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A multidimensional functional trait approach reveals the imprint of environmental stress in Mediterranean woody communities

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Abstract

Water availability is one of the most important factors determining species distribution, plant community structure and ecosystem functioning. We explore how the functional structure of Mediterranean woody plant communities varies along a regional gradient of aridity in the Andalusian region (south Spain). We question if communities located in more arid sites show more similarity in their functional structure when compared with communities located in wetter sites or if, instead, there is divergence in their functional spaces. We selected five aridity zones (three sampling sites per zone) and measured 13 traits of different functional dimensions (including leaf, stem and root traits) in 74 woody plant species. We quantified functional space differences using the n-dimensional niche space approach (hypervolume). We found a larger functional space for the wetter communities compared with the more arid communities, which showed greater overlap of the trait space occupation. Our results indicate that aridity acts as a key abiotic filter affecting various metrics of the community trait structure, in accordance with the plant economics spectrum. We have also documented consistent variation in the functional space, supporting lower functional diversity under more harsh climatic conditions. The trend of functional space variation along the aridity gradient was different when considering traits from only one plant organ. Thus, the filtering process driving the functional structure of the communities studied here largely depends on the trait axis considered; for example, the root dimension showed considerable variation in wet environments whereas the leaf dimension exhibited a larger functional space in the drier habitats.

Keywords: Aridity, dry shrubland, functional diversity, functional structure, hypervolume, plant traits.

Introduction

Trait-based approaches have proved fruitful to understand biodiversity effects on ecosystem processes and underlying physiological mechanisms (Mason and others 2005; Grime and others 2006; Garnier and others 2007; Mouillot and others 2011). However, they have been applied mostly in experimental conditions or along local environmental gradients (Bernard-Verdier and others 2012; Maire and others 2012; de la Riva and others 2016a). This impedes a thorough evaluation of ecosystem functionality along large-scale environmental gradients, a high priority for functional biogeography (Violle and others 2014). A notable exception refers to global modelling studies that classify ecosystems based on functional type diversity (Kleidon and Mooney 2000) and sometimes on plant functional traits (Heberling and Fridley 2012). However, these models typically refer to database approaches in which the real flora or trait plasticity is largely ignored. In other words, woody communities of a given biogeographic area are commonly described by a similar set of plant functional trait values without taking into account the species composition or intraspecific trait variation. In addition, the ecological strategies seem to be highly scale-dependent (Lamanna and others 2014; de la Riva and others 2016b), with functional strategies identified at smaller spatial scales not necessarily matching the patterns found at regional or global levels (Mokany and Roxburgh 2010; Funk and Cornwell 2013). Thus, there is an urgent need for a functional understanding of ecosystem variability at larger spatial scales, which would provide potential insights into both ecosystem and global change biology.

A trait-based approach is a relevant tool to evaluate plant responses to environmental changes since a given trait can be related straightforwardly to abiotic or biotic constraints (Garnier and Navas 2012). However, the application of this approach to plant communities has been challenged recently (Laughlin 2014; Lamanna and others 2014) based on the idea that, instead of using single traits, studying whole-phenotype responses is more useful to understand the filtering effects of environmental factors on natural communities (Laughlin 2014; Carmona and others 2016). The use of trait information of the different plant organs (leaves, stems, roots and seeds), however may offer complementary information on plant functional responses to the environment (Laughlin 2014). In this regard, root traits have been generally overlooked in studies of functional structure (i.e. the composition and diversity of functional traits; Mouillot and others 2011), despite the important role of root attributes in several key ecosystem processes (Craine and others

2003). Although there is a growing interest in investigating the role of root traits on plant community assembly (e.g. Laughlin and others 2010; Pérez-Ramos and others 2012; Kramer-Walter and others 2016; Navarro-Fernández and others 2016), the belowground compartment has been particularly ignored in studies at large spatial scales. For example, root trait data represent only 7% of the TRY database with respect to the leaf compartment (Laliberté 2017). Thus, given the multi-dimensionality of plant functions, the lack of consideration of several key functional traits, such as those related to belowground functioning, may strongly bias our estimation of community functional structure and diversity (Laughlin 2014).

Functional biodiversity changes have been frequently assessed using diversity indices that take into account different dimensions (Mason and others 2005; Villéger and others 2008): the range of functional trait variability in a given species assemblage (functional richness), the evenness of abundance distribution across species traits (functional evenness), and the divergence in the abundance distribution of functional traits (functional divergence). An alternative and recent approach to quantify the magnitude of the occupied functional space is the *n*-dimensional niche space method (Blonder and others 2014), based on the Hutchinson's multidimensional niche concept (Hutchinson 1957). Hutchinsonian niches are related with functional diversity and allow us to quantify niche spaces by assessing the functional trait hypervolumes that characterise the phenotypic spaces occupied by a set of species (Lamanna and others 2014). One of the main advantages of this method is that it can accurately measure the volume of a high-dimensional shape that may include holes or other complex geometrical features, which refine the measurement of the functional space better than linear and continuous dimensions (i.e. the convex hull model; Cornwell and others 2006). Also, the hypervolume algorithm permits measurement of the proportions of the hypervolumes that share the same functional space (see details in Material and Methods). Thus, the *n*-dimensional space makes it possible to predict functional redundancy within communities (overlap) as a result of the convergence towards a relatively small set of successful trait combinations (Grime 2006; Díaz and others 2016); or plant divergence and character displacement (the portion of unique hypervolume) as the result of niche shifts among species along environmental gradients (Violle and Jiang 2009). Therefore, it may allow inferring relevant processes such as competitive exclusion and niche differentiation (see Blonder and others 2014; Loranger and others 2016a). However, despite its great potential to provide a better understanding of the rules that govern

the process of community assembly, the approach based on hypervolume has been barely used in plant community studies (but see Lamanna and others 2014, Loranger and others 2016a).

In arid and semi-arid regions, water availability is one of the main limiting resources for plants (Padilla and Pugnaire 2007), affecting many aspects of plant fitness and therefore of species composition and distribution (Bréda and others 2006; Engelbrecht and others 2007). Arid conditions promote specific adaptations to the imposed climatic constraints, reflecting different functional trade-offs between nutrient acquisition, growth or life span (Reu and others 2011). Thus, communities in dry environments tend to be dominated by short, slow-growing species with higher tissue dry matter content and higher water-use efficiency, which is known as a conservative resource-uptake strategy (Wright and others 2004; Grubb and others 2015; de la Riva and others 2016a). In contrast, highly-productive ecosystems are dominated by plant

communities with tall, fast-growing species with a large absorption surface per unit of tissue biomass (high specific leaf area and specific root area values) and high photosynthetic capacity (high nitrogen or chlorophyll concentration), indicating an acquisitive resource-uptake strategy (Wright and others 2004; de la Riva and others 2016b). However, in spite of this general tendency in resource uptake strategies, some evidence suggests that different factors are able to drive opposite assembly processes for related traits (Mason and others 2011).

It has long been observed that the diversity of plant functional strategies (i.e. functional diversity) at a global scale is largely conditioned by climate (Kleidon and Mooney 2000; Thuiller and others 2006), likely because this is one of the main factor which determines resource availability (Schimel and others 1996; Arnell 1999). According to theory, greater functional diversity is expected in

Table 1. List of the 13 functional traits measured in this study, their abbreviations, units and main role in plant functioning.

Group	Trait	Abbreviation	Unit	Functional role
Leaf morphology	Leaf size	Lsize	cm ²	Light capture and growth rate
	Specific leaf area	SLA	m ² kg ⁻¹	Light capture and growth rate
	Leaf dry matter content	LDMC	g g ⁻¹	Physical resistance and stress tolerance
Stem morphology	Stem dry matter content	SDMC	g g ⁻¹	Resistance to physical hazards
	Stem wood density	SWD	g cm ⁻³	Physical resistance, growth rate and stress tolerance
Root morphology	Specific root length	SRL	m g ⁻¹	Water and nutrients acquisition
	Root dry matter content	RDMC	g g ⁻¹	Resistance to physical hazards
	Root tissue mass density	TMDr	g cm ⁻³	Physical resistance, growth rate and stress tolerance
Plant Size	Plant height	Pheight	m	Dispersal distance, light capture, aboveground competition
	Plant cover	Pcover	m ²	Dispersal distance, light capture, aboveground competition
Leaf Chemical	Leaf nitrogen concentration	LNC	%	Light capture and photosynthetic rate
	Leaf chlorophyll ¹	LChl	μg g ⁻¹	Light capture and photosynthetic rate
	Isotopic carbon fraction	δ ¹³ C	‰	Gas exchange and water-use efficiency

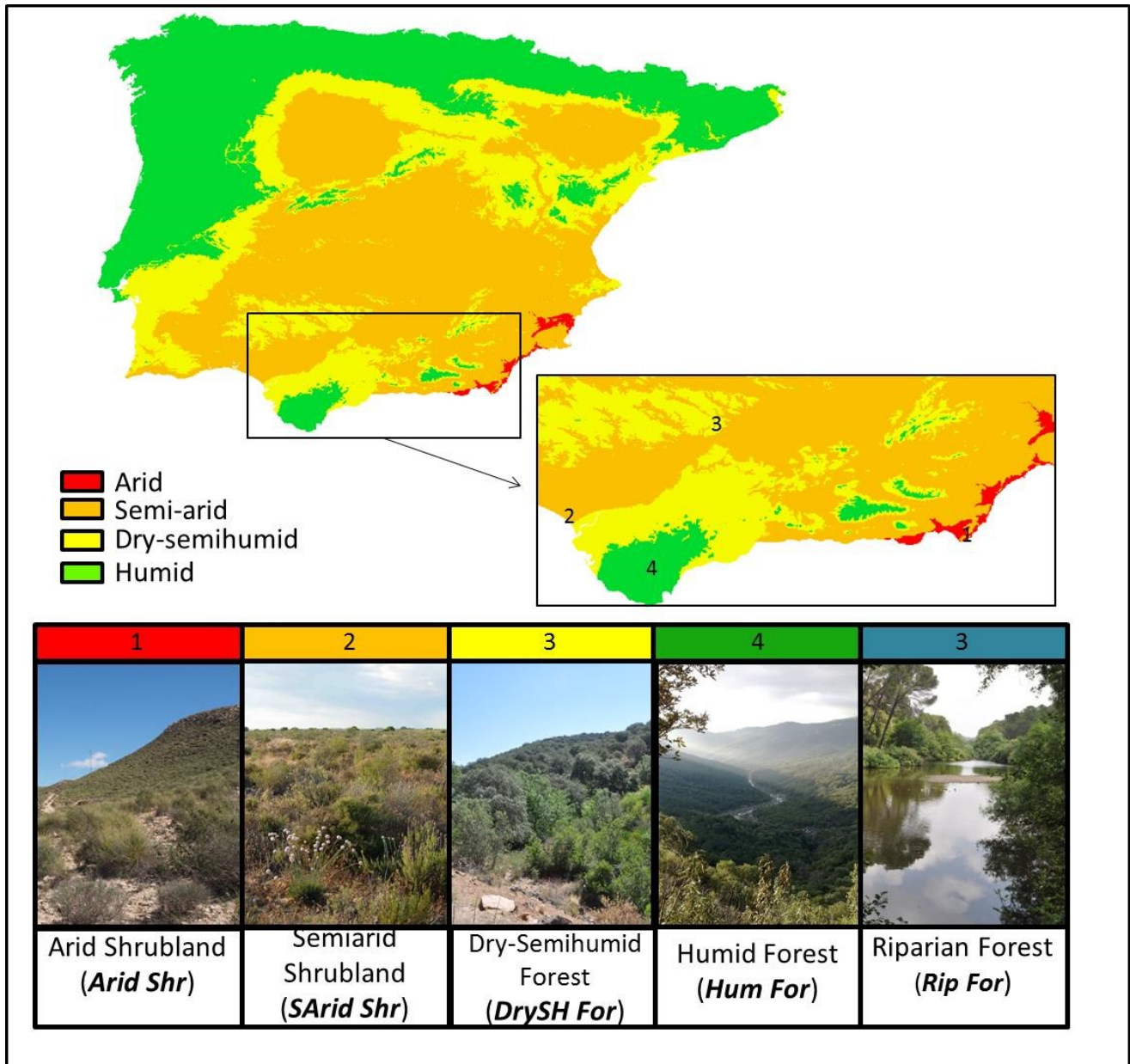


Figure 1. Location of the study zones (and their abbreviations) selected along the regional aridity gradient. The aridity index map was generated in ArcGis software 10.2 (Trabucco and Zomer 2009).

resource-rich and productive environments (Heywood 1995) as a result of strong interspecific competition, which promotes resource partitioning (limiting similarity hypothesis; MacArthur and Levins 1967). By contrast, in environments that are more resource-limited, plant adaptations to such stressful conditions are limited, constraining the phenotypic space and decreasing the plant functional diversity (Jacobsen and others 2008). However, and contrary to this general global pattern, some studies at lower scale have shown lower diversity (for both species and functional richness) in more-productive environments (Grime 2006; Pakeman 2011; de Bello and others 2013, Loranger and others 2016b). These apparently contradictory results may be explained because climate imposes constraints on a certain range of parameter values (Kleidon and Mooney 2000), but within the range of viable solutions for a particular environment the diversifi-

cation of successful strategies exists (de la Riva and others 2016b). Thus, there is a need to understand how arid conditions determine the functional structure and niche space volume of plant communities, and to test the initial hypothesis stating that the niche functional space of communities located at more arid sites is smaller than the hypervolume of communities inhabiting wetter sites.

In this paper, we explore a regional gradient of well-preserved Mediterranean woody plant communities, from dry to permanently-wet conditions, covering a wide natural area of water conditions in southern Spain. We measured a large set of plant traits, including root traits, representing the main functional dimensions of the vegetative phenotype. Using the n-dimensional niche space approach, we examined specifically: i) whether, and to what extent, the functional trait structure of different communities is sensitive to the regional aridity gradient; in particu-

lar, whether the communities exposed to harsher (drier) environmental conditions display smaller hypervolumes; and ii) whether the patterns obtained for all traits are congruent with the hypervolumes calculated for each independent dimension of the phenotype (i.e. leaf and root morphology or leaf chemical composition).

Material and methods

Study area

The study was conducted in five Mediterranean zones, dominated by woody plant communities (forests and shrublands) and located in Andalusia, southern Spain (87 597 km²), that encompass a wide range of precipitation (from 200 to 2000 mm year⁻¹; Fig. 1). To characterize the water availability of the different zones we use the Aridity index (Fig. 1), based on the ratio of Mean Annual Precipitation and Mean Annual Potential Evapo-Transpiration, using the datasets from the CGIAR consortium for spatial information (<http://www.cgiar-csi.org/>). According to the Global-Aridity datasets (Trabucco and Zomer 2009) the studied zones can be classified as follows: i) Arid zone at Cabo de Gata Natural Park, dominated by shrubs (e.g. *Anthyllis cytisoides*, *Helianthemum almeriense*) (hereafter **Arid Shr**); ii) Semi-Arid zone at Doñana National Park, dominated by shrubs on sandy soils (e.g. *Halimium comutatum*, *Stauracanthus genistoides*) (hereafter **SArid Shr**); iii) Dry-Semihumid zone in the Sierra Morena mountains, dominated by forest with drought-tolerant evergreen species (e.g. *Quercus ilex*, *Rosmarinus officinalis*) (hereafter **DrySH For**); iv) Humid zone at Los Alcornocales Natural Park, dominated by mixed forests of evergreen oaks (*Quercus suber*) and winter-deciduous oaks (*Quercus canariensis*) (hereafter **Hum For**); and v) Riparian Forest (hereafter **Rip For**) near the Guadiato River (Sierra Morena mountains, close to the **DrySH For** zone), with permanent water availability due to its proximity to a river channel and dominated by deciduous tree species (e.g. *Fraxinus angustifolia*, *Ulmus minor*). For simplicity we will refer to these five studied zones throughout the article using the acronyms.

Sampling design

Three sampling sites with a low anthropogenic influence and similar bedrock were selected (no more than 10 km between them) per each aridity zone. Four 20-m-long transects were set up randomly in each of the sampling sites, with a minimum distance of 10 m relative to one another and avoiding steep slopes. The area sampled in each of the five zones

or habitat types was around 1800 m² (600 m² per sampling site). Species composition and abundances were recorded using the “line interception method” (Canfield 1941). The cover of all woody individuals was estimated by identifying plants intercepted by a metric tape and recording intercept distances in each of the four 20-m transects (total abundance can exceed 20 m since the overlapping vegetation layers were taken into account). The mean relative abundance for each species and sampling site was calculated as the mean value of the four transects.

Trait measurements

For trait measurements, we selected all the species appearing in the transect excluding only those with a relative abundance below 0.5% since in these cases it was difficult to find at least six individuals per species in the sampling sites (12 species were excluded in total). This led to a total of 74 selected woody plant species, many of them occurring in more than one study zone (Appendix S1).

Healthy adults of the woody plant species were selected randomly during the peak of plant biomass (spring). We measured 13 key functional traits related to morphology (of leaf, stem and root), physiology (leaf chemical compounds) and plant size, covering the main plant functional dimensions (see functional roles in Table 1). All these trait measurements were carried out according to the criteria defined by Pérez-Harguindeguy and others (2013), varying the number of replicates per species and zone, for plant size (10), leaf traits (6), root traits (4), and chemical traits (1 combined value) according to trait variability and logistic limitations (the plant replicates were distributed among the three sampling sites per zone, wherever possible). For a detailed protocol of sample harvesting and trait measurements see de la Riva and others (2016a).

Leaf morphological traits.- Six individuals per species and aridity zone were chosen, on which the following leaf traits were measured: leaf size (Lsize); specific leaf area (SLA; leaf area per unit of leaf dry mass); and leaf dry matter content (LDMC; leaf dry mass per unit of water-saturated leaf fresh mass).

Stem morphological traits.- On the same six individuals per species and aridity zone, we measured the following stem traits: stem dry matter content (SDMC), which was obtained as the ratio between dry and saturated fresh mass; and stem wood density (WD), calculated as the stem dry mass divided by its fresh volume (which was calculated according to the Archimedes principle, i.e., measuring the volume of water displaced by the immersion of the stem).

Root morphological traits.- The fine roots (<

2 mm in diameter) of four individuals per species and aridity zone were used to measure belowground traits: specific root length (SRL, root length per unit of root dry mass), root dry matter content (RDMC, root dry mass per unit of water-saturated root fresh mass) and root tissue mass density (TMDr, root dry mass per root volume). The root area and root volume data were obtained by analysing the scanned root samples with WinRHIZO 2009 (Regent Instruments Inc., Quebec, Canada).

Plant size traits.- Plant height (Pheight) and cover (Pcover; canopy projection) were measured as functional traits commonly used to quantify plant size. Measurements were made using a metric tape on ten individuals per species (excepting some rare species, for which only six individuals were found, such as *Crataegus monogyna* in Sierra Morena, *Withania frutescens* in Cabo de Gata or *Phillyrea latifolia* in Alcornocales). For tall trees, plant height was estimated using the 'Christen height' meter, based on trigonometric principles (Klein 2007).

Leaf physiological and chemical traits.- Three chemical traits related to plant physiology were measured: leaf nitrogen concentration (LNC), leaf chlorophyll (LChl, the concentration of chlorophyll per unit of fresh leaf mass) and leaf carbon isotopic ratio ($\delta^{13}\text{C}$). LNC and LChl were measured on leaves of six individuals per species and aridity zone, whereas the $\delta^{13}\text{C}$ was analysed in a mixture of leaves from six different individuals per species and aridity zone.

Data analyses

To study the degree of trait variation and the correlations among them a general principal components analysis (PCA) was performed with the whole set of traits (13 variables) and for the 91 observations of woody plants (74 species, but some of them occurring in more than one zone). To explore differences in functional structure between the communities from the five aridity zones, we used a linear mixed model to calculate the differences among aridity zones for each trait, using species-mean trait values per zone (considering species as the random effect), followed by post hoc multiple pairwise comparisons (Tukey's test). Variables were log-transformed when necessary.

The total niche space of the community was calculated by the estimation of the n-dimensional hypervolume (Blonder and others 2014), from the trait space occupied by the total pool of species that were present in each aridity zone. In order to reduce the number of dimensions (which is recommended for this analysis), we first performed a PCA for each dimension (leaf, stem and root morphology, leaf chemical and plant size) separately. With the first PC axis of each dimension (which explained between 53 and 95 % of the variation; see more details in the results section), we calculated the hyper-

volume for each aridity zone using a multidimensional kernel density estimation (KDE) procedure (see Blonder and others 2014 for mathematical details). The units of the hypervolumes are reported as the standard deviations of centred and scaled log-transformed trait values, raised to the power of the number of trait dimensions used ($\text{sd}^{\text{number of dimensions}}$). We also calculated the overlap between the hypervolumes of each aridity zone with the correlation analysis of the "hypervolume" package, which compares the similarity between hypervolumes using the Sørensen index (intersection hypervolume divided by mean hypervolume for each pair of assemblages; see Blonder and others 2014). In addition, to observe if the functional trait overlap between aridity zones was related to species similarity, we also calculated the Sørensen index of similarity for species composition between each pair of aridity zones. A rarefaction analysis was performed to control for the effects of species richness on the hypervolume. Thus, for each zone, we built 100 randomised communities composed of species drawn (12 species) from the species pool of that aridity zone. Then, we calculated the hypervolume of each sample and performed a one-way ANOVA to compare the hypervolumes of the zones independently of species richness.

For a comparative purpose, we also calculated the three functional diversity indexes (FRich: functional richness; FEve: functional evenness; and FDiv: functional divergence) proposed by Mason and others (2005) and Villéger and others (2008). For that we used the loadings of the first PCA axis of each dimension (leaf, stem and root morphology, leaf chemical and plant size) in each sampling site (3 sampling sites per aridity zone). The functional richness reflects the amount (the difference between the maximum and minimum values) of functional trait variability in a given community. The functional evenness quantifies the equitability of abundance distribution across species trait values. The functional divergence captures the degree of differentiation in the abundance distribution of species functional traits (for more details see Mason and others 2005, Villéger and others 2008). We performed a one-way ANOVA and post hoc multiple pairwise comparisons (Tukey's test) to compare functional diversity indexes between aridity zones.

Next, in order to examine whether the hypervolume variations were consistent for different functional dimensions, we performed the same analysis for each dimension separately: leaf morphological (Lsize, SLA and LDMC), root (SRL, RDMC and TMDr) and leaf chemical traits (LNC, LChl and $\delta^{13}\text{C}$). We also performed the rarefaction analysis for each of these dimensions. Since the hypervolume analysis needs at least three variables, the stem and plant-size dimensions (with only two traits each) were discarded for these specific analyses.

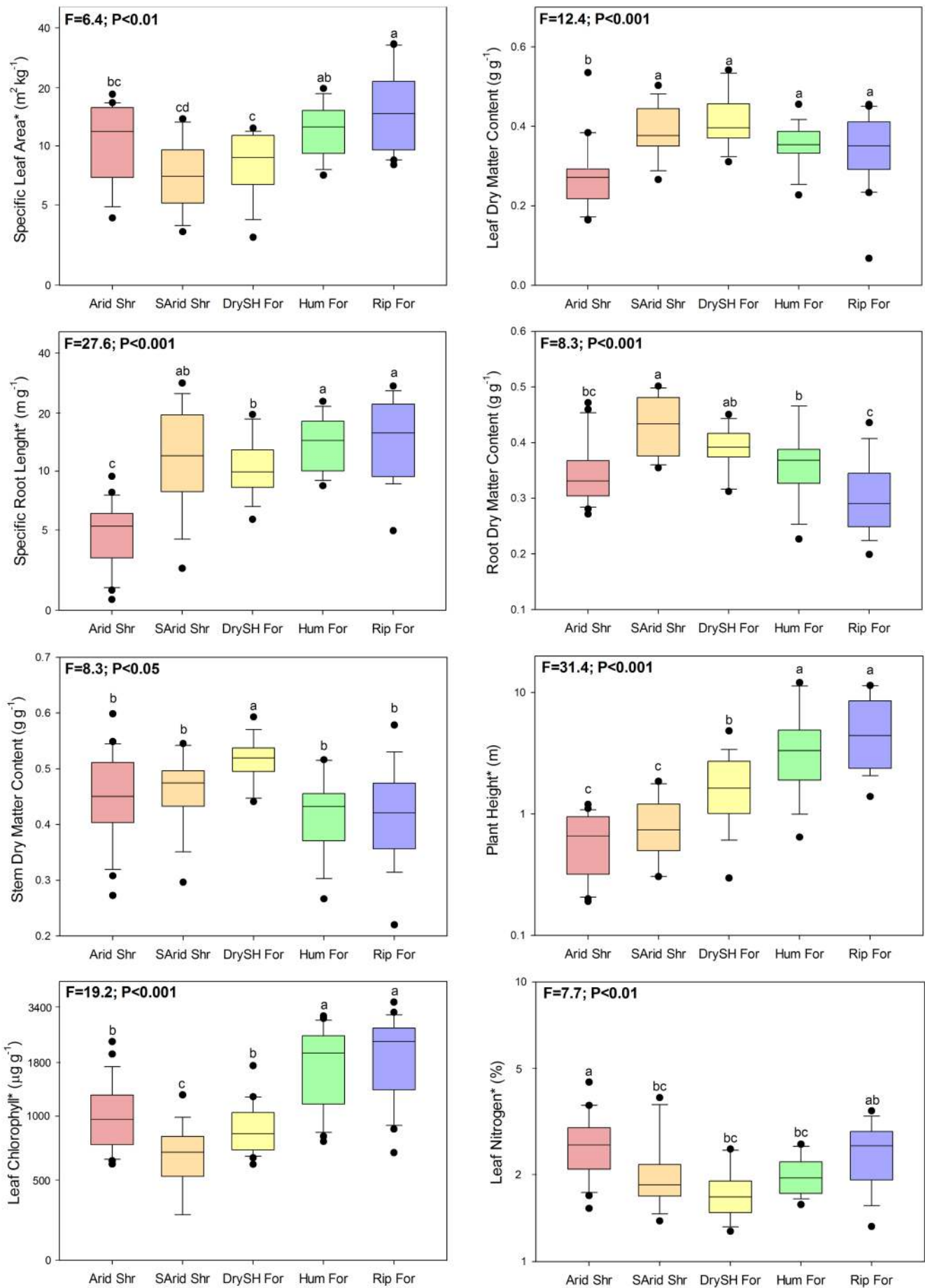


Figure 2. Average values for eight of the measured 13 functional traits in each aridity habitat. Box-plot of functional trait composition between habitats, calculated considering all the species sampled in each habitat. The line inside the box represents the median value, the box limits are the 25th and 75th percentiles, error bars show 10th and 90th percentiles, and filled symbols show outliers. Different letters indicate significant differences ($P < 0.05$) between habitats. Some traits were previously log-transformed (SLA, SRL, Pheight, LChl, LNC). The F and P values of the LMM analysis are also shown.

All the trait values were previously scaled by log-transformation to calculate the hypervolumes (Lamanna and others 2014).

All these analyses were conducted in the R 2.10.0 statistical platform (R Development Core Team, 2011), using the packages “vegan” (Oksanen, 2013), “hypervolume” (Blonder and others 2014), ‘nlme’ (Pinheiro and others 2015) and ‘FD’ (Laliberté and Shipley 2011).

Results

Functional trait variation along the aridity gradient

We detected high trait variability among the species composing the different sampled communities. The first PCA axis accounted for 37.6 % of overall variation (Appendix S2) and was related in one extreme (negative values) with species showing high values of traits representative of the resource acquisition strategy (SLA, Lsize, SRL, LChl, Pheight, and LN). At the opposite extreme (positive values), there were species with high values of traits representative of the resource-conservation strategy (LDMC, SDMC, WD, RDMC, TMDr and $\delta^{13}\text{C}$). The communities inhabiting wetter zones (*Hum For* and *Rip For*) were dominated by species having high values of leaf size (Lsize), specific leaf area (SLA), specific root length (SRL), leaf chlorophyll (LChl), plant height (Pheight) and plant cover (Pcover) (Fig. 2, Appendix S2 and S3). In contrast, the arid and semi-arid shrublands (*SArid Shr* and *Arid Shr*) were dominated by species with high values of stem wood density (SWD) and root dry matter content (RDMC) (higher in the semi-arid shrubland). Interestingly, the arid shrublands showed the lowest values of leaf dry matter content (LDMC) and the highest values of leaf nitrogen concentration (LNC) (close to those found in the riparian forest). For most of the measured traits, the *DrySH For* showed intermediate values or values similar to those of the arid and semi-arid shrublands. The only exception was SDMC, which had its highest value in the *DrySH For* (Fig. 2 and Appendix S3).

Functional diversity along the aridity gradient

We calculated the hypervolume space for each of the five habitats, considering five plant dimensions (leaf, stem and root morphology, leaf chemical and plant size). Since we measured several traits for each of these dimensions, we finally used a single PCA axis for each of them, which individually explained a large proportion of the total variance. We used these first axes of the PCA to determine the hypervolumes of the woody plant communities along the aridity gradient.

The results from the n-dimensional hypervolume approach show that the functional space was greatest for the riparian forest (Fig. 3A) in the five

plant dimensions (leaf, stem, root, leaf chemical and plant size). In addition, after standardising for species richness, the functional space showed significant variation along the aridity gradient, the hypervolume being significantly greater for the wet habitats than for the dry habitats ($P < 0.001$; Fig. 3B).

The functional richness (FRich) was significantly higher in the *Rip For* (Fig. 4) supporting the results from the niche hypervolume (Fig. 3B). However, across-habitat differences for both FEve and FDiv were marginally significant ($P < 0.06$), due to the divergent *Hum For* values (Fig. 3).

The degree of overlapping among the hypervolumes of the different communities was variable, ranging from 0 to 40% (Fig. 5). The overlap was greater between the dry environments (*Arid Shr* and *SArid Shr*) and lower when comparing these dry environments with the riparian forest. The lower values of the hypervolumes and the greater overlap among them in the driest environments indicate that the trait space occupation of different species is much less variable than in the wet zones. In spite of the high functional space overlap between dry environments, the percentage of similarity in species composition was lower than 20% (Fig. 5), while the similarity indices for species composition between the wet zones were higher (40%). As expected, species composition was very different among the wet (riparian and humid forest) and dry habitats (dry forest and arid and semi-arid shrublands).

Hypervolume space is dependent on functional dimensions

The hypervolume variations were different when we considered the plant organs or dimensions separately (Appendix S4 and Fig. 6) in comparison to the whole hypervolume described above. Thus, the dry communities showed the greatest functional space for the leaf morphology (*Arid Shr* = 19.5 sd^3 ; Fig. 6A) and chemical dimensions (*SArid Shr* = 0.98 sd^3 ; Fig. 6C), followed by the wet communities in both cases. However, the wet communities showed the highest values for the root dimension (*Rip For* = 2.93 sd^3 and *Hum For* = 1.85 sd^3 ; Fig. 6B). The dry semihumid forest displayed the smallest functional spaces in all cases.

Discussion

Functional trait variation along the regional aridity gradient

In this study, we have detected a consistent variation of several components of the functional trait structure (composition and diversity of functional traits; Mouillot and others 2011) in several Medite-

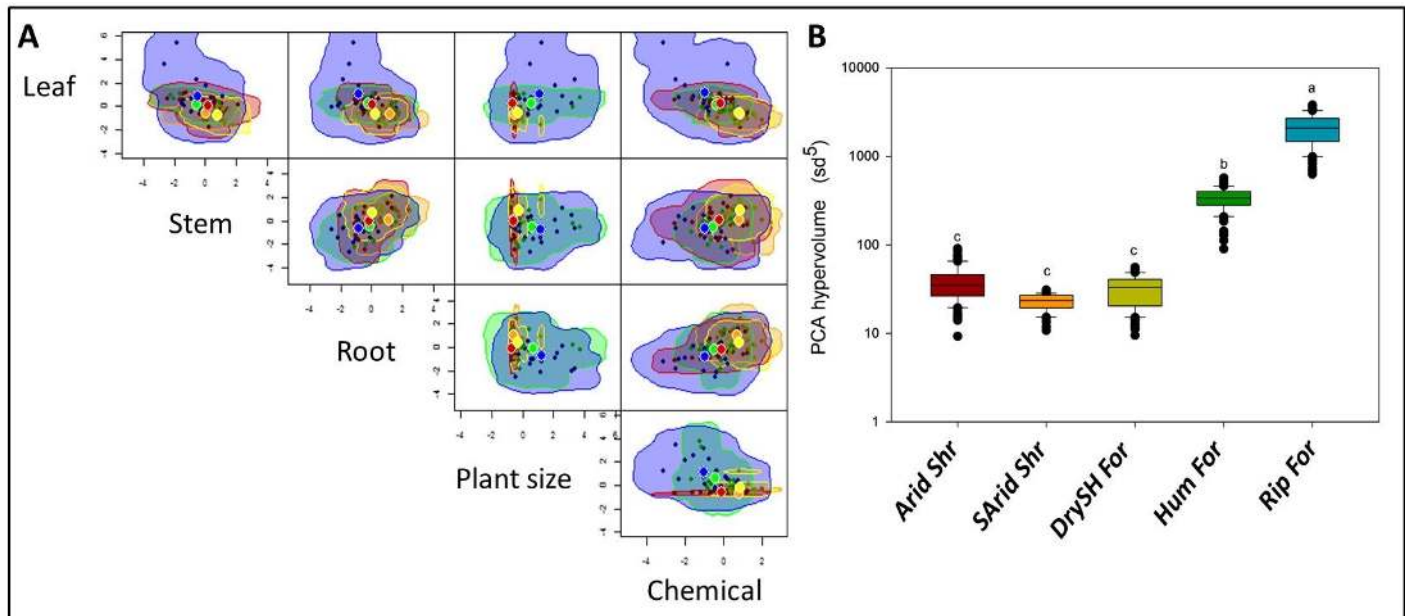


Figure 3. A) Estimated five-dimensional hypervolumes for the five habitats (see also Fig. 1). Each plant dimension was based on the first PCA axis of the different traits belonging to this dimension (Table 1). B) Size of the hypervolume of the five habitats along the regional gradient of water stress obtained by 100 randomised communities composed by 12 species from the total pool of each aridity zone. The line inside the box represents the median value, the box limits are the 25th and 75th percentiles, error bars show 10th and 90th percentiles, and filled symbols show outliers. Different letters indicate significant differences ($P < 0.05$) among habitats according to a one-way ANOVA ($P < 0.001$). Arid Shrublands –red-. Semiarid Shrublands -orange-, Dry Semihumid Forest -yellow-, Humid Forest -green-, Riparian Forest -blue-.

rranean woody plant communities over a regional environmental gradient. This provides useful insights about the effects of aridity as a main driver of plant community assembly in Mediterranean environments. Our results show that the variation in plant traits was strongly related to the plant economics spectrum theory, a notion broadly accepted at both the local (Freschet and others 2010; de la Riva and others 2016a,b; but see Wright and Sutton-Grier 2012) and global scale (Wright and others 2004). On the one hand, communities present in wet habitats (e.g. riparian and humid forest habitats) were dominated by fast-growing, acquisitive species (with high values of SLA, LChl, and plant size). These functional traits allow species to compete for space and light, which have been usually identified as the main limiting factors in productive ecosystems (Poorter and Markesteijn 2008; Bernard-Verdier and others 2012). On the other hand, plant communities inhabiting dry habitats (arid and semiarid shrublands) showed - in general - traits related to a drought tolerance strategy, such as small plant size, lower values of leaf size and SLA, and higher stem wood density (that is, slow growth rates and evergreen, sclerophyllous leaves). The general pattern obtained for the studied communities is consistent with previous studies in Mediterranean woody plant species at a local scale (Cornwell and Ackerly, 2009; de la Riva and others 2016a), where trait variation seemed to be related to the trade-off between conservation and acquisition of resources. Our results highlight the importance of water res-

triction as a major driver of functional trait distribution in Mediterranean environments at a larger (regional) spatial scale.

Variation in functional diversity and niche functional space along the regional aridity gradient

We have documented here a consistent variation in functional space (hypervolumes) along a regional gradient of aridity, with smaller hypervolumes in more stressful environments. These results are in accordance with previous studies that found lower

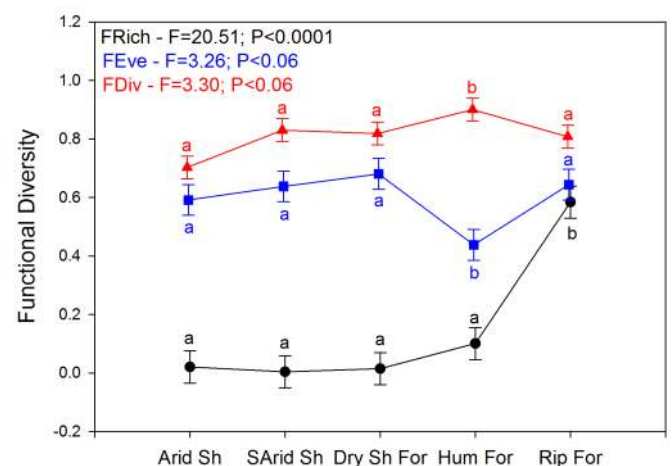


Figure 4. Differences in the functional diversity indexes (FRich: Richness, FEve: Evenness and FDiv: Divergence) among zones. Different letters denote significant differences between habitats (Tukey's test)

functional diversity under more stressful climatic conditions (Kleidon and Mooney 2000; Reu and others 2011). In dry conditions, woody plants may exhibit different sets of functional traits (Jacobsen and others 2008; Grubb and others 2015), but this diversification of strategies is limited within the range of viable traits that allow plants to persist in this arid environment (de la Riva and others 2016b). Thus, water scarcity limits the establishment of species that are not physiologically able to tolerate such abiotic constraints, reducing the range of functional traits. For example, water limitation would be expected to act as a filter, excluding from these environments fast-growing species (with a more exploitative strategy) and limiting the functional space to more conservative functional traits (Cornwell and Ackerly 2009; de la Riva and others 2016a). The main differences along the gradient were due to the increase in functional trait variability in wetter zones (higher FRich), reflecting the niche space variations among the species present in the different arid zones.

Multiple functional traits may be correlated due to evolutionary or biophysical constraints and trade-offs and hence represent meaningful syndromes or strategies (Reich and others 2003). Thus, the different traits and dimensions used show some correlations (see Appendix S2), which could limit our assessments, such a result of the lack of volume from the potential functional space that is not occupied by our traits (Díaz and others 2016). Still, the concentration into five dimensions and the lumpiness within that plane reflect the major trait range and functional roles that are relevant to estimate a wide range of the functional niche occupation.

In wetter zones (riparian and humid forests), where no water limitation exists, another secondary filter probably operates (Cingolani and others 2007). For example, in riparian and humid forests, the dense shade created by the most-dominant fast-

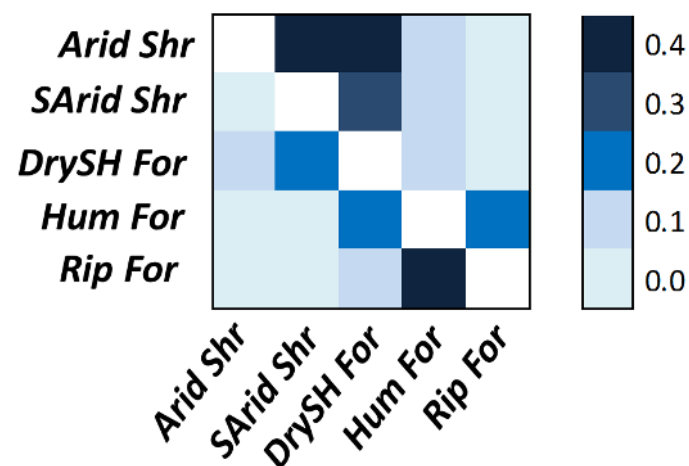


Figure 5. Values of the Sørensen similarity index calculated for the functional niche space (above the diagonal) and for the vegetation composition (below the diagonal).

growing species induces greater competition for light among them (de la Riva and others 2016a), promoting the acquisitive strategy as the most advantageous for coping with a competitive exclusion (Reich and others 1992; Mayfield and Levine 2010). However, in spite of that strong interspecific competition, we found larger functional space in the wet communities studied here. This could be due to several factors. First, the larger functional space of the communities inhabiting wetter habitats could result from niche differentiation (Ackerly and Cornwell 2007), that promotes the coexistence of species with different traits (Stubbs and Wilson 2004; Grime 2006). For example, the existence of different plant adaptations to cope with light competition, like lianas (i.e. *Hedera helix* or *Smilax aspera*) or plants with phyllodes (i.e. *Ruscus aculeatus*), is noteworthy. Secondly, in productive habitats, water availability and competition for light may promote the spatial aggregation of taller, resource-acquisitive species, facilitating the persistence of smaller and less-competitive species in the remaining open areas (Gross and others 2013). Thus, the gap spaces resulting from different disturbance processes (e.g. river floods or canopy tree death) could be relevant to the functional heterogeneity of these habitats (Biswas 2010), promoting the colonisation by some light-demanding species (i.e. *Cistus salvifolius*, *Pistacia lentiscus* or *Rhamnus lycioides*). As expected, similar patterns were observed when comparing the two approaches used in this study (functional richness and hypervolume approaches), although the kernel density (hypervolume) seemed to show greater sensitivity for functional trait space occupation among study zones than the convex hull model (FRich). However, these differences became weaker or disappeared when functional diversity (instead of the FRich and hypervolume approach) was calculated taking into account species abundances (FEve and FDiv). This could be explained because the range of functional trait variation of dominant species is similar between zones and there are no drastic changes in term of species dominance and species evenness for functional trait variation (Villéger and others 2010). As we previously observed, these results reinforce the strong influence of water restriction not only in functional trait distribution, but also in the range of functional trait variation of the dominant species. The marginal differences found in the functional diversity of *Hum For* could be due to the differences in the functional space occupied by the dominant species that share this environment with two contrasting growth form strategies; for instance tree species from genus *Quercus* (*Q. canariensis* and *Q. suber*) and vines (*Hedera helix* or *Smilax aspera*), which would increase the functional divergence to the detriment of evenness.

The communities of the dry environments (*Arid Shr*, *SArid Shr* and *DrySH For*) showed

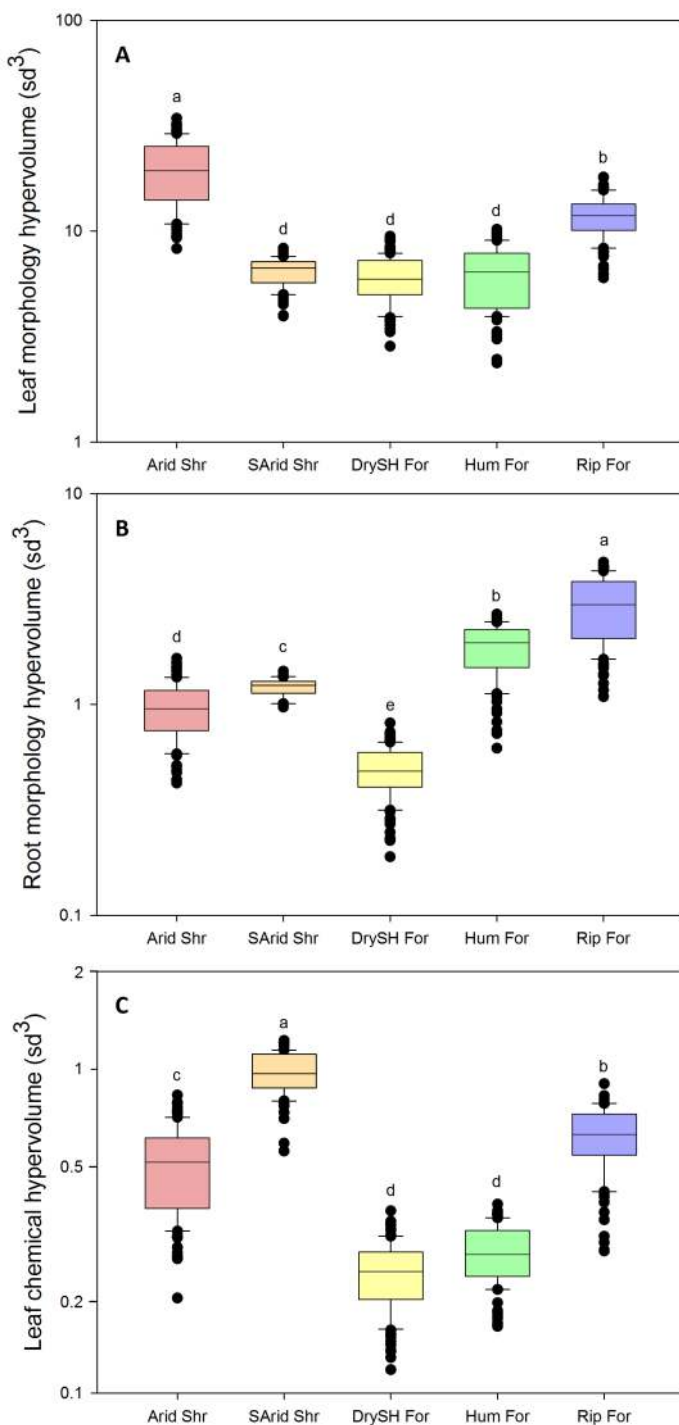


Figure 6. Size of the hypervolume variations for each plant dimension (leaf and root morphology and leaf chemical traits) in the five habitats studied along the regional gradient of water stress. Different letters indicate significant differences ($P < 0.05$) among habitats, according to post hoc multiple pairwise comparisons (Tukey's test). The ANOVA results were significant in all cases

smaller hypervolumes with a higher degree of overlap between them, in contrast to the communities from the wet environments. These results suggest that trait space occupation in wetter zones is much more variable than in the driest zones. Further, the hypervolumes of the dry communities showed higher overlaps in terms of functional structure than in terms of species composition (Fig. 5), and wet environments shared higher niche overlap for spe-

cies similarity than for functional structure. This suggests that there is a strong pressure for a similar resource-use strategy (Mason and others 2011), and supports the idea of aridity in Mediterranean regions as a potential convergence force clustering trait values at a regional scale (Gross and others 2013). In contrast, the wetter habitats (*Hum* and *Rip For*) showed higher similarity in species composition than in functional structure, which implies higher functional over-dispersion among these zones for the unshared species. Similar results were found by de Bello and others (2007), who suggested that the mechanisms related to community functional assembly do not necessarily match those promoting species coexistence. Hence, species richness indices may not be replaced always by indices of functional diversity (de Bello and others 2007).

Mismatch of niche functional spaces between different plant dimensions

The trends obtained for the multidimensional trait hypervolume were different when considering the plant dimensions separately. We found greater niche space in arid and semi-arid shrublands for the leaf morphology and chemical dimensions, respectively, while the wetter environments (*Hum For* and *Rip For*) showed greater hypervolumes for the root dimension. The lack of a general and congruent pattern when comparing results of different trait dimensions (i.e. leaf and root morphology) suggests that the functional diversity can depend largely on the niche axis considered (see also Loranger et al. 2016b) (although these differences could be also attributed to the proportion of variance that was not included in the PCA axes of the different plant dimensions, especially in the case of leaf chemical). Our results agree with those obtained by Mason and others (2011), who found dissimilar niche overlap for different traits related to similar aspects of plant strategy. As it has been hypothesized, the strength of filtering depends on the traits studied (Grime 2006), because filtering could affect differently the range of variation of each plant organ or dimension (de Bello and others 2013; Laughlin and others 2014). Therefore, within the range of viable functional traits that persist under particular environmental conditions, the diversification of successful strategies tends to exist (de la Riva and others 2016b), promoting species coexistence through the complementary uses of resources (Stubbs and Wilson 2004). For example, the soils of arid shrublands are very shallow and poor in nutrients (data not shown), which could be a strong constraint to greater root trait diversification (greater root hypervolume); however, at the leaf level different growth forms related to different resource-uptake and drought-survival strategies coexist (e.g. evergreen, and summer-deciduous shrubs; Gálmes and others

2005; Jacobsen and others 2008; Grubb and others 2015). Hence, according with the 'limiting similarity principle' (MacArthur and Levins 1967), some divergence of strategies exist as a result of resource partitioning (Cornwell and Ackerly 2009), but without compromising (necessarily) in the same way all plant dimensions and within the range of viable trait values for these particular abiotic conditions.

The lower functional diversity detected in the communities of the most stressful and arid habitats reflected a relatively homogeneous functional structure dominated by shrubs with a predominant resource-conservative strategy (see also Jacobsen and others 2008). However, other studies based on aboveground traits found a lower functional diversity in more benign conditions (Pakeman 2011; de Bello and others 2013). These contradictory results could arise from the comparison of different scales and different diversity indices or growth forms (i.e. herbaceous/woody species), which do not necessarily support the global patterns (de Bello and others 2007; Funk and Cornwell 2013). In the light of our results, the trait dimension considered could be also an important factor to take into account (Loranger and others 2016b). In this regard, most of the studies linking plant functional diversity and environmental factors are biased to above-ground traits, often ignoring the root dimension. Therefore, our results reinforce the importance of considering a multidimensional approach, which implies the inclusion of root attributes in the calculations of functional diversity, to better understand the role of aridity as a driver of community functional structure in Mediterranean environments.

Conclusions

Our study highlights the trait hypervolume approach as a useful tool to understand community assembly patterns and quantify species niches over a broad regional scale. In addition, our results show that the wettest ecosystems serve as a reservoir of functional diversity, mainly constituted by species with a predominantly acquisitive strategy and a deciduous leaf habit. By contrast, the greater functional diversity in the leaf dimension detected in the dry habitats studied may offer a wide range of possible adaptations to cope with water stress (Stubbs and Wilson 2004; Mason and others 2005), which could imply greater resilience in the face of increasing aridity. The fact that particular dimensions of the functional community structure respond differently along the aridity gradient makes this kind of study relevant to the modelling of vegetation responses to the ongoing climate change. However, more research along regional gradients worldwide is needed to better understand the community assembly process and to forecast the consequences of in-

creased aridity (according to IPCC 2013 predictions) for ecosystem functions and services.

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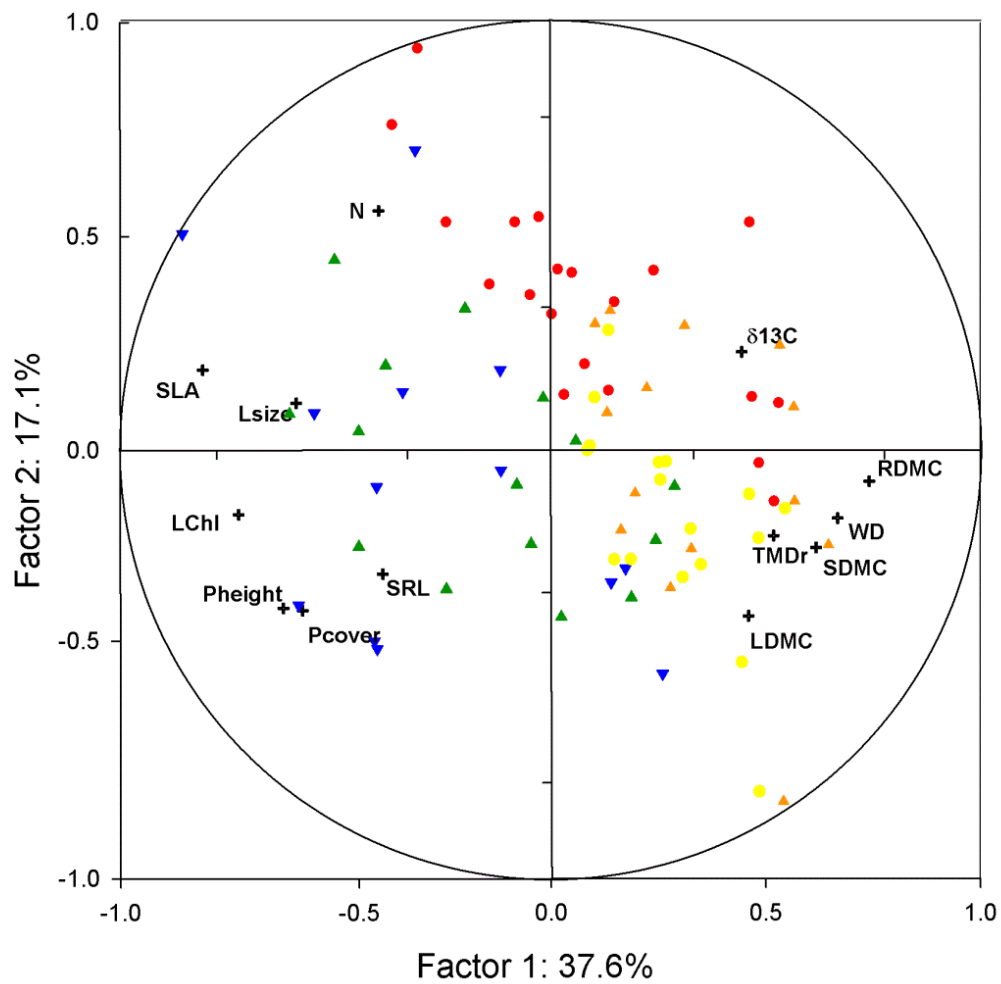
1 **Appendix S1.** List of the 74 woody plant species, family, life habit and their presence/absence in the five aridity zones.

Species	Family	Life habit	Cabo de Gata (Arid Shr)	Doñana (SArid Shr)	Sierra Morena (DrySH For)	Alcornocales (Hum For)	Guadiato River (Rip For)
<i>Alnus glutinosa</i>	Betulaceae	Tree					x
<i>Anthyllis citysoides</i>	Fabaceae	Shrub	x				
<i>Anthyllis terniflora</i>	Fabaceae	Shrub	x				
<i>Arbutus unedo</i>	Ericaceae	Arborescent-shrub			x	x	
<i>Armeria velutina</i>	Plumbaginaceae	Shrub		x			
<i>Artemisia barririeri</i>	Asteraceae	Shrub	x				
<i>Atractylis humilis</i>	Asteraceae	Shrub	x				
<i>Ballota hirsuta</i>	Lamiaceae	Shrub	x				
<i>Celtis australis</i>	Cannabaceae	Tree					x
<i>Cistus albidus</i>	Cistaceae	Shrub	x		x		
<i>Cistus crispus</i>	Cistaceae	Shrub			x		
<i>Cistus ladanifer</i>	Cistaceae	Shrub			x		
<i>Cistus libanotis</i>	Cistaceae	Shrub		x			
<i>Cistus monspeliensis</i>	Cistaceae	Shrub			x		
<i>Cistus salvifolius</i>	Cistaceae	Shrub			x	x	
<i>Coronilla juncea</i>	Fabaceae	Shrub	x				
<i>Crataegus monogina</i>	Rosaceae	Arborescent-shrub				x	x
<i>Cytisus grandiflorus</i>	Fabaceae	Shrub		x			
<i>Daphne gnidium</i>	Malvaceae	Shrub			x		
<i>Ephedra fragilis</i>	Ephedraceae	Shrub	x				
<i>Erica arborea</i>	Ericaceae	Shrub				x	
<i>Erica scoparia</i>	Ericaceae	Shrub		x			
<i>Ficus carica</i>	Moraceae	Tree					x
<i>Fraxinus angustifolia</i>	Oleaceae	Tree					x
<i>Fumana spidula</i>	Violaceae	Shrub	x				
<i>Genista hirsuta</i>	Fabaceae	Shrub			x		

<i>Halimium commutatum</i>	Malvaceae	Shrub		x				
<i>Halimium halimifolium</i>	Malvaceae	Shrub		x				
<i>Hedera helix</i>	Araliaceae	Vine					x	x
<i>Helianthemum almeriense</i>	Malvaceae	Shrub	x					
<i>Helianthemum syriacum</i>	Malvaceae	Shrub	x					
<i>Helichrysum stoechas</i>	Asteraceae	Shrub	x					
<i>Helycrisum picardii</i>	Asteraceae	Shrub			x			
<i>Hippocrepis scabra</i>	Fabaceae	Shrub	x					
<i>Juniperus phoenicea</i>	Cupressaceae	Arborescent-shrub			x			
<i>Launaea arborescens</i>	Asteraceae	Shrub	x					
<i>Lavandula multifida</i>	Lamiaceae	Shrub	x					
<i>Lavandula stoechas</i>	Lamiaceae	Shrub			x		x	
<i>Myrtus communis</i>	Mirtaceae	Shrub					x	
<i>Nerium oleander</i>	Apocynaceae	Arborescent-shrub						x
<i>Phlomis fruticosa</i>	Lamiaceae	Shrub					x	
<i>Phlomis purpurea</i>	Lamiaceae	Shrub	x				x	
<i>Phyllirea angustifolia</i>	Oleaceae	Arborescent-shrub					x	
<i>Phyllirea latifolia</i>	Oleaceae	Arborescent-shrub					x	x
<i>Pinus pinea</i>	Pinnaceae	Tree			x			
<i>Pistacia lentiscus</i>	Anacardiaceae	Arborescent-shrub					x	x
<i>Pistacia terebinthus</i>	Anacardiaceae	Arborescent-shrub					x	
<i>Populus alba</i>	Salicaceae	Tree						x
<i>Quercus cocifera</i>	Fagaceae	Arborescent-shrub					x	
<i>Quercus canariensis</i>	Fagaceae	Tree					x	
<i>Quercus ilex</i>	Fagaceae	Arborescent-shrub					x	
<i>Quercus suber</i>	Fagaceae	Tree					x	
<i>Rhamnus alaternus</i>	Rhamnaceae	Shrub					x	
<i>Rhamnus lycioides</i>	Rhamnaceae	Shrub						x
<i>Rhododendron ponticum</i>	Ericaceae	Shrub					x	
<i>Rosa canina</i>	Rosaceae	Shrub						x
<i>Rosmarinus officinalis</i>	Lamiaceae	Shrub	x		x		x	
<i>Rubus ulmifolius</i>	Rosaceae	Vine					x	

<i>Ruscus aculeatus</i>	Asparagaceae	Shrub			x	x
<i>Salix atrocinerea</i>	Salicaceae	Tree				x
<i>Sideritis pusilla</i>	Lamiaceae	Shrub	x			
<i>Smilax aspera</i>	Smilacaceae	Vine	x			x
<i>Stauracanthus genistoides</i>	Fabaceae	Shrub			x	
<i>Teucrium charidemi</i>	Lamiaceae	Shrub	x			
<i>Teucrium fruticans</i>	Lamiaceae	Shrub				
<i>Thymelaea hirsuta</i>	Malvaceae	Shrub	x			
<i>Thymus hyemalis</i>	Lamiaceae	Shrub	x			
<i>Thymus mastichina</i>	Lamiaceae	Shrub			x	
<i>Ulex australis</i>	Fabaceae	Shrub			x	
<i>Ulex parviflorus</i>	Fabaceae	Shrub	x			
<i>Ulmus minor</i>	Ulmaceae	Tree				x
<i>Viburnum tinus</i>	Adoxaceae	Arborescent-shrub			x	
<i>Vitis vinifera</i>	Vitaceae	Vine				x
<i>Withania frutescens</i>	Solanaceae	Shrub	x			

3 **Appendix S2.** Principal components analysis (PCA) showing the plant economics spectrum,
 4 from conservative (right) to fast-growing or acquisitive (left) species. 13 functional traits have
 5 been sampled from 91 observations. (Arid Shrublands –red-, Semiarid Shrublands -orange-, Dry
 6 Semihumid Forest -yellow-, Humid Forest -green-, Riparian Forest -blue-. SLA: Specific leaf
 7 area; Lsize: Leaf area; LDMC: Leaf dry matter content; N: Leaf nitrogen concentration; LChl:
 8 Leaf chlorophyll; $\delta^{13}\text{C}$: Leaf carbon isotope ratio; WD: Wood density; SDMC: Stem dry matter
 9 content; SRL: Specific root length; RDMC: Root dry matter content; TMDr: Root density;
 10 Pheight: Plant height; Pcover: Plant cover.



12 **Appendix S3.** Mean values and standard errors (SE) and results of linear mixed models between aridity zones for functional traits
 13 (species as random effect). Some traits have been log-transformed in order to fulfil statistic assumptions (*). Different letters indicate
 14 significant differences ($P < 0.05$) among habitats, according to post hoc multiple pairwise comparisons (Tukey's test).

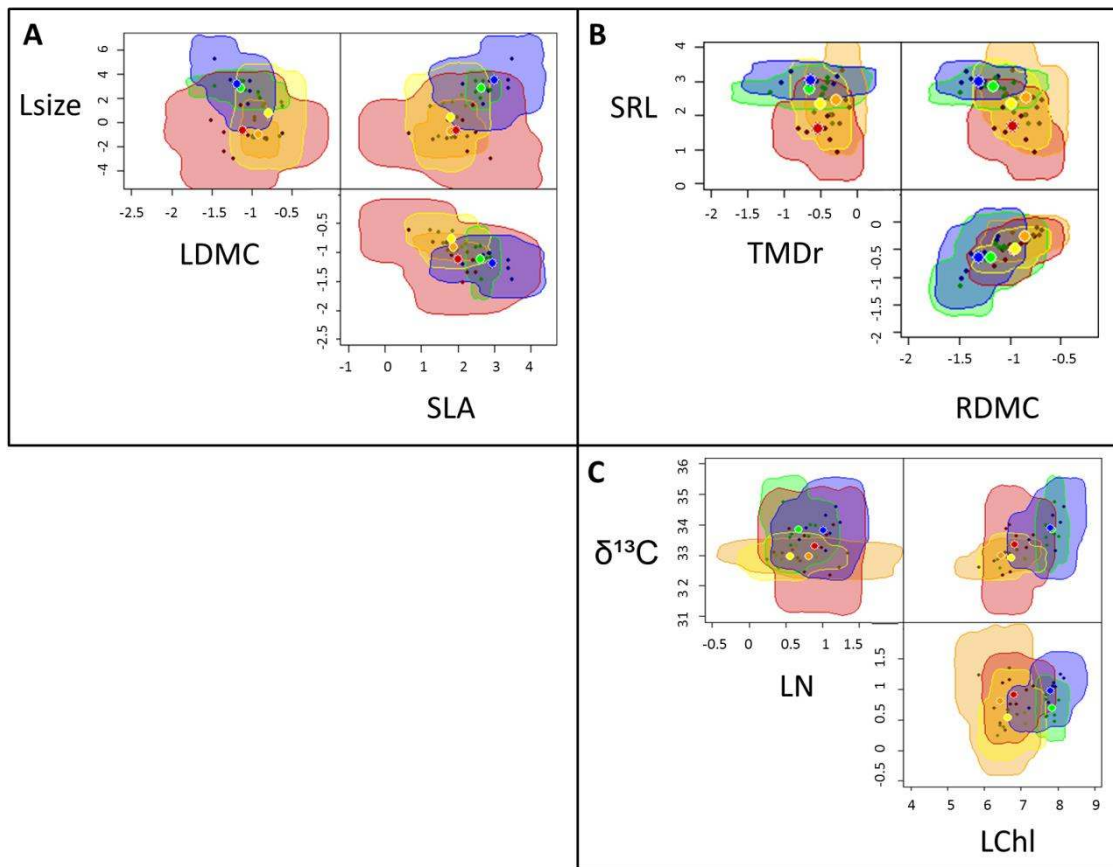
Trait	Arid Shr			SArid Shr			DrySH For			Hum For			Rip For			F	P
	Mean	SE		Mean	SE		Mean	SE		Mean	SE		Mean	SE			
Lsize*	1.26	± 0.28	c	0.64	± 0.20	c	3.10	± 2.17	b	11.8	± 2.17	a	26.6	± 10.6	a	12.2	<0.001
SLA*	11.27	± 0.92	bc	7.39	± 0.81	cd	8.51	± 0.65	c	12.5	± 0.84	ab	17.1	± 2.0	a	6.4	0.004
LDMC	0.27	± 0.017	b	0.38	± 0.01	a	0.41	± 0.15	a	0.35	± 0.05	a	0.35	± 0.08	a	12.4	<0.001
SWD	0.51	± 0.02	ab	0.53	± 0.08	ab	0.59	± 0.08	a	0.44	± 0.1	b	0.43	± 0.11	b	3	0.05
SDMC	0.44	± 0.01	b	0.46	± 0.06	b	0.51	± 0.01	a	0.41	± 0.07	b	0.41	± 0.08	b	8.3	0.04
SRL*	5.16	± 0.36	c	13.4	± 1.84	ab	10.8	± 0.87	b	14.3	± 1.05	a	16.1	± 6.32	a	27.6	<0.001
RDMC	0.34	± 0.01	bc	0.43	± 0.01	a	0.39	± 0.01	ab	0.36	± 0.02	b	0.3	± 0.01	c	8.3	0.001
TMDr	0.58	± 0.02	b	0.8	± 0.04	a	0.66	± 0.02	b	0.62	± 0.03	b	0.57	± 0.04	b	7.7	0.005
LN*	2.63	± 0.14	a	2.11	± 0.18	bc	1.77	± 0.08	bc	2.04	± 0.07	bc	2.47	± 0.14	ab	7.7	0.002
LChl*	1066.4	± 94.8	b	666	± 72.4	c	910.6	± 68.2	b	1873	± 180.4	a	2085.6	± 203.6	a	19.2	<0.001
$\delta^{13}C$	-28.6	± 0.3		-27.6	± 0.5		-27.6	± 0.28		-28.9	± 0.28		-28.4	± 0.15		2.7	ns
Pheight*	0.61	± 0.67	c	0.87	± 0.13	c	1.91	± 0.27	b	4.17	± 0.77	a	5.52	± 0.8	a	31.4	<0.001
Pcover*	0.83	± 0.16	d	0.78	± 0.21	d	4.39	± 1.68	c	12.1	± 4.27	b	22.6	± 4.36	a	27.1	<0.001

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17 **Appendix S4.** Estimated three-dimensional hypervolumes of the five aridity zones for each
18 independent plant dimension: **(A)** Leaf morphology, **(B)** Root morphology and **(C)** Leaf
19 chemical. Arid srhublands in red, Semi-Arid srhublands in orange, Dry-Semihumid forest in
20 yellow, Humid forest in green and Riparian forest in blue. SLA: Specific leaf area; Lsize: Leaf
21 area; LDMC: Leaf dry matter content; SRL: Specific root length; RDMC: Root dry matter
22 content; TMDr: Root density; LN: Leaf nitrogen concentration; LChl: Leaf chlorophyll; $\delta^{13}\text{C}$:
23 Leaf carbon isotope ratio.

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