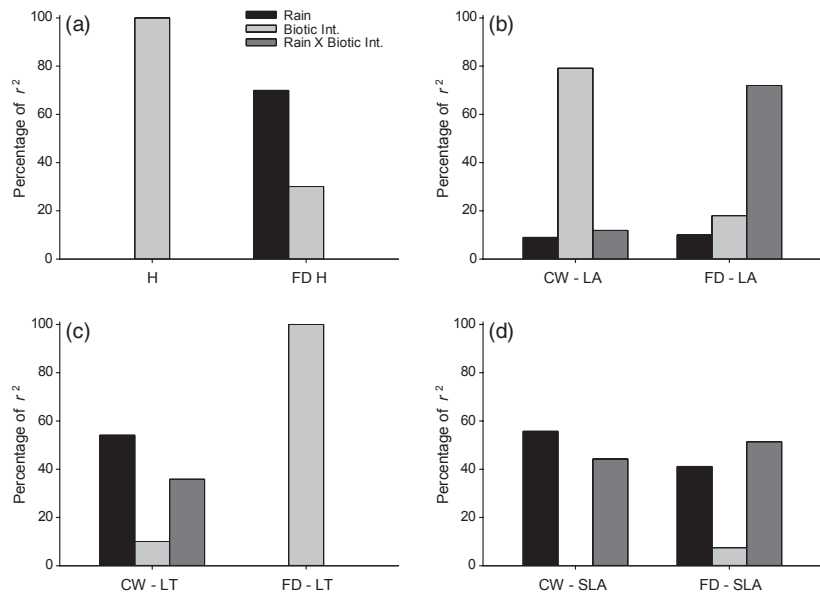


Fig. 5. Relative importance (percentage of model r^2) of rainfall (rain), biotic interactions (Biotic int.) and their interactions as predictors of the community-weighted trait (CWT) and the functional distance (FD) for (a) vegetative height (H), (b) leaf area (LA), (c) leaf thickness (LT) and (d) specific leaf area (SLA). See Table S2 for additional information on the models fitted.

of above- and below-ground plant parts (Westoby *et al.* 2002; Kerkhoff & Enquist 2006). At the community level, we observed a strong decrease in plant size and FD-H as a direct response to increasing aridity, suggesting that HF is taking place (Fig. 3, Díaz, Cabido & Casanoves 1998; Thuiller *et al.* 2004). Increasing water stress at the plant level is known to increase the risk of cavitation, which imposes the plant to exhibit lower stature as rainfall decreases (Enquist 2002). Plant height's response to aridity was mediated by ITV (as indicated by the different regression lines in Fig. 3b). The ITV effect might be due to the response of tall dominant shrubs such as *Q. coccifera*, for which the phenotype is altered along the aridity gradient, likely because of the genetic differentiation between populations of this species (Rubio de Casas *et al.* 2009). This result highlights the importance of taking ITV into account as an important factor when investigating trait-based community assembly (Violle *et al.* 2012).

The spatial trait dispersion found for height, with consistent spatial overdispersion and underdispersion of traits at the wettest and driest parts of the gradient, respectively, suggested a shift from competition to facilitation with increasing aridity (Fig. 4a), in accordance with the main prediction of the 'stress-gradient hypothesis' (Bertness & Callaway 1994). Spatial overdispersion patterns were systematically associated with high trait divergence at the community level, indicating that competition is likely to translate at the community level by promoting high ND and a spatial coexistence between functionally contrasted competitors (King & Woodell 1973; Fowler 1986; Haase *et al.* 1996). Our result contrasts with general observations from more mesic ecosystems (Grime 1973; Wedin & Tilman 1993; Schamp, Chau & Aarssen 2008; Gross *et al.* 2009), where asymmetric competition often leads to species exclusion and community-level trait convergence (Grime 1973; Tilman 1988; Schamp, Chau & Aarssen 2008; Gross *et al.* 2009). In semi-arid environments, inter- and intraspecific competition is an important factor in

explaining vegetation patterns (Tielbörger & Kadmon 2000; Gilad, Shachak & Meron 2007; Rietkerk & van de Koppel 2008). Competitive interactions for water may limit the spatial aggregation of tall competitors, reinforcing a patchy habitat where only less competitive species with small stature were able to persist in the remaining open areas (e.g. *Thymus vulgaris*; Fowler 1986; Haase *et al.* 1996; Gilad, Shachak & Meron 2007). On the contrary, facilitation did not translate into high trait divergence at the community level as expected (e.g. Gross *et al.* 2009). This result suggests that facilitation impacted only on subordinate or rare species (Bruno, Stachowicz & Bertness 2003; Liancourt, Callaway & Michalet 2005). Facilitation results from a cost-benefit relationship (Liancourt, Callaway & Michalet 2005) and is likely to occur only when the cost of having neighbours is lower than the benefits they can provide. Under dry conditions, small plants are more likely to benefit from the facilitation of taller nurse plants, as the competitive abilities of the latter should decrease with increasing abiotic stress, while the benefit of being close to a nurse plant might be maximized under high aridity levels (Bertness & Callaway 1994; Liancourt, Callaway & Michalet 2005; Maestre *et al.* 2009b).

The second axis reflected a trade-off for hydrological constraints at the leaf level according to the Corner's rule: highly branched species cannot develop large and long leaves to avoid leaf overlapping and maximize light interception (Westoby *et al.* 2002; Swenson & Enquist 2008). High leaf area generally leads to low water stress tolerances, whereas highly branched species with small leaves are better suited to arid environments (Westoby *et al.* 2002). At the community level, CW-LA and FD-LA followed quadratic responses to rainfall, indicating that HF is driven by contrasted mechanisms along the gradient (Figs. 3c,d). On the one hand, this quadratic relationship can be explained by the limitation of grass species abundances (e.g. *S. tenacissima*) due to competition with tall shrub at the highest rainfall levels, which

would lead to the exclusion of tall grass species from the community (Gasque & Garcia-Fayos 2004). On the other hand, the abundance of grasses such as *S. tenacissima* may decrease due to the increasing abiotic stress at the driest part of the aridity gradient (Armas, Kikvidze & Pugnaire 2009) where an underdispersed spatial pattern was recorded for leaf area (Fig. 4b). Similar to what was observed for plant height, spatial overdispersion of LA (Fig. 4) may indicate that competition is also important under intermediate levels of abiotic stress, and translated into an observed spatial coexistence between shrub and grass species and high ND.

For the third and four PCA axes, CW-LT decreased, while CW-SLA increased with aridity (Fig. 3e–h). These results indicated a shift in the dominant strategy along the rainfall gradient, from stress-tolerant strategies with thick leaves (Grime 1973; Frenette-Dussault *et al.* 2012) to stress avoidance strategies characterized by thin leaves and high SLA (Niinemets 2001; Poorter *et al.* 2009; Freschet *et al.* 2011). Sites located in the driest part of the gradient are dominated by fast-growing summer deciduous species (e.g. *Lavandula multifida* L., *Artemisia herba-alba* Asso., *Launaea arborescens* Murb.). These species are well adapted to dry environments as they can exploit the short growing season during late winter and spring, when cool temperatures and lower water stress allow plants to grow (Poorter *et al.* 2009). The decrease in abundance of stress-tolerant species at the driest end of the aridity gradient may point out that water stress becomes too strong for these perennial leaf species to support summer drought (Lillis & Fontanella 1992; Poorter *et al.* 2009).

Interestingly, we observed that the spatial distribution of SLA within communities changed from underdispersion in wetter sites to overdispersion in dry ones, suggesting a shift from facilitation to competition with increasing aridity (Fig. 4d). This result contrasted with predictions from the ‘SGH’ (Bertness & Callaway 1994) and results observed on plant height (Fig. 4a). They, however, agreed with other empirical and theoretical studies conducted in water-limited systems (Maestre, Valladares & Reynolds 2005; Maestre *et al.* 2009b; Gross *et al.* 2010). Facilitation is likely to benefit only to those species that are not well adapted to local abiotic conditions (Liancourt, Callaway & Michalet 2005; Gross *et al.* 2010). Under low aridity conditions, facilitation might only concern those exploitative species characterized by high SLA and perennial leaves, which cannot tolerate high aridity levels (Frenette-Dussault *et al.* 2012). These species (e.g. *Brachypodium retusum*, *Dactylis hispanica*) may persist under shrub canopies due to facilitation (Maestre, Cortina & Bautista 2004) and explain the observed spatial underdispersion of SLA observed under less arid conditions. The spatial overdispersion of SLA observed at the driest part of the gradient studied suggested that competition might be the prevailing force in dry conditions between well-adapted summer deciduous species and stress-tolerant shrubs.

We did not observe a clear response of FD-LT along the aridity gradient, although most of the communities exhibited a significant trait divergence (Fig. 3f). This suggests a coexistence of contrasted functional strategies with similar responses

to aridity (i.e. two stress-tolerant strategies either with thick leaves filled with water vs. dense leaves strategies, Poorter *et al.* 2009; Frenette-Dussault *et al.* 2012), which led to high trait divergence at the community level.

COMMUNITY-LEVEL IMPACT OF COMPETITION AND FACILITATION IN DRYLANDS

An important result from our study is that a shift from competition to facilitation appears to be trait dependent (See Fig. 6 for a synthesis of our results). While patterns observed on some traits (e.g. height) supported the ‘SGH’ (Bertness & Callaway 1994), others showed contrasting responses to aridity (Fig. 4). The trait dependency of the relationship between aridity vs the outcomes of biotic interactions may explain contrasted patterns of competition/facilitation previously observed along aridity gradients (e.g. Tielbörger & Kadmon 2000; see also Maestre, Valladares & Reynolds 2005 for a meta-analysis). Thus, our result provides a mechanistic explanation helping to solve this issue (see also Brooker *et al.* 2008; Maestre *et al.* 2009b for reviews): (i) competition and facilitation co-occurred within each community along the gradient but acted independently on different traits (Maire *et al.* 2012), and (ii) competition mainly impacted dominant species, while facilitation benefited subordinate or rare species (Bruno, Stachowicz & Bertness 2003).

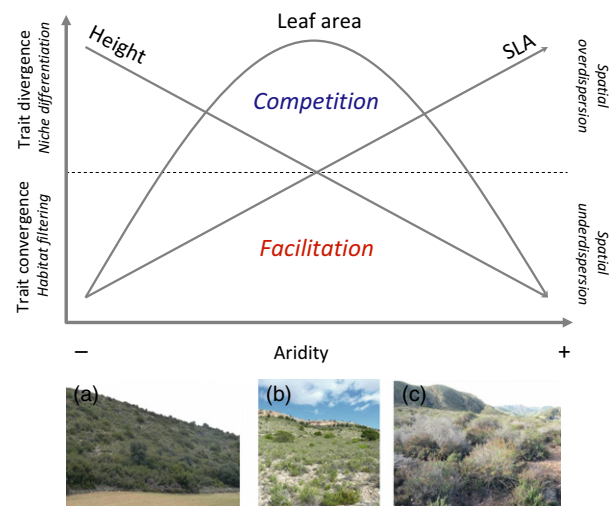


Fig. 6. The functional response of Mediterranean shrublands to aridity suggests an impact of biotic interactions on community structure. High trait convergence indicates the effect of habitat filtering (HF) along the aridity gradient. High trait divergence indicates niche differentiation (ND) among co-occurring species. Coexistence between functionally contrasted species is also suggested by the spatial dispersion of traits within communities. Along the aridity gradient, HF and ND jointly determined the functional structure of Mediterranean shrublands, acting independently on contrasted axes of plant specialization. Importantly, spatial analysis at the plant neighbourhood scale suggests that competition and facilitation impacted the whole community structure but acted differently on contrasted sets of traits. Competition impacted mostly the dominant plant species leading to high trait divergence at the community level, while facilitation impacted only subordinate and rare species (see main text for details).

The competition between dominant plant types seems to be constant along the aridity gradient, while the traits on which competition may act changed with aridity (Fig. 6). These results suggest that the type of resources for which competitors interact may change along the aridity gradient, consistently with theoretical predictions (Tilman 1988; Tilman & Pacala 1993) and previous empirical work in temperate grasslands (Wedin & Tilman 1993). At the wettest part of the gradient, tall shrubs may have a strong competitive effect for light availability within their neighbourhood (Gasque & Garcia-Fayos 2004; Armas & Pugnaire 2005). Under these conditions, smaller drought-tolerant species are only likely to persist in open areas (Fig. 4a). With increasing stress, the size of the plant and the functional divergence for height decreased, and the abundance of medium-sized grass species (e.g. *S. tenacissima*) increased. This translated into an intense competition, likely for soil resources (e.g. water, Armas & Pugnaire 2005), and a spatial avoidance between grasses and shrubs within communities is observed (Armas, Kikvidze & Pugnaire 2009; Fig. 4b). At the driest part of the gradient, stress-avoidant and summer deciduous species increased in abundance (Poorter *et al.* 2009), increasing the SLA of the shrubland communities. Under these conditions, competition during the growing season may favour the development of exploitative plant types, with high SLA and faster growth rate, which can out-compete locally slow-growing and more stress-tolerant shrubs (Fig. 4d). For all traits, competition between dominant plant types translated into high functional divergence at the community level indicative of high ND between competitors (Fig. 5).

Similar to competition, facilitation occurred all along the aridity gradient by acting on contrasted traits, but did not promote high functional divergence at the community level (Fig. 6). This result implies that facilitation likely impacted subordinate and rare species (Bruno, Stachowicz & Bertness 2003; Liancourt, Callaway & Michalet 2005). Thus, facilitation can be considered as an important factor maintaining high species diversity in semi-arid environments (Pugnaire, Armas & Maestre 2011). For instance, in semi-arid *S. tenacissima* steppes from Spain, Soliveres *et al.* (2011) found that facilitation by grasses (*S. tenacissima*) and shrubs (*Q. coccifera*) increased local species richness and that, similar to our results, the community-wide importance of these nurse plants remained constant along a rainfall gradient similar to the one studied here.

Together, our results emphasize that biotic interactions are likely to explain a non-negligible part of the functional variation observed along the aridity gradient (Fig. 5). In general, aridity seems to act as a convergence force clustering trait values of co-occurring species (e.g. low SLA and height value at the wettest and the driest part of the gradient, respectively). In contrast, competition (but not facilitation) appeared to explain the large functional diversity observed within drylands (Freschet *et al.* 2011). The effect of competition led, in some cases, to FD values above the null envelope (Fig. 3), indicating the effect of ND, while aridity led to FD values below the null envelope, suggesting the effect of HF. However, it is

important to keep in mind that CWT and FD values within the null envelope are not necessarily random but may highlight the opposite effect of aridity and competition on community trait distributions: the former clustered species traits towards an optimum value; the latter increased trait divergence between competitors. Together, these results highlighted the importance of identifying the relative effect of abiotic and biotic factors on community structure as their opposite effects may explain apparent random patterns, which are often found in trait-based community analyses (Cornwell & Ackerly 2009; Spasojevic & Suding 2012).

Conclusions

Our knowledge on the mechanisms driving the functional structure of arid and semi-arid ecosystems remains incomplete (Maestre *et al.* 2009a; Eldridge *et al.* 2011; Freschet *et al.* 2011; Frenette-Dussault *et al.* 2012), despite their ecological importance, extent and the ecosystem services that they provide to human populations (Safirel & Adeel 2005). Our community-level analysis indicated the overwhelming impact of deterministic process in structuring shrublands across a large aridity gradient in Spain. Consistent with our leading hypothesis, HF and ND appeared to be non-exclusive mechanisms, which together shape the functional structure of semi-arid communities (see Fig. 6). Together, our results highlighted the need to consider multiple traits to understand contrasted processes that jointly operate to shape natural communities (see also Spasojevic & Suding 2012).

By considering multiple scales to study community assembly, our approach also offers a practical way to separate the role of biotic interactions from the effect of abiotic factors in explaining the community-level patterns of trait divergence and convergence (Fig. 1). As such, our study constitutes an important step forward in the attempt to link biotic interactions to community structure (see also Cavieres & Badano 2009; Gross *et al.* 2009). Our results observed at the plant neighbourhood scale suggest that biotic interactions have an important impact on the structure of semi-arid communities; modifying species realized niches and abundance, and thus affecting the structure of the whole community. Overall, our study calls for a more mechanistic approach of community functional assembly (e.g. Savage, Webb & Norberg 2007; Gross *et al.* 2009), that is, to move from patterns of community trait divergence and convergence towards the examination of the underlying mechanisms acting at the individual scale.

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Supporting Information

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

Fig S1. The Mediterranean shrublands sampled along an aridity gradient from central to south-eastern Spain.

Fig S2. Aridity gradient.

Fig S3. Slope and aspect across selected sites.

Fig S4. Species relative abundance at the regional scale.

Table S1. Species name and trait values.

Table S2 Predicting community structure in response to rainfall and biotic interactions.