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Functional diversity enhances the resistance of ecosystem multifunctionality to aridity in Mediterranean drylands

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Summary

- We used a functional trait-based approach to assess the impacts of aridity and shrub encroachment on the functional structure of Mediterranean dryland communities (functional diversity (FD) and community-weighted mean trait values (CWM)), and to evaluate how these functional attributes ultimately affect multifunctionality (i.e. the provision of several ecosystem functions simultaneously).
- Shrub encroachment (the increase in the abundance/cover of shrubs) is a major land cover change that is taking place in grasslands worldwide. Studies conducted on drylands have reported positive or negative impacts of shrub encroachment depending on the functions and the traits of the sprouting or nonsprouting shrub species considered.
- FD and CWM were equally important as drivers of multifunctionality responses to both aridity and shrub encroachment. Size traits (e.g. vegetative height or lateral spread) and leaf traits (e.g. specific leaf area and leaf dry matter content) captured the effect of shrub encroachment on multifunctionality with a relative high accuracy ($r^2 = 0.63$). FD also improved the resistance of multifunctionality along the aridity gradient studied.
- Maintaining and enhancing FD in plant communities may help to buffer negative effects of ongoing global environmental change on dryland multifunctionality.

Introduction

Global change is altering biodiversity worldwide at an unprecedented rate, with important consequences for the functioning of natural ecosystems (Vitousek *et al.*, 1997; Chapin *et al.*, 2000). A response–effect framework based on plant functional traits has been proposed to explore the ecosystem-level consequences of local changes in biodiversity in response to ongoing global environmental change (global change hereafter; Lavorel & Garnier, 2002; Suding *et al.*, 2008). This approach states that changes in the functional structure of communities can partly affect ecosystem functioning ('indirect' effects, *sensu* Suding *et al.*, 2008), although global change drivers also alter such functioning directly (Asner *et al.*, 2004; Austin *et al.*, 2004; Zepp *et al.*, 2007). The influential 'mass ratio hypothesis' (Grime, 1998) considers that the traits of dominant species largely determine the effects of plant communities on ecosystem functioning. As such, trait-based studies have mainly focused on community-weighted mean values (CWM hereafter; Garnier *et al.*, 2004; Violle *et al.*, 2007; Suding *et al.*, 2008; see De Bello *et al.*, 2010; for a review). However, global change drivers can also affect the variance of the trait distributions within communities (here defined as 'functional diversity' (FD); see Laliberté & Legendre, 2010). High FD may reflect an increase in complementarity in resource use between species (Gross *et al.*, 2007b), thus improving ecosystem functioning (Díaz *et al.*, 2007).

Most studies investigating the relationship between the community functional structure and ecosystem functioning have studied one or a few ecosystem functions (see De Bello *et al.*, 2010 for a review). However, ecosystems are primarily valued because they provide multiple functions and services simultaneously (i.e. multifunctionality hereafter; Zavaleta *et al.*, 2010). Therefore, assessing how global change drivers may impact multifunctionality is crucial to understand the ecological consequences of global change (Reiss *et al.*, 2009; Zavaleta *et al.*, 2010; Cardinale *et al.*, 2012). In this context, high degrees of FD have been

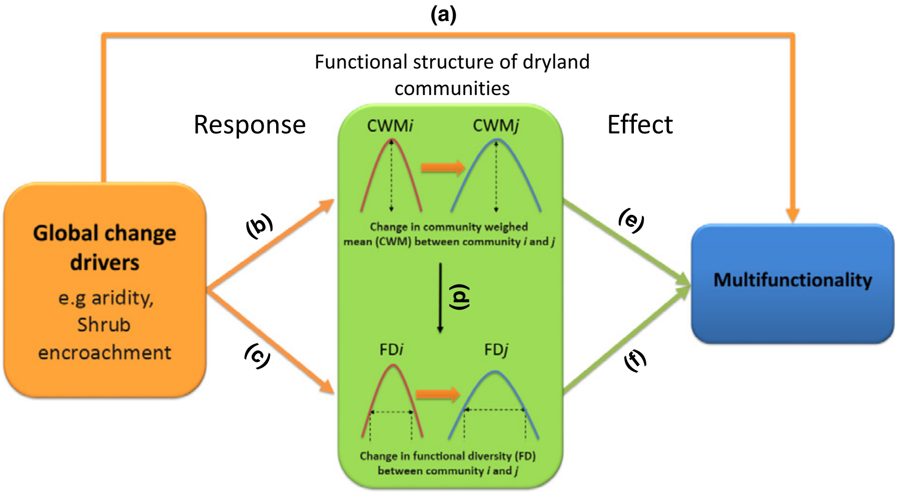

Fig. 1 Hypothetical relationships among aridity, shrub encroachment and the functional structure and multifunctionality of dryland communities. Aridity and shrub encroachment directly impact multifunctionality (a). The left part of the figure represents the response of the plant community to both variables (CWM, mean trait distribution, b; FD, functional diversity, c; and covariation between CWM and FD, d). Changes in community functional structure promote effects on multifunctionality via two nonexclusive mechanisms, mass ratio process (e) and niche complementary (f). The red unimodal distributions represent a hypothetical trait distribution within a community (*i*) in a given environmental condition. The blue distributions represent the impact on trait distribution produced by contrasting amounts of aridity and shrub encroachment in a community *j* compared with *i*. See Supporting Information Notes S1 for a detailed rationale of the different relationships depicted in the figure.

hypothesized as crucial for maintaining high multifunctionality (Mouillot *et al.*, 2011).

Arid, semiarid and dry-subhumid ecosystems (drylands hereafter) are currently impacted by climate change (Maestre *et al.*, 2012b) and shrub encroachment (Eldridge *et al.*, 2011). Shrub encroachment, that is, an increase in abundance and/or density of shrub species in grasslands (Schlesinger *et al.*, 1990), is a major land cover change that is occurring in drylands worldwide (Knapp *et al.*, 2008; Maestre *et al.*, 2009; Li *et al.*, 2013). This phenomenon has been found to promote dryland desertification by reducing plant biomass and species richness (Knapp *et al.*, 2008), increasing fire risk (Mitchley & Ispikoudis, 1999) and enhancing soil erosion (Schlesinger *et al.*, 1990). However, other studies have found positive effects of shrub encroachment on the richness of different organisms and on ecosystem functioning (see Eldridge *et al.*, 2011 for a review). Maestre *et al.* (2009) hypothesized that the functional traits of encroaching shrubs relative to those of the grasses being replaced are key determinants of the outcomes of shrub encroachment. Size-related traits of shrub species might be particularly important, as the replacement of grass species by tall and large shrubs (i.e. sprouting shrubs) enhances species richness and ecosystem functions such as nutrient/carbon (C) cycling and storage (Eldridge *et al.*, 2011; Quero *et al.*, 2013).

Climate change has been projected to increase aridity in drylands worldwide during this century (Feng & Fu, 2013). This can modify the traits of dominant shrub species, as well as the FD within communities (Gross *et al.*, 2013), because aridity generally favors small stress-tolerant and slow-growing shrub species with particular leaf traits, for example, thick evergreen leaves with low specific leaf area (SLA) and high leaf dry matter content (Ackerly *et al.*, 2002). However, these species can be replaced in the most arid Mediterranean ecosystems by stress-avoidant species characterized by summer deciduous leaves and an opposite trait strategy (Ackerly *et al.*, 2002; Gross *et al.*, 2013). Changes in leaf trait values may have important consequences on ecosystem functioning, as they determine the rate of resource capture and utilization (Garnier *et al.*, 2004) as well as litter decomposition (Kazakou *et al.*, 2006). Also, increasing aridity may select for small shrub species (Gross *et al.*, 2013) and limit the ability of tall sprouting shrubs to enhance multifunctionality. Finally, increasing aridity may also alter multifunctionality by modifying the FD within drylands (Gross *et al.*, 2013), because a positive effect of species diversity on multifunctionality has been found in global drylands (Maestre *et al.*, 2012a), and high FD has been hypothesized to improve the resistance of dryland ecosystems to aridity (Volaire *et al.*, 2014); this is the case because FD could increase the probability that some species will survive if environmental conditions change, and thus could maintain ecosystem functioning (Díaz & Cabido, 2001).

In this paper, we evaluated how aridity and shrub encroachment affect the functional structure of Mediterranean drylands, and assessed how changes in their functional structure ultimately drive variations in multifunctionality. We also quantified the relative contribution of mass ratio (reflected by CWM) vs niche complementarity (reflected by FD) processes on multifunctionality for multiple traits (size and leaf traits) using a confirmatory path analysis (Shipley, 2013; Fig. 1). We tested the following hypotheses: mass ratio and niche complementarity processes are important drivers of multifunctionality (Mouillot *et al.*, 2011); high FD will improve multifunctionality (Mouillot *et al.*, 2011); high FD will minimize the negative effects of aridity on multifunctionality (Cardinale *et al.*, 2012; Maestre *et al.*, 2012a); and the effects of aridity on multifunctionality will be modulated by the traits of shrubs which determine the outcome of shrub encroachments.

Materials and Methods

Study area

We surveyed 45 sites along an aridity gradient from central to southeast Spain (Supporting Information Fig. S1). Mean annual precipitation and temperature along this gradient ranged from 294 to 479 mm and from 12 to 18°C, respectively. Aridity (1 – aridity index; precipitation/potential evapotranspiration; Delgado-Baquerizo *et al.*, 2013) values range from 0.57 to 0.76, and are strongly correlated to both annual mean precipitation ($R^2 = 0.97$) and temperature ($R^2 = 0.89$) in the studied sites. Climatic data were extracted from the WorldClim global database (Hijmans *et al.*, 2005), while data to calculate the aridity index were obtained from Trabucco & Zomer (2009). All the studied sites were located on south-facing slopes, with slope values ranging from 1 to 22° (measured *in situ* with a clinometer), and had soils derived from limestone (Lithic Calciorthid; Soil Survey Staff, 1994). Vegetation at these sites was either a grassland dominated by *Stipa tenacissima* or a shrubland dominated by obligate-seeder shrubs such as *Rosmarinus officinalis* (hereafter nonsprouting shrubs, Fig. S2). Within grasslands and shrublands, we selected sites with and without tall sprouting shrubs (such as *Quercus coccifera*; Fig. S2; Table S1).

Vegetation sampling

We established a 30 × 30 m plot at each study site. Total plant cover within each plot was sampled by using four 30 m long transects located 8 m apart from each other, which were extended parallel to the slope. In each transect, the cover of every perennial species in 20 consecutive quadrats (1.5 × 1.5 m) was visually recorded. We focused on perennial plants as they represent most of the plant biomass in drylands (Whitford, 2002), and their cover is a good predictor of ecosystem functioning in these areas (Maestre & Escudero, 2009; García-Gómez & Maestre, 2011; Gaitán *et al.*, 2014). Species abundance per site was calculated as the sum of the cover measured in the 80 quadrats.

At each plot, we measured the traits of all the perennial plant species that accounted for at least 80% of the total plot cover, in decreasing order of relative abundance. These measurements were conducted on 10 randomly selected individuals per species during the peak of the vegetation growth season (spring). We assigned to each species and plot the average value of the individuals measured in that plot. In the case of the species for which we did not have local trait values we used the average trait values observed in the three nearest sites. Ten traits were measured following standardized protocols (Cornelissen *et al.*, 2003): plant architecture traits, including vegetative height (VH, cm), lateral spread (LS, cm^2), branching density (BD, number of main stems) and ramification (Br, number of ramifications per stem) (these traits are related to plant water-use efficiency and/or competitive ability; Westoby *et al.*, 2002); and leaf traits, including leaf area (LA, cm^2), leaf length (LL, cm), leaf width (LW, cm) and leaf thickness (LT, mm), all reflecting light interception and water stress tolerance (Westoby *et al.*, 2002), and SLA ($\text{cm}^2\ \text{g}^{-1}$) and leaf dry matter content (LDMC, g g^{-1}), which correlate with plant relative growth rate and nutrient acquisition and utilization (Wright *et al.*, 2004).

Soil sampling and analyses

Soil cores (0–7.5 cm depth) were sampled during the peak of the dry season (July–August) under the canopy of five randomly selected *S. tenacissima* and *R. officinalis* individuals, and five others in randomly selected open areas devoid of vascular vegetation. In those sites with sprouting shrubs, additional soil cores were sampled under the canopy of five randomly selected individuals of these shrubs. Hence, 10 or 15 soil samples, respectively, were collected per site.

Soil samples were sieved by a 2 mm mesh and air-dried for 1 month before laboratory analyses. For each soil sample, the following variables were quantified as described in Maestre *et al.* (2012a) and Delgado-Baquerizo *et al.* (2013): organic C, pentoses, hexoses, total nitrogen (N), total available N, amino acids, proteins, net potential mineralization rate, total phosphorus (P), available inorganic P, Olsen P (inorganic P – HCL 1M) and the activities of phosphatase and β-glucosidase. These variables constitute a good proxy for processes such as nutrient cycling, biological productivity, and build-up of nutrient pools, which are important determinants of ecosystem functioning in drylands (Whitford, 2002). Most of these processes are also considered to support ecosystem services, as other types of ecosystem services depend on them (MEA, 2005; Isbell *et al.*, 2011).

Data management

Community trait distribution For each measured trait, we calculated two complementary indices of functional structure: CWM and FD. CWM corresponds to the mean trait value of a community weighted by the relative abundance of each species, and reflects the trait values of the most dominant plant species in a given community. It was calculated with the following equation (Violle *et al.*, 2007):

$$\text{CWM}_j = \sum_i^n p_{ij} T_{ij} \qquad \text{Eqn 1}$$

where p_{ij} is the abundance of the species i in the community j, and T_{ij} is the mean trait value of the species i in the community j.

Functional diversity quantifies the degree of trait dispersion within a community (adapted from Laliberté & Legendre, 2010). Calculated for each trait separately, FD is similar to the variance of the community trait distribution weighted by the relative abundance of each species within the community. It was calculated as:

$$\text{FD}_j = \sum_i^n p_{ij} \left(\frac{|T_{ij} - \text{CWM}_j|}{\sum_i^n |T_{ij} - \text{CWM}_j|} \right) \qquad \text{Eqn 2}$$

where p_{ij} is the abundance of the species i in the community j, T_{ij} is the mean trait value of the species i in the community j, and

CWM_j is the community-weighted trait of the community j. High FD values suggest higher complementarity in resource used between species within a given community (Maire *et al.*, 2012).

Multifunctionality index Multifunctionality was estimated from all the soil variables measured using the M index of Maestre *et al.* (2012a). To obtain an M-value for each site, Z-scores were first calculated for each of the 13 soil variables estimated at the scale of each 30 × 30 m plot surveyed. These estimates were obtained by using a weighted average of the mean values observed in bare ground and vegetated areas, and weighted by their respective cover at each plot (Maestre *et al.*, 2012a). Raw data were normalized before calculations; a square root transformation normalized most of the variables evaluated. Following this, the Z-scores of the 13 soil variables were averaged to obtain M. This index provides a straightforward and easily interpretable measure of the ability of different communities to sustain multiple ecosystem functions simultaneously (Byrnes *et al.*, 2014). It is also statistically robust (Maestre *et al.*, 2012a), and is being increasingly used when assessing multifunctionality (Quero *et al.*, 2013; Bradford *et al.*, 2014; Pendleton *et al.*, 2014; Wagg *et al.*, 2014). We acknowledge that the use of M may preclude a detailed analysis of how particular species differ in their importance for different functions (Hector & Bagchi, 2007; Gotelli *et al.*, 2011), and that in this index declines in a particular process/function can theoretically be compensated for by increases in another process/function (something that has been criticized in the past; Gamfeldt *et al.*, 2008). However, we did not find that particular sites with high values of a single or a few functions had consistently low values of other functions (Table S2). Moreover, the relatively large number of variables employed to calculate M makes it relatively robust to outliers or atypical values. We also acknowledge that having variables that are highly correlated among them could make them somewhat redundant (albeit this also simplifies the interpretation of the values of M). However, in our dataset, only nine out of the 78 correlations between the soil variables evaluated had r-values higher than 0.7, suggesting that redundancy is not very high within our data (Table S2). Finally, our estimates of M are highly related to other multifunctionality indices (Fig. S3). Thus, our results and conclusions are robust to the choice of metric used to estimate multifunctionality.

Statistical analyses

Functional variation between dryland communities We conducted a principal component analysis (PCA) with Varimax rotation using the CWM and FD values of all the traits measured. These analyses were done separately for CWM and FD. We used the PCA coordinates in those components with an eigenvalue > 1 to measure the CWM and the FD of each community. This procedure allowed us to identify the plant strategy spectrum along which traits covary across species and communities (Maire *et al.*, 2012). It has also the advantage to consider only independent variables in further analyses. CWM values were normalized using log transformation before PCA analyses.

Community responses to aridity and shrub encroachment We used a stepAICc procedure (following Grace, 2006) to evaluate the relationship between either CWM or FD (response variables) and aridity, abundance of sprouting shrubs and abundance of nonsprouting shrubs (predictors). As the functional response to aridity is not necessarily linear (Gross *et al.*, 2013), a quadratic term was introduced if needed. The best model was selected based on the Akaike information criterion (AICc; Akaike, 1973). To evaluate the relative importance of aridity and shrub encroachment as drivers of the functional structure of the studied communities, we conducted a variance decomposition analysis based on the sum of squares of the selected models. Note that we also initially included slope in our models, as it has important effects on water availability in drylands (Gómez-Plaza *et al.*, 2001). However, this variable was not retained in any model based on an AICc model selection ($P > 0.05$ in all cases, data not shown). Therefore, we removed slope as a predictor in our models because it does not explain additional variation over that explained by aridity and functional structure.

Direct and indirect effects of aridity and shrub encroachment on multifunctionality To test for relationships among CWM, FD, aridity, shrub encroachment, and multifunctionality, we conducted a confirmatory path analysis using a d-sep approach (Shipley, 2009; Laliberté & Tylianakis, 2012). This methodology allows some of the limitations of standard structural equation models to be relaxed, including nonnormal data distribution, nonlinear relationships between variables and small sample sizes (Grace, 2006; Shipley, 2009). The d-sep approach is based on an acyclic graph that depicts the hypothetical relationships and independence claims between variables, where the latter are tested using the C statistic (see Fig. 1 and Notes S1 for the detailed rationale of our analyses). We tested three main alternative hypotheses, where multifunctionality responses to aridity and shrub encroachment are driven by CWM only (mass ratio hypothesis); FD only (niche complementary hypothesis); and the interplay of mass ratio and niche complementarity processes (combined hypothesis). To simplify the *a priori* models used, a stepAICc procedure was first conducted to select the predictors that explained most of the variability found in multifunctionality (see Table S3). When several models were not rejected, we used the AICc procedure adapted for confirmatory path analysis to select the best model (Shipley, 2013). Finally, standardized path coefficients were used to measure the direct, indirect, and total effects of the predictors (Grace & Bollen, 2005).

As multiple traits can potentially act simultaneously on multifunctionality through contrasted mechanisms (e.g. mass ratio and niche complementarity in the case of the combined hypothesis), their respective effects on multifunctionality responses to aridity might be difficult to isolate. Thus, we ran a sensitivity analysis on the best selected model to highlight the relative contribution of multiple traits to the observed multifunctionality in response to aridity and shrub encroachments. To do this, we used the parameters of the best model to estimate multifunctionality values along the aridity gradient studied under different scenarios, which were created by manipulating the abundances of nonsprouting and sprouting shrubs. The first scenario considered only the effects of aridity by fixing the abundance of both shrub types at 0%. The second scenario focused on the interplay between aridity and encroachment by nonsprouting shrubs. For this, we fixed the abundance of sprouting shrubs at 0%, and simulated the effects of aridity on nonsprouting shrubs. In the third scenario we simulated the interactive effects of aridity and encroachment by sprouting shrubs. We fixed the abundance of sprouting shrubs at 30% (an average abundance that can be observed along the aridity gradient), and that of nonsprouting shrubs at 0% (to remove their effect from the simulation).

Principal component and stepAICc analyses were carried out using JMP 11 (SAS Institute, Cary, NC, USA); and d-sep analyses were conducted using the lm function in R (R Core Development Team, 2012).

Results

Functional structure of studied communities

The CWM of the studied communities segregated along two PCA components, which accounted for 62% of the total variance found in the data (Fig. 2a; Tables S4a, S5a). The first component (36% of the variance) separated communities according to their leaf trait values (hereafter CWM-leaf trait), with SLA and Br being negatively correlated to LDMC, LL and LA. The first PCA component was negatively correlated with the abundance of *S. tenacissima* ($r^2 = 0.82$, $P < 0.001$; dot scale in Fig. 2), and discriminated grasslands from shrublands. The second PCA component discriminated communities according to plant size traits (hereafter CWM-size trait), with VH, LW and LS being negatively correlated to BD.

Similarly to what was observed with CWM, the FD of the studied communities was explained by the two first PCA components, which accounted for 55% of the total variance in the data (Fig. 2b; Tables S4b, S5b). The first component (31% of the variance) discriminated communities according to the FD of traits related to plant size (hereafter FD-size trait), such as FD-Br, FD-LS, FD-LW and FD-VH. The second PCA component (24% of the variance) segregated communities according to the FD of leaf traits (hereafter FD-leaf traits), such as FD-SLA, FD-LDMC, and FD-LT.

Community response traits to aridity and shrub encroachment

The abundance of nonsprouting shrubs largely determined CWM-leaf traits (73% of the explained variance; Table 1) and the communities dominated by these species had higher CWM-SLA and -Br, and lower CWM-LDMC, -LL, and -LA. These traits were also significantly impacted by aridity and the abundance of sprouting shrubs, although to a lesser extent (8 and 19% of the explained model variance, respectively; Table 1). A quadratic relationship was observed between aridity and CWM-leaf traits (Table 1; Fig. S4). By contrast, CWM-size traits were mostly driven by the abundance of sprouting shrubs (Table 1). Communities with high CWM-size traits were those dominated by tall sprouting shrubs.

The abundance of sprouting shrubs largely impacted FD-size traits (97% of the variance explained), whose values peaked at intermediate values of nonsprouting shrub abundance (Table 1). Finally, variations in FD-leaf traits were driven by the interplay of aridity and shrub abundance (Table 1). A positive quadratic relationship between aridity and FD-leaf traits ($r^2 = 36\%$) indicated that the FD values of these traits peaked in low and high aridity conditions. Sprouting shrubs tended to have a negative impact on FD-leaf traits ($r^2 = 20\%$), while nonsprouting shrubs increased FD-leaf traits ($r^2 = 44\%$).

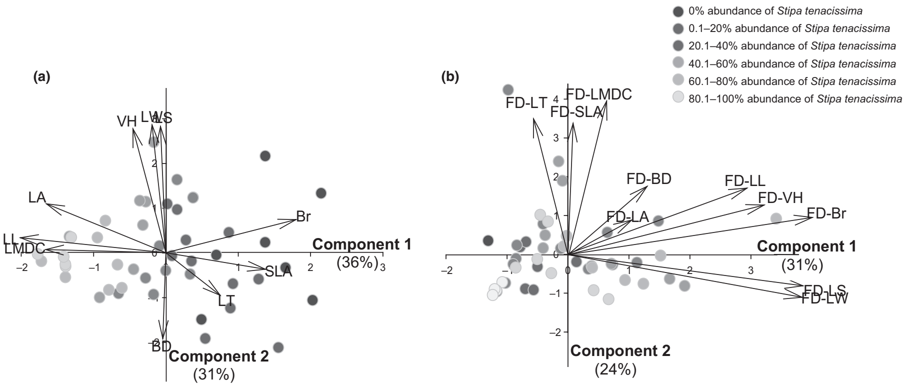

Fig. 2 Principal component analysis (PCA) of community-weighted mean trait (a) and functional diversity (FD) values (b). Light gray dots represent communities dominated by grass species, while dark gray dots are communities dominated by shrub species. BD, branching density (number of main stems); Br, number of ramifications per stem; LA, leaf area; LDMC, leaf dry matter content; LL, leaf length; LS, lateral spread; LT, leaf thickness; LW, leaf width; SLA, specific leaf area; VH, vegetative height. For each component we indicate the percentage of variance explained. See Supporting Information Table S4(a) for correlations among community-weighted trait values and Table S4(b) for correlations among functional diversity trait values. Furthermore, see Table S5(a) for correlation between community-weighted traits values and two mean components of a PCA (a) and Table S5(b) for the different functional diversity trait values and two mean components of the PCA (b).

Table 1 Results of the stepwise procedure to evaluate functional community responses to aridity and shrub encroachment for community-weighted mean (CWM) and functional diversity (FD) of leaf- and size-related traits.

	CWM-leaf traits					CWM-size traits					FD-leaf traits					FD-size traits				
Model r^2	0.9					0.63					0.32					0.72				
	Estimate	df	*F*-ratio	*P*-value	% of r^2	Estimate	df	*F*-ratio	*P*-value	% of r^2	Estimate	df	*F*-ratio	*P*-value	% of r^2	Estimate	df	*F*-ratio	*P*-value	% of r^2
Aridity	−6.842	1	28.08	< 0.0001	6.5						−7.755	1	5.39	0.0255	21.1					
Aridity^2	65.8141	1	8.35	0.0063	1.9						113.7509	1	3.72	0.0611	14.6					
Nonsprouting	0.0301	1	294.35	< 0.0001	68.2						0.0041	1	0.78	0.3837	3	−0.0001	1	0	0.958	0
Nonsprouting^2	0.0002	1	19.6	< 0.0001	4.5						−0.0005	1	10.52	0.0024	41.2	−0.0002	1	3.6	0.0651	2.8
Sprouting	0.0273	1	80.92	< 0.0001	18.8	0.0523	1	76.93	< 0.0001	100	−0.0207	1	5.11	0.0295	20	0.0817	1	78.1	< 0.0001	60.1
Sprouting^2																−0.0019	1	48.19	< 0.0001	37.1
Error		39					43					39					40			

We include a quadratic term when significant. Aridity, (1 − aridity index; precipitation/potential evapotranspiration); sprouting, sum of abundances of all sprouting shrubs; nonsprouting, sum of abundances of all shrubs except the sprouting shrubs; % of r^2, variance decomposition analysis based on the sum of squares. See Supporting Information Fig. S4 for details of the different relationships.

Linking community response traits to effect traits on multifunctionality

The model including the combined effects of CWM and FD (combined hypothesis) was the only model not rejected by the data (Fig. 3; Table S6). This model explained 62% of the variation in multifunctionality. Importantly, it highlighted that the effects of shrub encroachment on multifunctionality were mostly indirect via its effects on the functional structure of the plant community (Fig. 4).

While aridity had a direct effect on multifunctionality, it also had a large cascading effect by altering the functional structure of the studied communities. Aridity favored the abundance of nonsprouting shrubs, which resulted in higher values of CWM-leaf traits (Fig. 3). Shifting leaf trait values toward higher SLA had a strong adverse effect on multifunctionality. By contrast, the abundance of sprouting shrubs was independent of aridity. Increasing the abundance of these shrubs changed the value of CWM-size traits towards higher plant height. Such an increase did not directly impact multifunctionality, but had an indirect effect via the changes it promoted in FD (Fig. 3). Increasing the average size of the species in the community augmented the FD of size traits, although it decreased the FD of leaf traits, especially for intermediate values of CWM-size traits (quadratic relationship). It should be noted that communities showing a high variance in size traits were also characterized by high FD values of leaf traits. Increasing FD values of both leaf and size traits generally increased multifunctionality. However, a significant interaction between aridity and FD leaf traits was observed (Fig. 3). This indicates that the effect of these traits on multifunctionality shifted from positive to negative under high aridity conditions. Finally, sprouting and nonsprouting shrubs did not have a direct effect on multifunctionality (Fig. 4), suggesting that all their effects on multifunctionality were explained by the functional traits measured.

Model scenarios

In the sensitivity analyses of our final path model (Fig. 3), scenario 1 modeled the direct effect of aridity on multifunctionality as it had fixed zero abundance of both types of shrubs. In this case, multifunctionality directly decreased with increases in aridity (orange line, Fig. 5). In scenario 2, we modeled the effects of aridity on the abundance of nonsprouting shrubs (significant link in Fig. 3) and its consequences for multifunctionality. Increasing the abundance of nonsprouting shrubs augmented CWM-leaf traits, and strongly decreased multifunctionality, along the aridity gradient (green line, Fig. 5). Finally, in scenario 3 we fixed the abundance of sprouting shrubs to 30% to maintain high values of FD along the aridity gradient and to model its effects on multifunctionality. In this scenario, multifunctionality values remained high for most of the aridity gradient, declining only under high aridity conditions (red line, Fig. 5).

Discussion

Our study represents a first attempt to evaluate how multiple traits mediated dryland multifunctionality responses to two

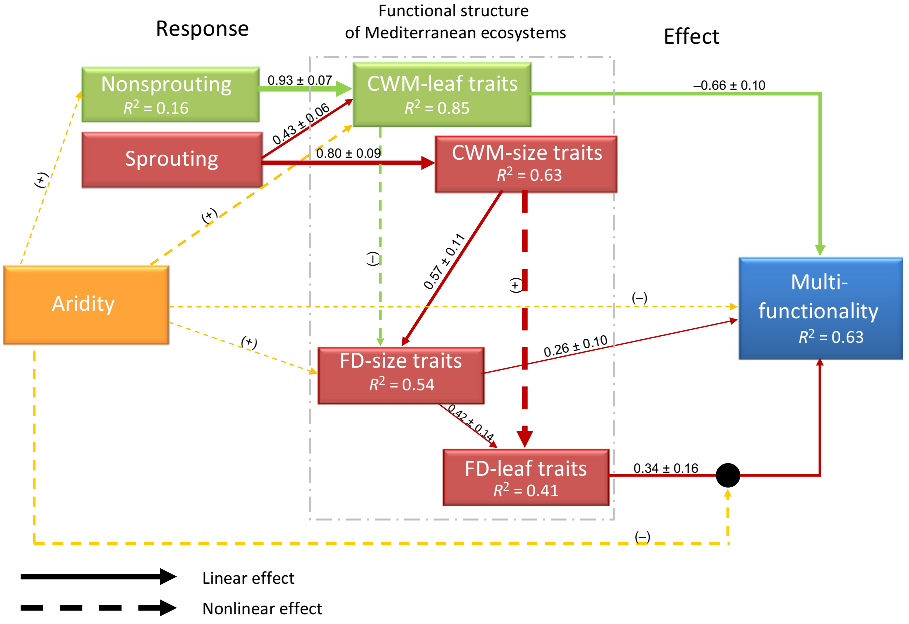

Fig. 3 Directed acyclic graph depicting the causal relationships between aridity (1 – aridity index; precipitation/potential evapotranspiration), the abundance of sprouting and nonsprouting shrubs, the functional structure of communities and multifunctionality. The width of each arrow is proportional to the standardized path coefficients. The solid arrows represent linear effects and the dashed arrows nonlinear effects (quadratic relationships). The black dot represents the interactive effects of aridity and functional diversity (FD) leaf traits on multifunctionality. For the nonlinear effects, the sign of the quadratic relationships is shown (positive (+) or negative (–)), whereas the standardized path coefficients for the latter are not available. CWM, community-weighted mean.

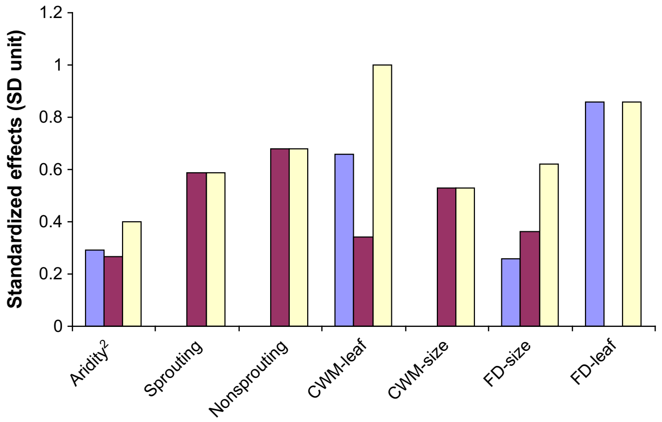

Fig. 4 Absolute effect sizes of the direct (blue bars), indirect (fuchsia bars), and total effects (sum of direct and indirect, yellow bars) of aridity (1 – aridity index; precipitation/potential evapotranspiration), the abundance of sprouting and nonsprouting shrubs and the functional structure of communities on multifunctionality. CWM, community-weighted mean; FD, functional diversity.

major global change drivers, that is, aridity and shrub encroachments. Dryland multifunctionality largely depends on the functional structure of the plant communities. Our results indicate that mass ratio and niche complementarity processes, as reflected by CWM and FD, respectively, were equally important as drivers of multifunctionality responses to both aridity and shrub encroachment (Fig. 3). Specifically, the two key findings from our study are that high FD improved the resistance of multifunctionality (i.e. the ability not to be affected by something, especially adversely; Oxford Dictionaries, 2014) to increases in aridity; and two sets of simple plant functional traits (size traits such as VH and leaf traits such as SLA or LDMC) can capture the effect of shrub encroachment on multifunctionality with a relative high accuracy. Thus, this set of traits can be particularly helpful to identify when and where shrub species affect multifunctionality positively or negatively, and to clarify the contrasted results previously found in the literature regarding the effects of shrub encroachment on ecosystem functioning (Eldridge *et al.*, 2011).

FD enhances multifunctionality in drylands

Functional diversity within dryland communities improved ecosystem multifunctionality, and accounted for a large fraction of the variation across communities (42% of the effect on multifunctionality; Fig. 4). This result contrasts with studies conducted in more mesic ecosystems, which highlighted the importance of CWM as a driver of ecosystem functioning (Garnier *et al.*, 2004; Díaz *et al.*, 2007; Mokany *et al.*, 2008). However, most studies conducted so far addressing the relationship between FD and ecosystem functioning have considered single ecosystem functions (e.g. productivity (Garnier *et al.*, 2004) or soil C (Laliberté & Tylianakis, 2012); for a review, see De Bello *et al.*, 2010). Our results suggest that FD and the associated niche complementarity might be particularly important when considering multiple ecosystem processes simultaneously (Mouillot *et al.*, 2011).

In temperate ecosystems, the effect of high FD on ecosystem functioning has generally been associated with higher resource acquisition rates (Van Ruijven & Berendse, 2005) and resource-use efficiency (Gross *et al.*, 2007a), temporal niche variability (Maire *et al.*, 2012) and plant soil feedbacks (Van Der Heijden *et al.*, 2008). While future experiments are needed to identify the underlying mechanisms supporting the positive relationship between FD and ecosystem multifunctionality reported here, our results suggest that FD may improve multifunctionality in drylands via two distinct pathways. First, increasing the FD of size traits can lead to regular spatial distributions of plants according to their size (Gross *et al.*, 2013), with tall individuals being

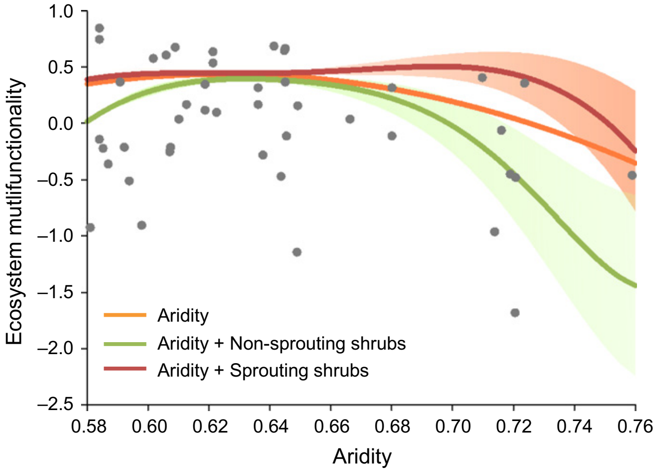

Fig. 5 Results of the sensitivity analysis carried out to evaluate the relationships between multifunctionality and aridity (1 – aridity index; precipitation/potential evapotranspiration) under different scenarios varying the abundance of shrub species. Scenario 1 (orange line), grassland multifunctionality responses to aridity without shrubs; scenario 2 (green line), the abundance of nonsprouting shrubs is increased in grasslands and the abundance of sprouting shrubs is fixed at 0%; and scenario 3 (red line), the abundance of sprouting and nonsprouting shrubs is fixed at 30 and 0%, respectively. The shaded areas surrounding the lines are the 95% confidence intervals. The gray dots represent the position of the communities sampled around the aridity gradient.

regularly spaced between each other. Such spatial distributions, which are characteristic of dryland communities (Fowler, 1986), can limit runoff and maximize soil infiltration and heterogeneity (Valentin *et al.*, 1999), thus enhancing species diversity (Soliveres *et al.*, 2011) and maximizing plant growth and ecosystem functioning (Puigdefábregas *et al.*, 1999). Secondly, high leaf trait diversity indicates the occurrence of contrasting leaf strategies (Westoby *et al.*, 2002) commonly found in Mediterranean systems (e.g. stress avoidance vs tolerance; Ackerly *et al.*, 2002; Freschet *et al.*, 2011). Differences in the leaf strategy of co-occurring species may have strong positive effects on ecosystem processes such as productivity (Gross *et al.*, 2007a), C cycling (Milcu *et al.*, 2014) and litter decomposition rates (Bardgett & Shine, 1999; Cornwell *et al.*, 2008). For instance, some studies have shown that increasing the FD of litter positively influences microbial communities (Zak *et al.*, 2003) and litter decomposition rates (Vos *et al.*, 2013), two potentially important factors for maintaining and improving dryland multifunctionality.

Multiple traits mediate the impact of mass ratio processes on multifunctionality

By considering multiple traits, our study showed that the outcomes of shrub encroachment can be explained by size-related and leaf traits. Shrub encroachment by sprouting shrubs species (such as *Q. coccifera*) had a positive cascading effect on multifunctionality, which was mediated by increasing CWM-size trait values (Fig. 3), in accordance with Maestre *et al.* (2009). Increasing plant size in dryland communities has been shown to be strongly associated with an increase in FD-size traits locally, and with a high spatial heterogeneity of plant biomass within communities (Gross *et al.*, 2013), two features that can have potential positive effects on ecosystem functioning, as discussed earlier. Maestre *et al.* (2009) showed how large *Quercus* species can increase the availability of local soil resources under their canopy in semiarid *S. tenacissima* grasslands. The positive effects of these shrubs on local resources have been shown to increase species diversity of the whole community (Maestre *et al.*, 2009; Soliveres *et al.*, 2011), an important parameter reinforcing the positive effect of sprouting shrubs on multifunctionality (Quero *et al.*, 2013). Our results complement previous findings by illustrating how sprouting shrubs can enhance FD within dryland communities, ultimately affecting multifunctionality.

The CWM-leaf trait values increased with an increase in the abundance of nonsprouting shrubs (Table 1; Fig. S4). This had a negative impact on multifunctionality, particularly in the most arid part of the gradient. The negative effect of fast-growing species on multifunctionality can be explained by a negative plant soil feedback, as suggested by Garnier *et al.* (2004). Negative relationships between SLA and soil nutrient contents have previously been found in Mediterranean French grasslands (Garnier *et al.*, 2004) and along successional vegetation stages, where fast-growing species are replaced by slow-growing species (Berendse, 1990). Higher growth and nutrient acquisition rates may accelerate nutrient uptake from the soil (Lavorel & Garnier, 2002). At the same time, plants with higher SLA may produce litter with higher decomposition rates (Kazakou *et al.*, 2006). Together with the reduction of litter accumulation per unit of soil surface, these effects may accelerate nutrient loss at the scale of the whole ecosystem (Garnier *et al.*, 2004). This may be particularly true in the most arid part of the aridity gradient, where the typical characteristics of the semiarid Mediterranean climate are worsened. For instance, the high variability of interannual precipitation distribution promotes increases in water runoff during short periods (Martínez-Mena *et al.*, 2001) and increases soil erosion that might accelerate nutrient loss (Martínez-Mena *et al.*, 2002). In addition, the negative effect of fast-growing summer deciduous species on multifunctionality can be amplified via an effect on FD-size traits (e.g. the negative link between CWM-leaf traits and FD-size traits in Fig. 3). Summer deciduous species with a stress avoidance strategy can outcompete the more stress-tolerant grass and shrub species (Gross *et al.*, 2013) by producing allelopathic compounds (as has been found for species such as *Artemisia herba-alba*; Escudero *et al.*, 2000). Competition between fast- and slow-growing species may decrease the abundance of slow-growing sprouting shrubs and modify the size and spatial distribution of plant biomass within communities (Gross *et al.*, 2013). This situation may decrease the positive effects of sprouting shrubs on FD, accelerating species loss and affecting the functioning of the whole ecosystem (Maestre *et al.*, 2009).

Importance of FD for ecosystem resistance to increasing aridity

The sensitivity analysis allowed us to explore how aridity interacts with plant functional community structure to determine multifunctionality (Fig. 5). While aridity had a direct detrimental effect on multifunctionality (scenario 1, Fig. 5; Delgado-Baquerizo *et al.*, 2013), this negative effect was further reinforced by the increase in abundance of nonsprouting shrubs, as favored by increasing aridity (scenario 2, Fig. 5). Moreover, we found an interactive effect of aridity and FD-leaf traits on multifunctionality (Fig. 3), suggesting that the effects FD-leaf traits shifted from positive to negative as aridity increased. At low aridity, high FD-leaf traits may reflect the coexistence between fast-growing species characterized by perennial leaves (e.g. *Brachypodium retusum*), and stress-tolerant shrub or grass species (Frenette-Dussault *et al.*, 2012) that maximized ecosystem multifunctionality. By contrast, under high aridity conditions, the increase in FD-leaf traits observed reflected the increase in abundance of nonsprouting shrubs (see the selection effect in Loreau & Hector, 2001), characterized by the high value of leaf traits (i.e. fast-growing species with summer deciduous leaves; Gross *et al.*, 2013) that may negatively affect ecosystem functioning.

An important result of our study was that high FD (enhanced by the occurrence of sprouting shrubs in grasslands) strongly delayed the collapse of multifunctionality under high aridity conditions. This was suggested by our sensitivity analysis (Fig. 5) where high FD-size traits were generally able to buffer the negative effects of aridity on multifunctionality, hence increasing the ecosystem resistance to aridity. Our results agree with previous experimental studies showing how higher species or FD can improve ecosystem resistance to global change drivers such as climate or land-use changes (Hooper *et al.*, 2005; Isbell *et al.*, 2011; Cardinale *et al.*, 2012). Understanding how the attributes of biotic communities mediate the resistance of ecosystem structure and functioning to global change drivers is a major focus of current ecological research. By identifying how fundamental attributes of biotic community predict ecosystem multifunctionality, our findings can be particularly useful for developing mechanistic models aiming to predict ecosystem resistance to climate change in drylands, which will increase the degree of aridity experienced by these ecosystems worldwide (Feng & Fu, 2013).

We standardized our sampling design by selecting sites with similar soil, slopes, and aspect (south-facing slopes). Local variation in topo-edaphic conditions could, however, alter plant community structure (Fonseca *et al.*, 2000; Gross *et al.*, 2008) and multifunctionality. For instance, while we did not find any significant effect of slope on multifunctionality, other local factors such as slope, aspect, soil texture or bedrock type could affect water availability (Fonseca *et al.*, 2000; Gómez-Plaza *et al.*, 2001; Delgado-Baquerizo *et al.*, 2013). Evaluating how local topo-edaphic factors interact with climatic/land use factors to determine the functional structure of dryland communities and their effect on multifunctionality is an important research objective for the future.

Concluding remarks

Our work suggests that the functional traits of dominant species and their diversity within communities modulate changes in multifunctionality in Mediterranean ecosystems along gradients of aridity and shrub encroachment. We showed that maintaining and enhancing FD (promoted by sprouting shrubs) in these ecosystems may help to buffer negative effects of climate change on multifunctionality. We also identified key traits that can accurately predict the outcome of shrub encroachment. Our results contribute to resolving the existing debate in the literature on the contrasting effects of shrub encroachment in drylands worldwide (Schlesinger *et al.*, 1990; Maestre *et al.*, 2009). On the one hand, traits related to the size of the plant species reflected the abundance of sprouting shrubs, which positively feed back on multifunctionality via their positive effect of FD. On the other hand, leaf traits such as SLA were related to the abundance of nonsprouting shrubs, which negatively impacted multifunctionality (particularly at the driest part of the aridity gradient studied). These results suggest that high values of SLA may typify those shrub species that are commonly associated with land degradation and desertification in drylands (Eldridge *et al.*, 2011).

Our results can be used to develop specific trait-based management and restoration programs (Sandel *et al.*, 2011; Laughlin, 2014) aiming to buffer the effects of climate change and shrub encroachment on multifunctionality. For instance, reintroducing/favoring the development of plants with low SLA and/or large size, such as sprouting shrubs, and enhancing local FD would reverse or limit the negative effects of increasing aridity and seasonal fast-growing summer deciduous plant species on multifunctionality.

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Fig. S1 Map with the location of the study sites along the aridity gradient evaluated.

Fig. S2 Differences between nonsprouting and sprouting shrubs.

Fig. S3 Relationships between our multifunctionality index (*M*) based on the average of *Z*-scores of ecosystem functions and other multifunctionality indices.

Fig. S4 Responses to aridity and shrub encroachment of community-weighted traits (CWM) and functional diversity (FD) evaluated with leaf- and size-related traits.

Table S1 Main characteristics of the study sites

Table S2 Results of Pearson correlation coefficients between the different soil variables (our surrogates of ecosystem functions) used to calculate the multifunctionality index

Table S3 Stepwise procedure to evaluate the responses of community-weighted mean (CWM) and functional diversity (FD) evaluated with leaf- and size-related traits to aridity and shrub encroachment

Table S4 Results of Pearson correlation coefficients among community-weighted trait values and functional diversity (FD) trait values

Table S5 Results of Pearson correlation coefficients between community-weighted (CWM) trait values and two mean components of a principal component analysis (component 1, CWM-leaf traits; component 2, CWM-size traits); and functional diversity (FD) trait values and two mean components of a principal component analysis (component 1, FD-size traits; component 2, FD- leaf traits)

Table S6 Conditional independence tests applied in the different hypothesis of the d-sep model implied by the hypothesized path models

Notes S1 Rationale of the different relationships depicted in Fig. 1.

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