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

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Title: 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 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 non-sprouting shrub species considered.
- Functional diversity 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 ($r^2=0.63$). Functional diversity also improved the resistance of multifunctionality along the aridity gradient studied.
- Maintaining and enhancing functional diversity in plant communities may help to buffer negative effects of ongoing global environmental change on dryland multifunctionality.

Keywords: aridity, community-weighted mean, drylands, functional diversity, global change, multifunctionality, shrub encroachment, traits.

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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 complementary 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

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change (Reiss *et al.*, 2009; Zavaleta *et al.*, 2010; Cardinale *et al.*, 2012). In this context, high levels of FD have been hypothesized as crucial for maintaining high multifunctionality (Mouillot *et al.*, 2011).

Arid, semi-arid 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, i.e. 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 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 functional diversity within communities (Gross *et al.*, 2013), because aridity generally favors small stress-tolerant and slow-growing shrub species with particular leaf traits, e.g. thick evergreen leaves with low specific leaf area and high leaf dry matter content (Ackerly *et al.*, 2002). However, these species can be

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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: (i) a positive effect of species diversity on multifunctionality has been found in global drylands (Maestre *et al.*, 2012a), and (ii) high FD has been hypothesized to improve the resistance of dryland ecosystems to aridity (Volaire *et al.*, 2014); this is so because FD could increase the probability that some species will survive if environmental conditions change, and thus could maintain ecosystem functioning (Díaz & Cabido, 2001).

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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: (i) mass ratio and niche complementarity processes are important drivers of multifunctionality (Mouillot *et al.*, 2011), (ii) high functional diversity will improve multifunctionality (Mouillot *et al.*, 2011), (iii) high functional diversity will minimize the negative effects of aridity on multifunctionality (Cardinale *et al.*, 2012; Maestre *et* *al.*, 2012a), and (iv) 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 south-east Spain (Fig. S1). Mean annual precipitation and temperature along this gradient ranged from 294 mm to 479 mm and from 12 ºC to 18 ºC, 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 and Zomer (2009). All the studied sites were located on south-facing slopes, with slope values ranging from 1º to 22º (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 non-sprouting shrubs, Fig. S2). Within grasslands and shrublands, we selected sites with and without tall sprouting shrubs (such as *Quercus coccifera*; Fig. S2). The cover of sprouting shrubs in both grasslands and shrublands were similar along the aridity gradient studied (Table S1).

Vegetation sampling

We established a 30 m x 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,

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which were extended parallel to the slope. In each transect, the cover of every perennial species in 20 consecutive quadrats (1.5 m x 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 a decreasing order of relative abundance. These measurements were conducted on ten 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): (i) plant architecture traits: 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); (ii) 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 specific leaf area (SLA, $cm^2 g^{-1}$) 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

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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 other 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 one month prior to 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 N, total available N, aminoacids, proteins, net potential mineralization rate, total 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 buildup 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).

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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):

$$\mathrm{CWT_j} = \sum_{i}^{n} p_{ij} T_{ij} \qquad \text{(eqn. 1)}$$

where p_{ij} is the abundance of the species i in the community j and T_{ij} 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:

$$\mathrm{FD_j} = \sum_{i}^{n} p_{ij} \left(\frac{\left| T_{ij} - CWT_j \right|}{\sum_{i}^{n} \left| T_{ij} - CWT_j \right|} \right) \qquad \text{(eqn. 2)}$$

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 CWT_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 a *M* value for each site, Z scores were first calculated for each of the 13 soil variables estimated at the scale of each 30 m × 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 prior to 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

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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; Pendleton *et al.*, 2014; Wagg *et al.*, 2014; Bradford *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 (e.g., 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; e.g. 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 for other functions (Table S4). 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 S4). Finally, our estimates of *M* are highly related to other multifunctionality indices (Fig S4). 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

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CWM and FD. We used the PCA coordinates in those components with an eigenvalue higher than one to measure the CWM and the FD of each community. This procedure allowed us to identify the plant strategy spectrum along which traits co-vary 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 non-sprouting shrubs (predictors). Since the functional response to aridity is not necessarily linear (e.g., 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

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To test for relationships between 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 relaxing some of the limitations of standard structural equation models, including non-normal data distribution, non-linear 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 Appendix 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: (i) CWM only (mass ratio hypothesis); (ii) FD only (niche complementary hypothesis); and (iii) 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 S2). When several models were not rejected, we used the AICc procedure adapted for confirmatory path analysis to select the best model (Shipley, 2013). Finally, standardised 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 so, we used the parameters of the best model to estimate multifunctionality values along the aridity

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gradient studied under different scenarios, which were created by manipulating the abundances of non-sprouting 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 non-sprouting shrubs. To do so, we fixed the abundance of sprouting shrubs at 0%, and simulated the effects of aridity on non-sprouting 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 non-sprouting shrubs at 0% (to remove their effect from the simulation).

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

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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). The first component (36% of the variance) separated communities according to their leaf trait values (hereafter CW-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 value < 0.001; dot scale in Fig. 2), and discriminated grasslands from shrublands. The second PCA component discriminated communities according to plant size traits (hereafter CW-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). 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.

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Community response traits to aridity and shrub encroachment

The abundance of non-sprouting shrubs largely determined CW-leaf traits (73% of the explained variance, Table 1) and the communities dominated by these species had higher CW-SLA and -Br, and lower CW-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 CW-leaf traits (Table 1). In contrast, CW-size traits were mostly driven by the abundance of sprouting shrubs (Table 1). Communities with high CW-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 levels of non-sprouting 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 at low and high aridity levels. Sprouting shrubs tended to have a negative impact on FD-leaf traits (r^2=20%), while non-sprouting shrubs increased FD-leaf traits (r^2=44%).

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 and Table S3). 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 favoured the abundance of non-sprouting shrubs, which resulted in higher values of CW-leaf traits (Fig. 3). Shifting leaf trait values toward higher SLA had a strong adverse effect on multifunctionality. In contrast, the abundance of sprouting shrubs was independent from aridity. Increasing the abundance of these shrubs changed the value of CW-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, though decreased the FD of leaf traits, especially for intermediate values of CW-size traits (quadratic relationship). It must 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 non-sprouting 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.

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Model scenarios

In the sensitivity analyses of our final path model (Fig. 3), scenario 1 modelled 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 modelled the effects of aridity on the abundance of non-sprouting shrubs (significant link in Fig. 3) and its consequences for multifunctionality. Increasing the abundance of non-sprouting shrubs augmented CW-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 functional diversity 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).

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DISCUSSION

Our study represents a first attempt to evaluate how multiple traits mediated dryland multifunctionality responses to two major global change drivers, i.e. 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: (i) 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; (ii) two sets of simple plant functional traits (size traits like VH and leaf traits like 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).

Functional diversity 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 addressing the relationship between FD and ecosystem functioning conducted so far have considered single ecosystem functions (e.g. productivity, Garnier *et al.*, 2004 or soil carbon, Laliberté & Tylianakis, 2012, see also de Bello *et al.*, 2010 for a review). 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 been generally associated to 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

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results suggest that FD may improve multifunctionality in drylands via two distinct pathways:

(i) Increasing the functional diversity of size traits can lead to regular spatial distributions of plants according to their size (Gross *et al*., 2013), with tall individuals being regularly spaced between each other. Such spatial distributions, which are characteristic of dryland communities (Fowler, 1986), can limit runoff and maximise soil infiltration and heterogeneity (Valentin *et al*., 1999), thus enhancing species diversity (Soliveres *et al*., 2011) and maximising plant growth and ecosystem functioning (Puigdefábregas *et al.* 1999).

(ii) 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), carbon 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 CW-size trait values (Fig. 3), in

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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 above. Maestre *et al.* (2009) showed how large *Quercus* species can increase the availability of local soil resources under their canopy in semi-arid *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 functional diversity within dryland communities, ultimately affecting multifunctionality.

CW-leaf trait values increased with an increase in the abundance of non-sprouting shrubs (Table 1). 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

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most arid part of the aridity gradient, where the typical characteristics of the semi-arid 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 CW-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 functional diversity, accelerating species loss and affecting the functioning of the whole ecosystem (Maestre *et al.*, 2009).

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Importance of functional diversity for ecosystem resistance to increasing aridity

The sensitivity analysis allowed us to explore how aridity interplays 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 non-sprouting shrubs, as favoured 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 levels, 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 (Frennette-Dussault *et al.*, 2012) that maximised ecosystem multifunctionality. In contrast, under high aridity conditions, the increase in FD-leaf traits observed reflected the increasing in abundance of non-sprouting shrubs (see selection effect in Loreau & Hector, 2001), characterized by high value of leaf traits (i.e. fast growing species with summer deciduous, 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 functional diversity 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 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

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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; Gomez-plaza *et al.*, 2001; Delgado-Baquerizo *et al.*, 2013). Evaluating how local topo-edaphic factors interplay with climatic/land use factors to determine the functional structure of dryland communities and their effect on multifunctionality represents an important research front for the future.

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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 predict accurately the outcome of shrub encroachment. Our results contribute to resolve the existing debate in the literature on the contrasted effects of shrub encroachment in drylands worldwide (e.g. 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 feedback on multifunctionality via their positive effect of FD. On the other hand, leaf traits such as SLA were related to the abundance of non-sprouting 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 to advance 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/favouring the development of plants with low SLA and/or high size, such as sprouting shrubs, and enhancing local functional diversity would reverse or limit the negative effects of increasing aridity and seasonal fast growing summer deciduous plant species on multifunctionality.

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Table 1. Results of the stepwise procedure to evaluate functional community responses to aridity and shrub encro weighed mean (CWM) and functional diversity (FD) of leaf and size-related traits. We included a quadratic term wher aridity index [precipitation/potential evapotranspiration]); Sprouting: Sum of abundances of all sprouting shrubs; abundances of all shrubs except the sprouting shrubs; est: Estimate; DF: degree of freedom; % of r^2: variance decompo the sum of squares. See Fig. S3 for details of the different relationships.

	CW-leaf traits					CW-size traits					FD-leaf traits					
Model r^2	0.9					0.63					0.32					
	est	DF	Fratio	Pvalue	% of r^2	est	DF	Fratio	Pvalue	% of r^2	est	DF	Fratio	Pvalue	% of r^2	est
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	
Non-sprouting	0.0301	1	294.35	<0.0001	68.2						0.0041	1	0.78	0.3837	3	-0.0001
Non-sprouting^2	0.0002	1	19.6	<0.0001	4.5						-0.0005	1	10.52	0.0024	41.2	-0.0002
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
Sprouting^2																-0.0019
Error		39					43					39				

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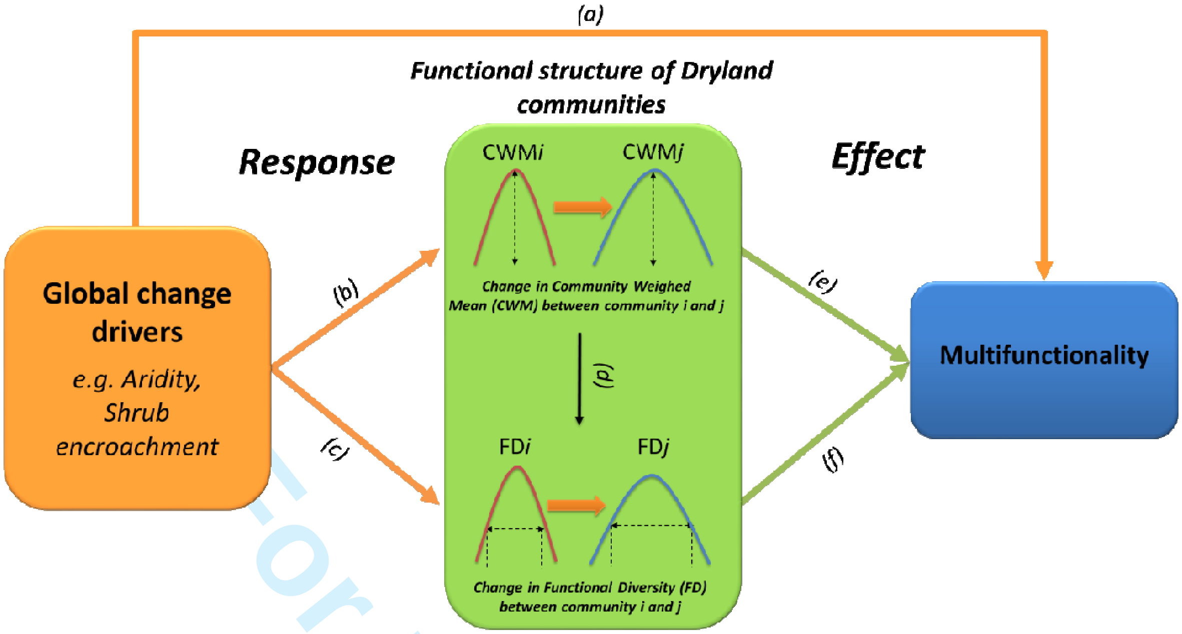

Fig. 1. Hypothetical relationships between aridity, shrub encroachment and the functional structure and multifunctionality of dryland communities. Aridity and shrub encroachment directly impact multifunctionality (a). The left part of the figure represents the response of the plant community to both variables (CWM: mean trait distribution [b]; FD: functional diversity [c]; and co-variation between CWT and FD [d]). Changes in community functional structure promote effects on multifunctionality via two non-exclusive 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 contrasted levels of aridity and shrub encroachment in a community *j* compared to community *i*. See Appendix S1 for a detailed rationale of the different relationships depicted in the figure.

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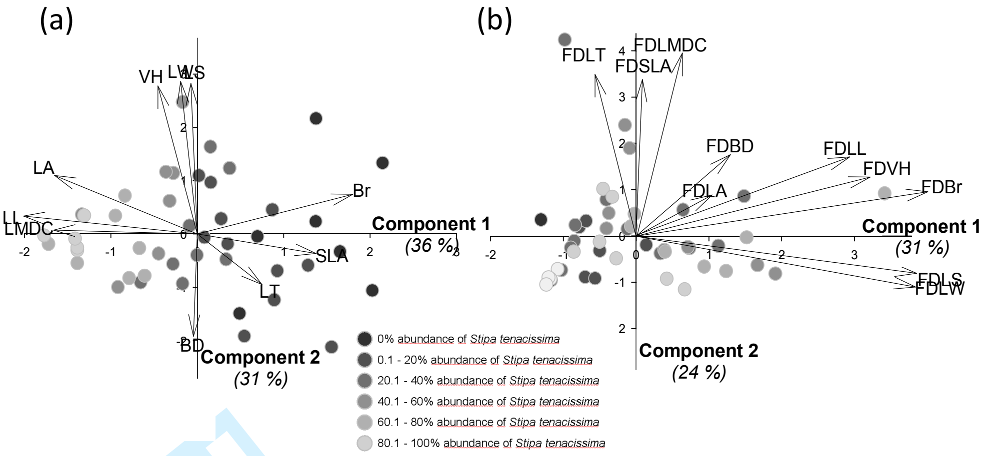

Fig. 2. Principal component analysis (PCA) of Community-Weighted Mean Trait (a) and Functional Diversity values (b). Light grey dots represent communities dominated by grass species, dark dots are communities dominated by shrub species. BD = branching density (number of main stems); Br = number of ramifications 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 % of variance explained. See Table S5a for correlations among Community-Weighted Trait values and Table S5b for correlations among Functional Diversity Trait values. Furthermore, see Table S6a for correlation between Community-Weighted Traits values and two mean components of a PCA (a) and Table S6b for the different Functional Diversity Traits value traits values and two mean components of the PCA (b).

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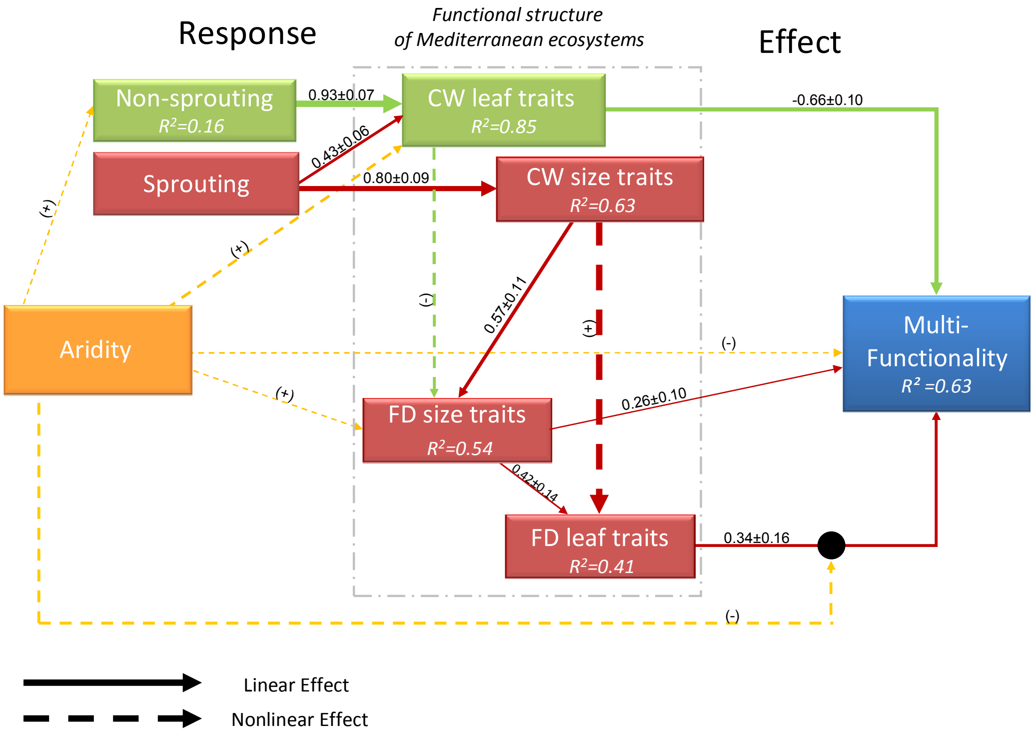

Fig. 3. Directed acyclic graph depicting the causal relationships between aridity (1-aridity index [precipitation/potential evapotranspiration]), the abundance of sprouting and non-sprouting shrubs, the functional structure of communities and multifunctionality. The width of each arrow is proportional to the standardized path coefficients. The continuous arrows represent linear effects and the discontinuous arrows non-linear effects (quadratic relationships). The black dot represents the interactive effects of aridity and FD leaf traits on multifunctionality. For the non-linear effects the sign of the quadratic relationships is shown (positive (+) or negative (-), whereas the standardized path coefficients for the latter are not available. CW = Community Weighted Mean, and FD = Functional Diversity.

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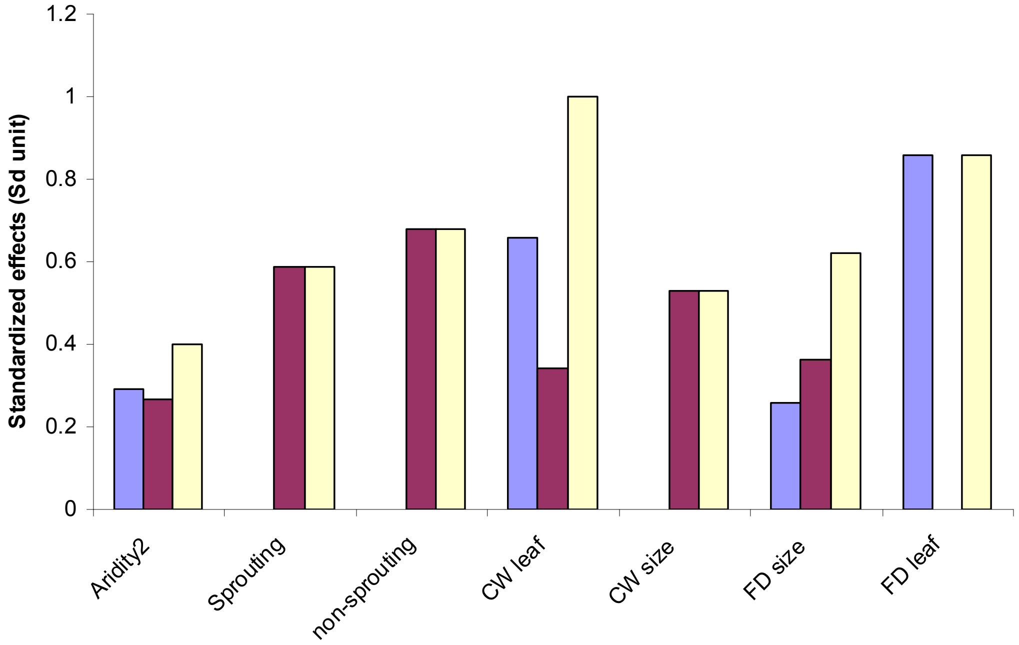

Fig. 4. Absolute effect sizes of the direct (blue bars), indirect (fuchsia bars), and total effects (sum of direct and indirect, yellow bars) of aridity (1- aridity index [precipitation/potential evapotranspiration]), the abundance of sprouting and non-sprouting shrubs and the functional structure of communities (CW = Community Weighted Mean and FD = Functional Diversity) on multifunctionality.

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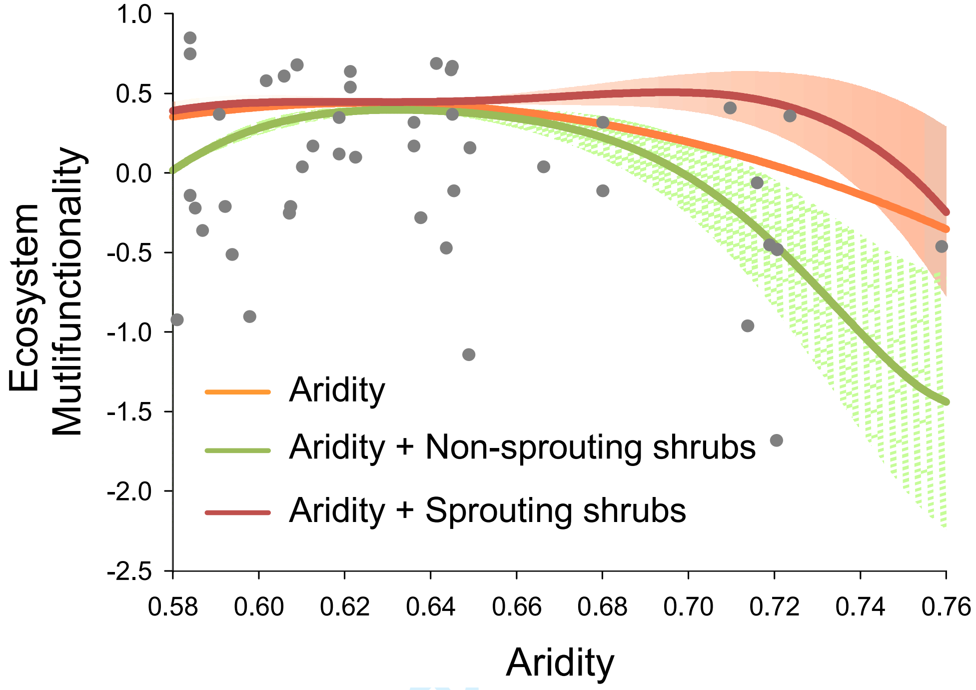

Fig. 5. Results of the sensitivity analysis carried out to evaluate the relationships between multifunctionality and aridity (1- aridity index [precipitation/potential evapotranspiration]) under different scenarios varying the abundance of shrub species. Scenario 1 (orange line) = grassland multifunctionality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

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SUPPORTING INFORMATION

The following Supporting Information is available for this article:

Appendix S1. Rationale of the different relationships depicted in Figure 1.

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

Figure S2. Differences between non-sprouting and sprouting shrubs.

Figure S3. Responses to aridity and shrub encroachment of community weighed traits (CWT) and functional diversity (FD) evaluated with leaf and size related traits.

Figure S4. Relationships between our multifunctionality index (*M*) based on the average of Z-scores of ecosystem functions and other multifunctionality indices.

Table S1. Main characteristics of the study sites.

Table S2. Stepwise procedure to evaluate the responses of community weighed mean (CWM) and functional diversity (FD) evaluated with leaf and size related traits to aridity and shrub encroachment.

Table S3. Conditional independence tests applied in the different hypothesis of the d-sep model implied by the hypothesized path models.

Table S4. Results of Pearson correlation coefficients between the different soil variables (our surrogates of ecosystem functions) used to calculate the multifunctionality index.

Table S5. Results of Pearson correlation coefficients among a) community-weighted trait values and b) functional diversity (FD) trait values.

Table S6. Results of Pearson correlation coefficients between a) community-weighted (CW) traits values and two mean components of a Principal Component Analysis (component 1: CW-leaf traits and component 2: CW-size traits); b) functional diversity (FD) traits values and two mean components of a Principal Component Analysis (component 1: FD-size traits and component 2: FD- leaf traits).

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Appendix S1. Rationale of the different relationships depicted in Figure 1.

In the main text, we proposed a conceptual figure (Fig. 1) that summarizes causal relationship between aridity, shrub encroachment, dryland functional community structure and multifunctionality. This figure is adapted to drylands from the "response effect framework" developed by Lavorel & Garnier (2002). Below we describe the *a priori* justifications for all links (arrows) leading to endogenous variables (box with one or more arrows leading to it) present in Fig. 1 in the main text.

While aridity can directly alter ecosystem functioning (arrow f; Delgado-Baquerizo *et al.*, 2013), the response-effect framework states that ecosystem responses to global change drivers are largely mediated by 'indirect effects' via changes in functional community structure, i.e. both community weighted mean (CWM) (Suding *et al.*, 2008) and functional diversity (Díaz *et al.,* 2007). We first detail how aridity and shrub encroachment may impact the functional structure of dryland communities via two non-exclusive mechanisms (habitat filtering, Keddy, 1992; Maire *et al.*, 2012 and niche differentiation, Maire *et al.*, 2012) (RESPONSE), then explain how those changes may cascaded on multifunctionality (EFFECT). Justifications for each arrow are grouped together for each endogenous variable.

RESPONSE

Arrow a: In drylands, aridity has been reported to decrease the size of the plants and to select species with slow growth rate (Cornwell & Ackerly, 2009; Freschet *et al.*, 2011). However, for extreme aridity values, slow-growing and stress-tolerant species can be replaced by fast growing summer deciduous species (stress avoidance species; (Freschet *et al.*, 2011; Gross *et al.*, 2013). Shrub encroachment in grasslands impacts on the functional structure of drylands by increasing plant size (Eldridge *et al.*, 2011), especially when encroachers are sprouting shrub species (Quero *et al.*, 2013). Shrub

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encroachment can also impact leaf traits such as specific leaf area and C:N ratio compared to grasslands. The impact in leaf traits depends on the species implies in shrub encroachment, i.e. *Quercus coccifera* decrease C:N ratio compared to *Stipa tenacissima* (dominant species in grassland) (Ferran *et al.,* 2005).

Arrow b: aridity can favor high functional diversity (FD) by promoting contrasted functional strategies to deal with stress, i.e. stress avoidance vs. stress tolerant species.

Arrow c: co-variation between changes in CWM and FD can be observed in drylands due to the effect of biotic interactions (Gross *et al*., 2013). High functional diversity can occur because dominant competitors with contrasted functional traits values can spatially coexist within communities (Gross *et al*., 2013). Facilitation has also been proposed to promote high FD (Gross *et al*., 2009) since well adapted dominant plant species promote the persistence of mal-adapted plants under their canopy (Valiente-Banuet *et al.,* 2006; Butterfield & Briggs, 2011; Gross *et al*., 2013). For instance, tussock grass species such as *Stipa tenacissima* and tall sprouting shrubs (e.g. *Quercus coccifera*) have been shown to increase species richness (Maestre *et al*., 2009; Soliveres *et al*., 2011; Quero *et al*., 2013) and functional diversity (Gross *et al*., 2013) in drylands as a result of facilitation (Maestre *et al*., 2001; García-Fayos & Gasque, 2002; Amat *et al*., in press).

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EFFECT

Arrow d: in contrast, sprouting shrubs have been shown to increase multifunctionality because their particular functional traits maximize multiple processes such as water acquisition, water use efficiency, litter accumulation, and carbon storage (Maestre *et al*., 2009; Eldridge *et al*., 2011). Non-sprouting shrubs have been shown to decrease multifunctionality, and in some cases accelerate desertification processes (Kefi *et al*., 2007; Quero *et al*., 2013). However, which traits mediate these effects is currently unknown.

Arrow e: recent studies have shown that species diversity may increase ecosystem multifunctionality (e.g. Gamfeldt *et al.*, 2008; Zavaleta *et al*., 2010; Maestre *et al*., 2012; Vos *et al*., 2013). Mediterranean ecosystem are generally characterized by high functional diversity respective to other biomes (Freschet *et al*., 2011) which, together with the fact that functional diversity may increase ecosystem multifunctionality, suggests that functional diversity might be important in driving multiple ecosystem processes in drylands.

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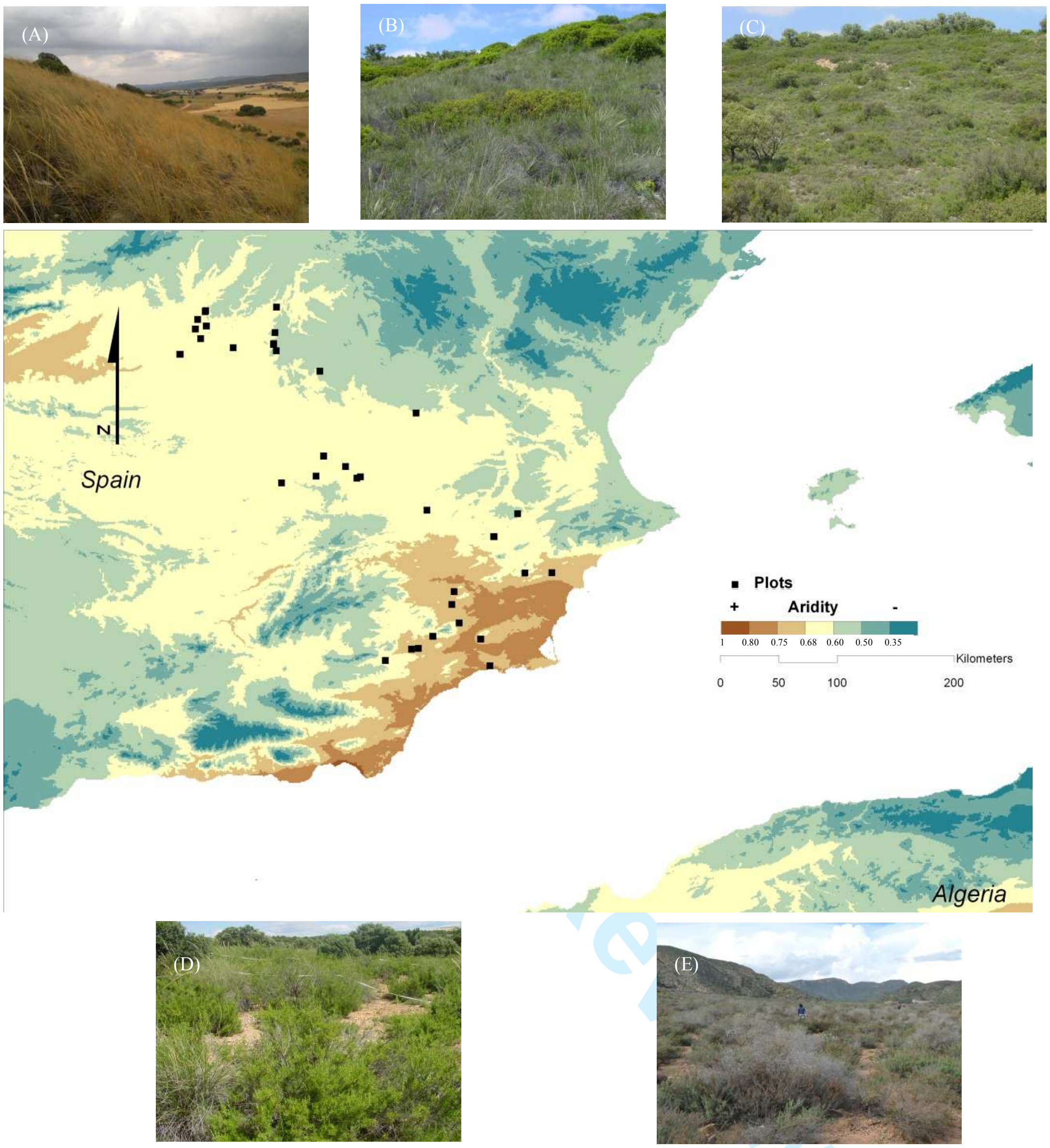

Figure S1. Map with the location of the study sites along the aridity gradient evaluated. Pictures indicate examples of the different types of communities along the aridity gradient (1- aridity index [precipitation/potential evapotranspiration]): (A) Grassland dominated by *Stipa tenacissima*; (B) Grassland with sprouting shrubs; (C) Shrublands dominated by *Rosmarinus officinalis* with sprouting shrubs; (D) Shrublands dominated by *Rosmarinus officinalis* with *Stipa tenacissima*; (E) Shrublands dominated by summer deciduous shrubs species.

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Sprouting shrubs:	**Non-sprouting shrubs:**
- Resprout after a fire - Long-lived species - They have a well-developed root system because they occupy the same space for a long time.	-Obligate seeders (survive fire as a dormant seed pool in the soil) -Suffer mortality after fires - Do not have a well-developed root system
Examples of species: *Quercus coccifera, Juniperus oxycedrus Pistacia lentiscus* and *Rhamnus lycioides*	Examples of species: *Rosmarinus officinalis*, *Artemisia herba-alba* and *Globularia alypum*
	
Quercus coccifera	*Rosmarinus officinalis*

Figure S2. Differences between non-sprouting and sprouting shrubs (based on Keeley & Zedler 1978).

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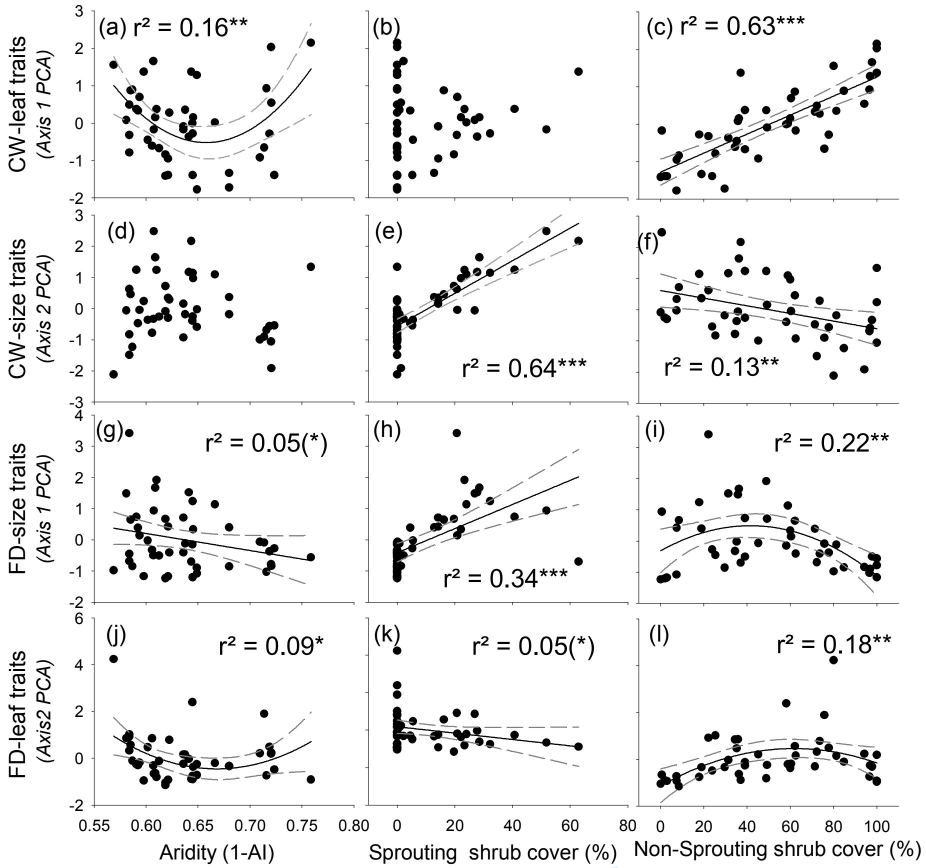

Figure S3. Responses to aridity (1- aridity index [precipitation/potential evapotranspiration]) and shrub encroachment of community weighed traits (CWT) and functional diversity (FD) evaluated with leaf and size related traits. Co-variations among traits are shown in Fig. 2 for CWT and FD. Community responses to: aridity (1-Aridity Index [AI]) are shown in panels (a, d, g, j); responses to shrub encroachment separating sprouting shrub and non-sprouting shrub are shown in panels (b, e, h, k) and (c, f, i, l) respectively. The black solid line indicates significant ($P < 0.05$) relationships; the grey dash lines show 95% confidence intervals in these cases. We provided the R^2 of the linear regression in each panel. (*) $P< 0.09$; * $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$.

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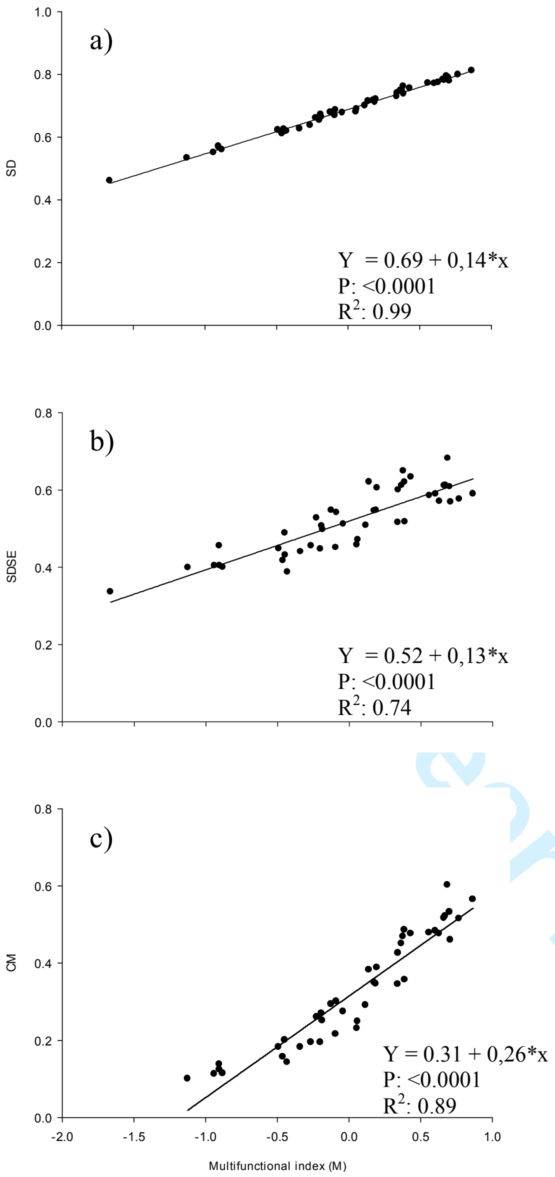

Figure S4. Relationships between our multifunctionality index based on the average of Z-scores of ecosystem functions and other multifunctionality indices: a) the average of multiple functions, previously standardized by dividing by the maximum (SD, Mouillot *et al*., 2011); b) this average minus the standard deviation (SDSE, Pasari *et al*., 2011); and (c) the cross-multiplied ten soil variables previously standarized by dividing by the maximum (CM, Bowker *et al*., 2013).

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Table S1. Main characteristics of the study sites. Climate variables were extracted from the Worldclim global database (www.worldclim.org) and Global Aridity Index (Trabucco and Zomer, 2009).

COD	LAT	LON	ELE	SLO	AMT	RAI	AI	ARIDITY	CBA	TCT	NSS	SS
1	37º35'35.04"N	1º13'56.57"W	76	4.25	17.8	294	0.241	0.759	55.750	44.250	100.000	0.000
2	37°47'57.23"N	1°18'13.80"W	405	21.00	16.5	339	0.277	0.724	60.875	36.792	23.920	5.234
3	38°03'55.91"N	1°31'37.33"W	445	7.75	16.1	341	0.279	0.721	65.568	34.432	94.271	1.301
4	38º09'54.31"N	1º30'32.36"W	446	14.00	16.0	345	0.280	0.720	70.417	28.500	100.000	0.000
5	37°55'23.46"N	1°28'12.62"W	443	2.34	16.1	344	0.281	0.719	41.208	57.875	77.811	0.000
6	37°43'36.22"N	1°47'04.56"W	476	9.15	15.9	339	0.284	0.716	48.250	46.708	96.607	0.000
7	37°43'16.79"N	1°50'13.15"W	487	0.50	15.9	341	0.286	0.714	41.208	27.083	75.812	0.000
8	37°48'01.14"N	1°18'19.54"W	406	15.75	16.1	353	0.290	0.710	50.917	36.750	45.242	0.101
9	37°49'16.16"N	1°40'25.49"W	654	2.88	15.1	378	0.320	0.680	50.250	48.750	18.977	12.824
10	37°49'17.92"N	1°40'20.26"W	651	1.25	15.1	378	0.320	0.680	55.083	44.917	29.648	0.000
11	38°18'30.88"N	0°57'47.68"W	504	15.40	15.5	398	0.334	0.666	47.944	27.621	58.922	23.991
12	39°02'54.74"N	2°13'49.56"W	779	4.50	13.7	415	0.351	0.649	53.167	46.500	7.421	0.000
13	37°38'02.03"N	2°02'22.61"W	863	15.96	14.4	405	0.351	0.649	62.146	37.686	96.874	0.000
14	39°07'39.03"N	2°20'42.50"W	780	11.75	13.8	420	0.355	0.645	58.333	40.583	60.038	22.109
15	39°59'31.33"N	3°37'08.21"W	597	14.50	14.5	412	0.355	0.645	16.075	66.758	17.909	32.187
16	39°59'33.27"N	3°37'21.13"W	579	10.25	14.5	412	0.355	0.645	43.417	48.708	1.998	0.000
17	39°12'27.14"N	2°30'53.16"W	750	1.75	13.8	422	0.355	0.645	50.000	48.250	58.179	0.000
18	39°02'17.65"N	2°15'28.45"W	806	8.25	13.6	423	0.357	0.644	58.070	41.930	37.077	62.923
19	39°12'31.60"N	2°30'50.71"W	752	3.50	13.8	426	0.359	0.641	31.850	62.775	31.337	27.736
20	38°47'30.67"N	1°43'03.70"W	845	16.25	13.5	422	0.362	0.638	56.000	31.167	81.305	0.850
21	40°21'17.25"N	2°52'38.77"W	625	10.25	13.6	405	0.364	0.636	49.625	45.208	62.574	0.000
22	40°21'16.74"N	2°52'42.07"W	629	8.00	13.6	405	0.364	0.636	41.250	57.417	49.258	14.229
23	39°03'10.77"N	2°34'20.10"W	851	4.75	13.4	446	0.378	0.622	42.500	57.500	73.618	0.000
24	40°12'31.61"N	3°25'08.99"W	621	14.75	14.0	432	0.379	0.621	18.558	57.858	7.506	14.238
25	40°12'31.82"N	3°25'05.49"W	616	22.00	14.0	432	0.379	0.621	18.167	63.877	2.924	0.000

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26	40°11'09.64"N	3°30'10.31"W	615	17.75	14.1	429	0.381	0.619	40.825	56.633	8.584	19.673
27	40°11'09.96"N	3°30'12.47"W	617	17.50	14.1	429	0.381	0.619	26.100	67.233	0.116	0.000
28	40°19'11.97"N	3°25'36.61"W	631	18.75	13.9	436	0.388	0.613	29.292	49.800	39.086	0.000
29	40°15'36.74"N	3°29'07.82"W	667	21.75	13.9	437	0.390	0.610	34.250	62.625	48.925	23.337
30	40°19'36.26"N	3°25'26.11"W	650	20.75	13.8	439	0.391	0.609	30.375	53.917	36.285	28.510
31	40°06'43.61"N	3°27'46.77"W	735	18.50	13.7	441	0.393	0.607	35.583	64.417	0.667	51.772
32	39°00'05.34"N	2°50'17.28"W	903	3.25	13.2	467	0.393	0.607	73.188	24.134	97.801	2.199
33	38°35'18.98"N	1°11'58.12"W	815	18.50	13.9	444	0.394	0.606	50.125	42.292	34.445	0.000
34	38°35'17.60"N	1°12'13.62"W	833	14.50	13.7	454	0.398	0.602	51.661	36.191	35.269	5.469
35	39°00'35.82"N	2°39'46.40"W	945	6.23	13.0	468	0.402	0.598	79.500	15.167	100.000	0.000
36	39°52'38.65"N	2°47'17.05"W	833	14.75	12.9	458	0.406	0.594	41.205	55.267	60.353	20.866
37	40°22'09.69"N	3°23'19.23"W	715	12.75	13.1	453	0.408	0.592	43.792	56.208	71.422	4.502
38	40°09'29.88"N	2°53'20.75"W	811	21.00	12.8	448	0.409	0.591	35.845	63.977	39.060	40.724
39	38°45'54.99"N	1°01'12.60"W	770	10.75	14.0	457	0.413	0.587	55.333	38.500	84.806	0.000
40	39°32'19.20"N	1°48'08.23"W	905	8.50	12.4	466	0.415	0.585	57.729	34.195	62.174	16.180
41	40°04'5.62"N	2°54'02.61"W	899	18.75	12.6	462	0.416	0.584	21.958	67.833	22.202	20.648
42	40°04'24.98"N	2°53'56.71"W	895	21.50	12.5	465	0.416	0.584	29.833	60.500	25.365	0.000
43	39°51'42.62"N	2°32'37.48"W	870	14.75	12.5	479	0.416	0.584	49.750	50.000	72.257	0.000
44	40°01'04.90"N	2°52'45.67"W	878	20.00	12.5	470	0.419	0.581	43.178	56.155	35.845	26.909
45	37°53'32.49"N	1°42'11.46"W	1024	21.75	13.1	468	0.431	0.569	42.919	36.424	80.084	0.000

COD = Code of the plot, LAT = latitude (WGS84 datum), LON = longitude (WGS84 datum), ELE = elevation (m), SLO = slope (°), AMT = annual mean temperature, RAI = annual precipitation, AI = Aridity index (precipitation/potential evapotranspiration), ARIDITY = 1-AI, CBA= Cover of bare areas (%), TCT = total perennial cover (%), NSS= Relative cover of non-sprouting shrubs (%), SS= Relative cover of sprouting shrubs (%).

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Literature Cited

Hijmans RJ, Cameron SE, Parra JL, Jones PG, Jarvis A. 2005. Very high resolution interpolated climate surfaces for global land areas. *International journal of climatology* **25:** 1965–1978.

Trabucco A, Zomer RJ. 2009. Global Aridity Index (Global-Aridity) and Global Potential Evapo-Transpiration (Global-PET) Geospatial Database. CGIAR Consortium for Spatial Information. Published online, available from the CGIAR-CSI GeoPortal at: http://www.csi.cgiar.org

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Table S2. Stepwise procedure to evaluate the responses of community weighed mean (CWM) and functional diversity (FD) evaluated with leaf and size related traits to aridity (1- aridity index [precipitation/potential evapotranspiration]) and shrub encroachment. We evaluated a quadratic term when it was significant. We also assessed the effect of slope on multifunctionality; this variable was not selected in any *a priori* models (data not shown) and thus was removed from the final analyses. Est: direction of relationship; DF: degree of freedom; % of r^2: variance decomposition analysis based on the sum of squares.

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	model mass ratio (hypothesis i)				**model niche complementary (hypothesis ii)**				**model combined hypothesis (hypothesis iii)**			
Model r^2	0.46				0.25				0.63			
	Est	DF	Fratio	Pvalue	Est	DF	Fratio	Pvalue	Est	DF	Fratio	Pvalue
Aridity(Ari)	-2.4	1	3.2	0.0824	1.8	1	0.6	0.4394	-1.2	1	0.5	0.4817
Ari^2					-110.7	1	8.2	0.0069	-47.7	1	2.7	0.1090
CW-leaf traits	-0.4	1	32.8	<0.0001					-0.4	1	39.7	<0.0001
CW-size traits	0.1	1	4.8	0.0345								
Ari*CW-leaf traits												
Ari*CW-size traits												
Ari^2*CW-leaf traits												
Ari^2*CW-size traits												
FD-leaf traits					0.1	1	1.0	0.3213	0.2	1	4.3	0.0460
FD-size traits					0.2	1	5.2	0.0288	0.1	1	7.1	0.0111
Ari*FD-leaf traits					-1.8	1	1.2	0.2775	-2.1	1	3.3	0.0762
Ari*FD-size traits												
Ari^2*FD-leaf traits					-65.8	1	4.7	0.0368	-84.8	1	15.4	0.0004
Ari^2*FD-size traits												
error		41				38				37		

Table S3. Conditional independence tests applied in the different hypothesis of the d-sep model implied by the hypothesized path models.

D-sep claim of Independence	**Model formula $**	**Ho**	***P***	**C statistic**	***P* of C (df)**
Mass ratio (hypothesis i)				43.01	0.058 (30)
(NSS;SS) |{ARI^2}	SS ~ NSS + ARI^2	NSS =0	0.0623		
(NSS; CWM2)|{SS, ARI^2 }	CWM2 ~ NSS + SS + ARI^2	NSS=0	0.3794		
(NSS; FD1)|{ARI^2,CWM1^2 ,CWM2}	FD1 ~ NSS + ARI^2 + CWM1^2 + CWM2	NSS=0	0.5485		
(NSS; FD2)|{ARI^2, CWM2^2 , FD1}	FD2 ~ NSS + ARI^2 + CWM2^2 + FD1	NSS=0	0.428		
(NSS; M)|{ARI^2, CWM1, CWM2}	M ~ NSS + ARI^2 + CWM1 + CWM2	NSS=0	0.7582		
(ARI;SS)|{Ø}	SS ~ ARI	ARI=0	0.1553		
(SS; FD2)|{CWM2^2, FD1}	FD2 ~ SS + CWM2^2 + FD1	SS=0	0.7035		
(SS; FD1)|{ARI^2, CWM1^2 , CWM2}	FD1 ~ SS + ARI^2 + CWM1^2 + CWM2	SS=0	0.4695		
(SS; M)|{ARI^2, CWM1, CWM2}	M ~ SS + ARI^2 + CWM1 + CWM2	SS=0	0.3703		
(ARI;CWM2)|{SS}	CWM2 ~ ARI + SS	ARI=0	0.226		
(ARI; FD2)|{CWM2^2, FD1}	FD2 ~ ARI + CWM2^2 + FD1	ARI=0	0.4835		
(CWM1; CWM2)|{SS,NSS, ARI}	CWM2 ~ CWM1 + SS + NSS + ARI	CWM1=0	0.1478		
(CWM1;FD2)|{SS,NSS, ARI, CWM2^2, FD1}	FD2 ~ CWM1 + SS + NSS + ARI + CWM2^2 + FD1	CWM1=0	0.7359		
(FD1; M)|{CWM1^2, CWM2, ARI^2}	M~ FD1 + CWM1^2 + CWM2 + ARI^2	FD1=0	0.5956		
(FD2; M)|{CWM1, CWM2^2, ARI^2, FD1}	M ~ FD2 + CWM1 + CWM2^2 + ARI^2 + FD1	FD2=0	0.0008		
Niche complementary (hypothesis ii)				86.34	<0.0001 (30)
(NSS;SS) |{ARI^2}	SS ~ NSS + ARI^2	NSS =0	0.0623		
(NSS; CWM2)|{SS, ARI^2 }	CWM2 ~ NSS + SS + ARI^2	NSS=0	0.3794		
(NSS; FD1)|{ARI^2,CWM1^2 ,CWM2}	FD1 ~ NSS + ARI^2 + CWM1^2 + CWM2	NSS=0	0.5485		
(NSS; FD2)|{ARI^2, CWM2^2 , FD1}	FD2 ~ NSS + ARI^2 + CWM2^2 + FD1	NSS=0	0.428		

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(NSS; M)|{ARI^2, FD1, FD2+(AI*FD^2)+(AI2*FD^2)}	M ~ NSS + ARI^2 + FD1 + FD2 + (AI*FD^2) + (AI2*FD^2)	NSS=0	<0.0001		
(ARI;SS)|{Ø}	SS ~ ARI	ARI=0	0.1553		
(SS; FD2)|{CWM2^2, FD1}	FD2 ~ SS + CWM2^2 + FD1	SS=0	0.7035		
(SS; FD1)|{ARI^2, CWM1^2 , CWM2}	FD1 ~ SS + ARI^2 + CWM1^2 + CWM2	SS=0	0.4695		
(SS; M)|{ARI^2, FD1, FD2+(AI*FD^2)+(AI2*FD^2)}	M ~ SS + ARI^2 + FD1 + FD2 + (AI*FD^2) + (AI2*FD^2)	SS=0	0.1372		
(ARI;CWM2)|{SS}	CWM2 ~ ARI + SS	ARI=0	0.226		
(ARI; FD2)|{CWM2^2, FD1}	FD2 ~ ARI + CWM2^2 + FD1	ARI=0	0.4835		
(CWM1; CWM2)|{SS,NSS, ARI}	CWM2 ~ CWM1 + SS + NSS + ARI	CWM1=0	0.1478		
(CWM1;FD2)|{SS,NSS, ARI, CWM2^2, FD1}	FD2 ~ CWM1 + SS + NSS + ARI + CWM2^2 + FD1	CWM1=0	0.7359		
(CWM1; M)|{ARI^2, NSS, SS, FD1, FD2+(AI*FD^2)+(AI2*FD^2)}	M~ CWM1 + ARI^2 + NSS + SS + FD1 + FD2 + (AI*FD^2) + (AI2*FD^2)	FD1=0	<0.0001		
(CWM2; M)|{ARI^2, SS, FD1, FD2+(AI*FD^2)+(AI2*FD^2)}	M ~ CWM2 + ARI^2 + SS + FD1 + FD2 + (AI*FD^2) + (AI2*FD^2)	FD2=0	0.2424		
Combined hypothesis (hypothesis iii)				26.97	0.520 (28)
(NSS;SS) |{ARI^2}	SS ~ NSS + ARI^2	NSS =0	0.0623		
(NSS; CWM2)|{SS, ARI^2 }	CWM2 ~ NSS + SS + ARI^2	NSS=0	0.3794		
(NSS; FD1)|{ARI^2,CWM1^2 ,CWM2}	FD1 ~ NSS + ARI^2 + CWM1^2 + CWM2	NSS=0	0.5485		
(NSS; FD2)|{ARI^2, CWM2^2 , FD1}	FD2 ~ NSS + ARI^2 + CWM2^2 + FD1	NSS=0	0.428		
(NSS; M)|{ARI^2, CWM1, FD1, FD2+(AI*FD2)+(AI^2*FD2)}	M ~ NSS + ARI^2 + CWM1 + FD1 + FD2 + (AI*FD2) + (AI^2*FD2)	NSS=0	0.5217		
(ARI;SS)|{Ø}	SS ~ ARI	ARI=0	0.1553		
(SS; FD2)|{CWM2^2, FD1}	FD2 ~ SS + CWM2^2 + FD1	SS=0	0.7035		
(SS; FD1)|{ARI^2, CWM1^2 , CWM2}	FD1 ~ SS + ARI^2 + CWM1^2 + CWM2	SS=0	0.4695		
(SS; M)|{ARI^2, CWM1, FD1, FD2+(AI*FD2)+(AI^2*FD2)}	M ~ SS + ARI^2 + CWM1 + FD1 + FD2 + (AI*FD^2) + (AI2*FD^2)	SS=0	0.974		
(ARI;CWM2)|{SS}	CWM2 ~ ARI + SS	ARI=0	0.226		
(ARI; FD2)|{CWM2^2, FD1}	FD2 ~ ARI + CWM2^2 + FD1	ARI=0	0.4835		

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(CWM1; CWM2)|{SS,NSS, ARI}	CWM2 ~ CWM1 + SS + NSS + ARI	CWM1=0	0.1478
(CWM1;FD2)|{SS,NSS, ARI, $CWM2^2$, FD1}	FD2 ~ CWM1 + SS + NSS + ARI + $CWM2^2$ + FD1	CWM1=0	0.7359
(CWM2; M)|{ARI^2, SS, CWM1,FD1, FD2+(AI*FD2)+(AI^2*FD2)}	M ~ CWM2 + ARI^2 + SS + CWM1 + FD1 + FD2 + (AI*FD^2) + (AI2*FD^2)	FD2=0	0.8082

Notes: Key to variables: NSS = non-sprouting shrubs, SS = sprouting shrubs, ARI = (1-aridity index [precipitation/potential evapotranspiration]), CWM1 = community weighted leaf trait, CWM2 = community weighted size trait, FD1 = functional dispersion size trait, FD2 = functional dispersion leaf trait, M = Multifunctionality index. $ = The associated mixed model regression for each d-sep claim using the lm function in R to test the independence claims. The *P* value is obtained by comparing the value of the C statistic for each hypothesis to a chi-square distribution with the same degrees of freedom – note that a model is rejected if the C statistic is significantly different from the χ^2 value.

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Table S4. Results of Pearson correlation coefficients between the different soil variables (our surrogates of ecosystem functions) used to calculate the multifunctionality index.

	ORC	HEX	PEN	BGL	TP	P_HCL	AVP	FOS	TON	AVN	AMI	PRO
ORC												
HEX	0.45**											
PEN	0.03	0.02										
BGL	0.48**	0.64**	-0.20									
TP	-0.09	-0.25	-0.11	-0.03								
P_HCL	-0.41**	-0.21	-0.24	0.07	0.12							
AVP	0.00	0.16	-0.29	0.36*	0.45**	0.10						
FOS	0.72**	0.55**	-0.03	0.67**	-0.09	-0.17	0.10					
TON	0.88**	0.46**	-0.10	0.64**	0.10	-0.29	0.14	0.76**				
AVN	0.52**	0.60**	-0.06	0.84**	-0.01	-0.12	0.24	0.63**	0.69**			
AMI	0.52**	0.72**	-0.21	0.80**	-0.03	-0.10	0.28	0.60**	0.66**	0.82**		
PRO	0.17	0.64**	0.00	0.55**	-0.19	-0.13	0.07	0.30*	0.26	0.47**	0.42**	
MIN	0.40**	0.50**	-0.29	0.71**	0.10	0.06	0.35*	0.47**	0.53**	0.61**	0.77**	0.16

Significance levels are as follows: * $p < 0.05$ and ** and $p < 0.01$.

ORC: organic carbon; HEX: hexoses; PEN: pentoses; BGL: β-glucosidase extracellular activity; TP: total phosphate; P_HCL: Olsen phosphate (inorganic P – HCL 1M); AVP: available inorganic phosphate; FOS: phosphatase activity; TON: total nitrogen; AVN: total available nitrogen; AMI: aminoacids; PRO: proteins and MIN: net potential mineralization rate.

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Table S5. Results of Pearson correlation coefficients among a) community-weighted trait values and b) functional diversity (FD) trait values.

a)	SLA	VH	LA	LT	LW	LMDC	Br	BD	LS
SLA									
VH	-0.30*								
LA	-0.49**	0.41**							
LT	0.05	-0.34*	-0.30*						
LW	-0.09	0.71**	0.40**	-0.28					
LMDC	-0.72**	0.17	0.56**	-0.33*	0.09				
Br	0.35*	-0.04	-0.56**	0.31*	0.13	-0.54**			
BD	0.22	-0.48**	-0.33*	0.18	-0.41**	0.00	-0.20		
LS	-0.10	0.78**	0.25	-0.24	0.83**	0.02	0.17	-0.32*	
LL	-0.54**	0.29	0.77**	-0.31*	0.19	0.70**	-0.83**	0.09	0.14

b)	FDSLA	FDVH	FDLA	FDLT	FDLW	FDLMDC	FDBr	FDBD	FDLS
FDSLA									
FDVH	0.27								
FDLA	0.23	-0.05							
FDLT	0.43**	0.08	-0.02						
FDLW	-0.13	0.43**	0.25	-0.16					
FDLMDC	0.35*	0.22	0.18	0.64**	-0.06				
FDBr	0.14	0.58**	0.06	0.06	0.58**	0.23			
FDBD	0.25	0.51**	-0.16	0.20	-0.07	0.21	0.27		
FDLS	-0.13	0.47**	0.01	-0.14	0.71*	-0.07	0.57**	0.26	
FDLL	0.27	0.25	0.43**	0.06	0.37*	0.45**	0.59**	-0.04	0.28

Significance levels are as follows: * $p < 0.05$ and ** and $p < 0.01$.

SLA = specific leaf area; VH = vegetative height; LA = leaf area; LT = leaf thickness; LW = leaf width; LDMC = leaf dry matter content; Br = number of ramifications per stem; BD = branching density (number of main stems); LS = lateral spread; LL = leaf length.

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Table S6. Results of Pearson correlation coefficients between a) different community-weighted (CW) traits values and two mean components of a Principal Component Analysis (component 1: CW-leaf traits and component 2: CW-size traits); b) different functional diversity (FD) traits values and two mean components of a Principal Component Analysis (component 1: FD-size traits and component 2: FD- leaf traits).

a)	CW-leaf traits	CW-size traits
SLA	0.69**	-0.14
VH	-0.23	0.87**
LA	-0.77**	0.36*
LT	0.38*	-0.34*
LW	-0.08	0.90**
LMDC	-0.85**	0.02
Br	0.84**	0.23
BD	-0.02	-0.64**
LS	-0.01	0.89**
LL	-0.94**	0.08

b)	FD-size traits	FD- leaf traits
FDSLA	0.02	0.74**
FDVH	0.69**	0.29
FDLA	0.19	0.20
FDLT	-0.14	0.78**
FDLW	0.84**	-0.22
FDLMDC	0.09	0.83**
FDBr	0.84**	0.21
FDBD	0.26	0.39**
FDLS	0.84**	-0.19
FDLL	0.57**	0.38*

Significance levels are as follows: * $p < 0.05$ and ** and $p < 0.01$.

SLA = specific leaf area; VH = vegetative height; LA = leaf area; LT = leaf thickness; LW = leaf width; LDMC = leaf dry matter content; Br = number of ramifications per stem; BD = branching density (number of main stems); LS = lateral spread; LL = leaf length.

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