



Swansea University
Prifysgol Abertawe



Cronfa - Swansea University Open Access Repository

This is an author produced version of a paper published in :

New Phytologist

Cronfa URL for this paper:

<http://cronfa.swan.ac.uk/Record/cronfa20625>

Paper:

Valencia, E., Maestre, F., Le Bagousse-Pinguet, Y., Quero, J., Tamme, R., Börger, L., García-Gómez, M. & Gross, N. Functional diversity enhances the resistance of ecosystem multifunctionality to aridity in Mediterranean drylands. *New Phytologist*, 206(2), 660-671.

<http://dx.doi.org/10.1111/nph.13268>

This article is brought to you by Swansea University. Any person downloading material is agreeing to abide by the terms of the repository licence. Authors are personally responsible for adhering to publisher restrictions or conditions. When uploading content they are required to comply with their publisher agreement and the SHERPA RoMEO database to judge whether or not it is copyright safe to add this version of the paper to this repository.

<http://www.swansea.ac.uk/iss/researchsupport/cronfa-support/>



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

Journal:	<i>New Phytologist</i>
Manuscript ID:	NPH-MS-2014-18486.R1
Manuscript Type:	MS - Regular Manuscript
Date Submitted by the Author:	n/a
Complete List of Authors:	Valencia-Gómez, Enrique; Universidad Rey Juan Carlos, Área de Biodiversidad y Conservación Móstoles, Madrid, Spain Maestre, Fernando; Universidad Rey Juan Carlos, Área de Biodiversidad y Conservación, Departamento de Ciencias Le Bagousse-Pinguet, Yoann; University of South Bohemia, Department of Botany, Faculty of Science Quero, José; Universidad de Córdoba, Campus de Rabanales, Departamento de Ingeniería Forestal Escuela Técnica Superior de Ingeniería Agronómica y de Montes Tamme, Riin; University of Tartu, Department of Botany, Institute of Ecology and Earth Sciences Börger, Luca; Swansea University, Department of Biosciences, College of Science Garcia, Miguel; Universidad Rey Juan Carlos, Área de Biodiversidad y Conservación Gross, Nicolas; INRA/CNRS, USC1339
Key Words:	Aridity, Community-weighted mean, Drylands, Functional diversity, Global change, Multifunctionality, Shrub encroachment, Traits

1 **Full paper**

2 **Title:** Functional diversity enhances the resistance of ecosystem multifunctionality to
3 aridity in Mediterranean drylands

4

5 Enrique Valencia-Gómez^{1*}, Fernando T. Maestre¹, Yoann Le Bagousse-Pinguet², José
6 Luis Quero³, Riin Tamme⁴, Luca Börger⁵, Miguel García-Gómez^{1,6} and Nicolas Gross^{7,8}

7

8 ¹Área de Biodiversidad y Conservación, Departamento de Biología y Geología, Física y
9 Química Inorgánica, Escuela Superior de Ciencias Experimentales y Tecnología,
10 Universidad Rey Juan Carlos, C/ Tulipán s/n, 28933 Móstoles, Spain.

11 ²Department of Botany, Faculty of Science; University of South Bohemia, Branisovska
12 31, CZ-370 05 Ceske Budejovice, Czech Republic.

13 ³Departamento de Ingeniería Forestal Escuela Técnica Superior de Ingeniería
14 Agronómica y de Montes Universidad de Córdoba Campus de Rabanales Crta. N-IV
15 km. 396 C.P. 14071, Córdoba, Spain.

16 ⁴Department of Botany, Institute of Ecology and Earth Sciences, University of Tartu,
17 Lai 40, Tartu, Estonia

18 ⁵Department of Biosciences, College of Science, Swansea University, Singleton Park,
19 Swansea, SA2 8PP, UK.

20 ⁶Departamento de Ingeniería y Morfología del Terreno, Escuela Técnica Superior de
21 Ingenieros de Caminos, Canales y Puertos, Universidad Politécnica de Madrid, Calle
22 Profesor Aranguren s/n, 28040 Madrid, Spain.

23 ⁷INRA, USC1339 Chizé (CEBC), F-79360, Villiers en Bois, France.

24 ⁸Centre d'étude biologique de Chizé, CNRS - Université La Rochelle (UMR 7372), F-
25 79360, Villiers en Bois, France.

26 *Corresponding author: Enrique Valencia Gómez: valencia.gomez.e@gmail.com

27

28 Total word in the main text: 6026; Summary: 187/200; Introduction: 913; Materials and

29 Methods: 2083; Results: 852; Discussion: 1883; Acknowledgments: 95

30 5 Figures, 1 Tables and 11 Appendices in Supporting information

31

For Peer Review

32 **SUMMARY**

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

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

56

57 INTRODUCTION

58 Global change is altering biodiversity worldwide at an unprecedented rate, with
59 important consequences for the functioning of natural ecosystems (Vitousek *et al.*,
60 1997; Chapin *et al.*, 2000). A response-effect framework based on plant functional traits
61 has been proposed to explore the ecosystem-level consequences of local changes in
62 biodiversity in response to ongoing global environmental change (global change
63 hereafter; Lavorel & Garnier 2002; Suding *et al.*, 2008). This approach states that
64 changes in the functional structure of communities can partly affect ecosystem
65 functioning (“indirect” effects, *sensu* Suding *et al.*, 2008), although global change
66 drivers also alter such functioning directly (Asner *et al.*, 2004; Austin *et al.*, 2004; Zepp
67 *et al.*, 2007). The influential “mass-ratio hypothesis” (Grime, 1998) considers that the
68 traits of dominant species largely determine the effects of plant communities on
69 ecosystem functioning. As such, trait-based studies have mainly focused on community-
70 weighted mean values (CWM hereafter; Garnier *et al.*, 2004; Violle *et al.*, 2007; Suding
71 *et al.*, 2008; see de Bello *et al.*, 2010 for a review). However, global change drivers can
72 also affect the variance of the trait distributions within communities (here defined as
73 “functional diversity” [FD], see Laliberté & Legendre, 2010). High FD may reflect an
74 increase in complementary in resource use between species (Gross *et al.*, 2007b), thus
75 improving ecosystem functioning (Díaz *et al.*, 2007).

76 Most studies investigating the relationship between the community functional
77 structure and ecosystem functioning have studied one or a few ecosystem functions (see
78 de Bello *et al.*, 2010 for a review). However, ecosystems are primarily valued because
79 they provide multiple functions and services simultaneously (i.e. multifunctionality
80 hereafter; Zavaleta *et al.*, 2010). Therefore assessing how global change drivers may
81 impact multifunctionality is crucial to understand the ecological consequences of global

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

85 Arid, semi-arid and dry-subhumid ecosystems (drylands hereafter) are currently
86 impacted by climate change (Maestre *et al.*, 2012b) and shrub encroachment (Eldridge
87 *et al.*, 2011). Shrub encroachment, i.e. an increase in abundance and/or density of shrub
88 species in grasslands (Schlesinger *et al.*, 1990), is a major land cover change that is
89 occurring in drylands worldwide (Knapp *et al.*, 2008; Maestre *et al.*, 2009; Li *et al.*,
90 2013). This phenomenon has been found to promote dryland desertification by reducing
91 plant biomass and species richness (Knapp *et al.*, 2008), increasing fire risk (Mitchley
92 & Ispikoudis, 1999) and enhancing soil erosion (Schlesinger *et al.*, 1990). However,
93 other studies have found positive effects of shrub encroachment on the richness of
94 different organisms and on ecosystem functioning (see Eldridge *et al.*, 2011 for a
95 review). Maestre *et al.* (2009) hypothesized that the functional traits of encroaching
96 shrubs relative to those of the grasses being replaced are key determinants of the
97 outcomes of shrub encroachment. Size-related traits of shrub species might be
98 particularly important, as the replacement of grass species by tall and large shrubs (i.e.
99 sprouting shrubs) enhances species richness and ecosystem functions such as
100 nutrient/carbon cycling and storage (Eldridge *et al.*, 2011; Quero *et al.*, 2013).

101 Climate change has been projected to increase aridity in drylands worldwide
102 during this century (Feng & Fu, 2013). This can modify the traits of dominant shrub
103 species, as well as the functional diversity within communities (Gross *et al.*, 2013),
104 because aridity generally favors small stress-tolerant and slow-growing shrub species
105 with particular leaf traits, e.g. thick evergreen leaves with low specific leaf area and
106 high leaf dry matter content (Ackerly *et al.*, 2002). However, these species can be

107 replaced in the most arid Mediterranean ecosystems by stress-avoidant species
108 characterized by summer deciduous leaves and an opposite trait strategy (Ackerly *et al.*,
109 2002; Gross *et al.*, 2013). Changes in leaf trait values may have important consequences
110 on ecosystem functioning, as they determine the rate of resource capture and utilization
111 (Garnier *et al.*, 2004) as well as litter decomposition (Kazakou *et al.*, 2006). Also,
112 increasing aridity may select for small shrub species (Gross *et al.*, 2013) and limit the
113 ability of tall sprouting shrubs to enhance multifunctionality. Finally, increasing aridity
114 may also alter multifunctionality by modifying the FD within drylands (Gross *et al.*,
115 2013) because: (i) a positive effect of species diversity on multifunctionality has been
116 found in global drylands (Maestre *et al.*, 2012a), and (ii) high FD has been hypothesized
117 to improve the resistance of dryland ecosystems to aridity (Volaire *et al.*, 2014); this is
118 so because FD could increase the probability that some species will survive if
119 environmental conditions change, and thus could maintain ecosystem functioning (Díaz
120 & Cabido, 2001).

121 In this paper, we evaluated how aridity and shrub encroachment affect the
122 functional structure of Mediterranean drylands, and assessed how changes in their
123 functional structure ultimately drive variations in multifunctionality. We also quantified
124 the relative contribution of mass ratio (reflected by CWM) vs. niche complementarity
125 (reflected by FD) processes on multifunctionality for multiple traits (size and leaf traits)
126 using a confirmatory path analysis (Shipley, 2013; Fig. 1). We tested the following
127 hypotheses: (i) mass ratio and niche complementarity processes are important drivers of
128 multifunctionality (Mouillot *et al.*, 2011), (ii) high functional diversity will improve
129 multifunctionality (Mouillot *et al.*, 2011), (iii) high functional diversity will minimize
130 the negative effects of aridity on multifunctionality (Cardinale *et al.*, 2012; Maestre *et*

131 *al.*, 2012a), and (iv) the effects of aridity on multifunctionality will be modulated by the
132 traits of shrubs which determine the outcome of shrub encroachments.

133

134 **MATERIALS AND METHODS**

135 **Study area**

136 We surveyed 45 sites along an aridity gradient from central to south-east Spain (Fig.
137 S1). Mean annual precipitation and temperature along this gradient ranged from 294
138 mm to 479 mm and from 12 °C to 18 °C, respectively. Aridity (1- aridity index
139 [precipitation/potential evapotranspiration]; Delgado-Baquerizo *et al.*, 2013) values
140 range from 0.57 to 0.76, and are strongly correlated to both annual mean precipitation
141 ($R^2 = 0.97$) and temperature ($R^2 = 0.89$) in the studied sites. Climatic data were
142 extracted from the WorldClim global database (Hijmans *et al.*, 2005), while data to
143 calculate the aridity index were obtained from Trabucco and Zomer (2009). All the
144 studied sites were located on south-facing slopes, with slope values ranging from 1° to
145 22° (measured in situ with a clinometer), and had soils derived from limestone (Lithic
146 Calciorthid; Soil Survey Staff, 1994). Vegetation at these sites was either a grassland
147 dominated by *Stipa tenacissima* or a shrubland dominated by obligate-seeder shrubs
148 such as *Rosmarinus officinalis* (hereafter non-sprouting shrubs, Fig. S2). Within
149 grasslands and shrublands, we selected sites with and without tall sprouting shrubs
150 (such as *Quercus coccifera*; Fig. S2). The cover of sprouting shrubs in both grasslands
151 and shrublands were similar along the aridity gradient studied (Table S1).

152

153 **Vegetation sampling**

154 We established a 30 m x 30 m plot at each study site. Total plant cover within each plot
155 was sampled by using four 30 m long transects located 8 m apart from each other,

156 which were extended parallel to the slope. In each transect, the cover of every perennial
157 species in 20 consecutive quadrats (1.5 m x 1.5 m) was visually recorded. We focused
158 on perennial plants as they represent most of the plant biomass in drylands (Whitford,
159 2002), and their cover is a good predictor of ecosystem functioning in these areas
160 (Maestre & Escudero, 2009; García-Gómez & Maestre 2011; Gaitán *et al.*, 2014).
161 Species abundance per site was calculated as the sum of the cover measured in the 80
162 quadrats.

163 At each plot, we measured the traits of all the perennial plant species that
164 accounted for at least 80% of the total plot cover, in a decreasing order of relative
165 abundance. These measurements were conducted on ten randomly selected individuals
166 per species during the peak of the vegetation growth season (spring). We assigned to
167 each species and plot the average value of the individuals measured in that plot. In the
168 case of the species for which we did not have local trait values we used the average trait
169 values observed in the three nearest sites. Ten traits were measured following
170 standardized protocols (Cornelissen *et al.*, 2003): (i) plant architecture traits: vegetative
171 height VH (cm), lateral spread LS (cm²), branching density (BD, number of main
172 stems) and ramification (Br, number of ramifications per stem). These traits are related
173 to plant water use efficiency and/or competitive ability (Westoby *et al.*, 2002); (ii) leaf
174 traits, including leaf area (LA, cm²), leaf length (LL, cm), leaf width (LW, cm) and leaf
175 thickness (LT, mm), all reflecting light interception and water stress tolerance (Westoby
176 *et al.*, 2002), and specific leaf area (SLA, cm² g⁻¹) and leaf dry matter content (LDMC, g
177 g⁻¹), which correlate with plant relative growth rate and nutrient acquisition and
178 utilization (Wright *et al.*, 2004).

179

180 **Soil sampling and analyses**

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

187 Soil samples were sieved by a 2 mm mesh and air dried for one month prior to
188 laboratory analyses. For each soil sample, the following variables were quantified as
189 described in Maestre *et al.* (2012a) and Delgado-Baquerizo *et al.* (2013): organic C,
190 pentoses, hexoses, total N, total available N, aminoacids, proteins, net potential
191 mineralization rate, total P, available inorganic P, Olsen P (inorganic P – HCL 1M) and
192 the activities of phosphatase and β -glucosidase. These variables constitute a good proxy
193 for processes such as nutrient cycling, biological productivity, and buildup of nutrient
194 pools, which are important determinants of ecosystem functioning in drylands
195 (Whitford, 2002). Most of these processes are also considered to support ecosystem
196 services, as other types of ecosystem services depend on them (MEA, 2005; Isbell *et al.*,
197 2011).

198

199 **Data management**

200 *Community trait distribution*

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

206
$$CWT_j = \sum_i^n p_{ij} T_{ij} \quad (\text{eqn. 1})$$

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

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

213
$$FD_j = \sum_i^n p_{ij} \left(\frac{|T_{ij} - CWT_j|}{\sum_i^n |T_{ij} - CWT_j|} \right) \quad (\text{eqn. 2})$$

214 where p_{ij} is the abundance of the species i in the community j , T_{ij} is the mean trait value
215 of the species i in the community j , and CWT_j is the community-weighted trait of the
216 community j . High FD values suggest higher complementarity in resource used between
217 species within a given community (Maire *et al.*, 2012).

218

219 *Multifunctionality index*

220 Multifunctionality was estimated from all the soil variables measured using the
221 M index of Maestre *et al.* (2012a). To obtain a M value for each site, Z scores were first
222 calculated for each of the 13 soil variables estimated at the scale of each $30 \text{ m} \times 30 \text{ m}$
223 plot surveyed. These estimates were obtained by using a weighted average of the mean
224 values observed in bare ground and vegetated areas, and weighted by their respective
225 cover at each plot (Maestre *et al.*, 2012a). Raw data were normalized prior to
226 calculations; a square root transformation normalized most of the variables evaluated.
227 Following this, the Z scores of the 13 soil variables were averaged to obtain M . This

228 index provides a straightforward and easily interpretable measure of the ability of
229 different communities to sustain multiple ecosystem functions simultaneously (Byrnes
230 *et al.*, 2014). It is also statistically robust (Maestre *et al.*, 2012a), and is being
231 increasingly used when assessing multifunctionality (Quero *et al.*, 2013; Pendleton *et al.*,
232 2014; Wagg *et al.*, 2014; Bradford *et al.*, 2014). We acknowledge that the use of M
233 may preclude a detailed analysis of how particular species differ in their importance for
234 different functions (e.g., Hector & Bagchi, 2007; Gotelli *et al.*, 2011), and that in this
235 index declines in a particular process/function can theoretically be compensated for by
236 increases in another process/function (something that has been criticized in the past; e.g.
237 Gamfeldt *et al.*, 2008). However, we did not find that particular sites with high values of
238 a single or a few functions had consistently low values for other functions (Table S4).
239 Moreover, the relatively large number of variables employed to calculate M makes it
240 relatively robust to outliers or atypical values. We also acknowledge that having
241 variables that are highly correlated among them could make them somewhat redundant
242 (albeit this also simplifies the interpretation of the values of M). However, in our dataset
243 only nine out of the 78 correlations between the soil variables evaluated had r values
244 higher than 0.7, suggesting that redundancy is not very high within our data (Table S4).
245 Finally, our estimates of M are highly related to other multifunctionality indices (Fig
246 S4). Thus, our results and conclusions are robust to the choice of metric used to estimate
247 multifunctionality.

248

249 **Statistical analyses**

250 *Functional variation between dryland communities*

251 We conducted a principal component analysis (PCA) with Varimax rotation using the
252 CWM and FD values of all the traits measured. These analyses were done separately for

253 CWM and FD. We used the PCA coordinates in those components with an eigenvalue
254 higher than one to measure the CWM and the FD of each community. This procedure
255 allowed us to identify the plant strategy spectrum along which traits co-vary across
256 species and communities (Maire *et al.*, 2012). It has also the advantage to consider only
257 independent variables in further analyses. CWM values were normalized using log-
258 transformation before PCA analyses.

259

260 *Community responses to aridity and shrub encroachment*

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

275

276 *Direct and indirect effects of aridity and shrub encroachment on multifunctionality*

277 To test for relationships between CWM, FD, aridity, shrub encroachment, and
278 multifunctionality, we conducted a confirmatory path analysis using a d-sep approach
279 (Shipley, 2009; Laliberté & Tylianakis, 2012). This methodology allows relaxing some
280 of the limitations of standard structural equation models, including non-normal data
281 distribution, non-linear relationships between variables and small sample sizes (Grace,
282 2006; Shipley, 2009). The d-sep approach is based on an acyclic graph that depicts the
283 hypothetical relationships and independence claims between variables, where the latter
284 are tested using the C statistic (See Fig. 1 and Appendix S1 for the detailed rationale of
285 our analyses). We tested three main alternative hypotheses, where multifunctionality
286 responses to aridity and shrub encroachment are driven by: (i) CWM only (mass ratio
287 hypothesis); (ii) FD only (niche complementary hypothesis); and (iii) the interplay of
288 mass-ratio and niche complementarity processes (combined hypothesis). To simplify
289 the *a priori* models used, a stepAICc procedure was first conducted to select the
290 predictors that explained most of the variability found in multifunctionality (see Table
291 S2). When several models were not rejected, we used the AICc procedure adapted for
292 confirmatory path analysis to select the best model (Shipley, 2013). Finally,
293 standardised path coefficients were used to measure the direct, indirect, and total effects
294 of the predictors (Grace & Bollen, 2005).

295 As multiple traits can potentially act simultaneously on multifunctionality
296 through contrasted mechanisms (e.g. mass ratio and niche complementarity in the case
297 of the combined hypothesis), their respective effects on multifunctionality responses to
298 aridity might be difficult to isolate. Thus, we ran a sensitivity analysis on the best
299 selected model to highlight the relative contribution of multiple traits to the observed
300 multifunctionality in response to aridity and shrub encroachments. To do so, we used
301 the parameters of the best model to estimate multifunctionality values along the aridity

302 gradient studied under different scenarios, which were created by manipulating the
303 abundances of non-sprouting and sprouting shrubs. The first scenario considered only
304 the effects of aridity by fixing the abundance of both shrub types at 0%. The second
305 scenario focused on the interplay between aridity and encroachment by non-sprouting
306 shrubs. To do so, we fixed the abundance of sprouting shrubs at 0%, and simulated the
307 effects of aridity on non-sprouting shrubs. In the third scenario we simulated the
308 interactive effects of aridity and encroachment by sprouting shrubs. We fixed the
309 abundance of sprouting shrubs at 30% (an average abundance that can be observed
310 along the aridity gradient), and that of non-sprouting shrubs at 0% (to remove their
311 effect from the simulation).

312 Principal component analysis and stepAICc analyses were carried out using JMP
313 11 (The SAS Institute, Cary, North Carolina, USA); d-sep analyses were conducted
314 using the `lm` function in R (R Core Development Team, 2012).

315

316 **RESULTS**

317 **Functional structure of studied communities**

318 The CWM of the studied communities segregated along two PCA components, which
319 accounted for 62% of the total variance found in the data (Fig. 2a). The first component
320 (36% of the variance) separated communities according to their leaf trait values
321 (hereafter CW-leaf trait), with SLA and Br being negatively correlated to LDMC, LL
322 and LA. The first PCA component was negatively correlated with the abundance of *S.*
323 *tenacissima* ($r^2=0.82$, P value < 0.001; dot scale in Fig. 2), and discriminated grasslands
324 from shrublands. The second PCA component discriminated communities according to
325 plant size traits (hereafter CW-size trait), with VH, LW and LS being negatively
326 correlated to BD.

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

334

335 **Community response traits to aridity and shrub encroachment**

336 The abundance of non-sprouting shrubs largely determined CW-leaf traits (73% of the
337 explained variance, Table 1) and the communities dominated by these species had
338 higher CW-SLA and -Br, and lower CW-LDMC, -LL, and -LA. These traits were also
339 significantly impacted by aridity and the abundance of sprouting shrubs, although to a
340 lesser extent (8% and 19% of the explained model variance, respectively; Table 1). A
341 quadratic relationship was observed between aridity and CW-leaf traits (Table 1). In
342 contrast, CW-size traits were mostly driven by the abundance of sprouting shrubs
343 (Table 1). Communities with high CW-size traits were those dominated by tall
344 sprouting shrubs.

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

352

353 **Linking community response traits to effect traits on multifunctionality**

354 The model including the combined effects of CWM and FD (combined hypothesis) was
355 the only model not rejected by the data (Fig. 3 and Table S3). This model explained
356 62% of the variation in multifunctionality. Importantly, it highlighted that the effects of
357 shrub encroachment on multifunctionality were mostly indirect via its effects on the
358 functional structure of the plant community (Fig. 4).

359 While aridity had a direct effect on multifunctionality, it also had a large
360 cascading effect by altering the functional structure of the studied communities. Aridity
361 favoured the abundance of non-sprouting shrubs, which resulted in higher values of
362 CW-leaf traits (Fig. 3). Shifting leaf trait values toward higher SLA had a strong
363 adverse effect on multifunctionality. In contrast, the abundance of sprouting shrubs was
364 independent from aridity. Increasing the abundance of these shrubs changed the value of
365 CW-size traits towards higher plant height. Such an increase did not directly impact
366 multifunctionality, but had an indirect effect via the changes it promoted in FD (Fig. 3).
367 Increasing the average size of the species in the community augmented the FD of size
368 traits, though decreased the FD of leaf traits, especially for intermediate values of CW-
369 size traits (quadratic relationship). It must be noted that communities showing a high
370 variance in size traits were also characterized by high FD values of leaf traits.
371 Increasing FD values of both leaf and size traits generally increased multifunctionality.
372 However, a significant interaction between aridity and FD leaf traits was observed (Fig.
373 3). This indicates that the effect of these traits on multifunctionality shifted from
374 positive to negative under high aridity conditions. Finally, sprouting and non-sprouting
375 shrubs did not have a direct effect on multifunctionality (Fig. 4), suggesting that all their
376 effects on multifunctionality were explained by the functional traits measured.

377

378 **Model scenarios**

379 In the sensitivity analyses of our final path model (Fig. 3), scenario 1 modelled the
380 direct effect of aridity on multifunctionality as it had fixed zero abundance of both types
381 of shrubs. In this case, multifunctionality directly decreased with increases in aridity
382 (orange line, Fig. 5). In scenario 2, we modelled the effects of aridity on the abundance
383 of non-sprouting shrubs (significant link in Fig. 3) and its consequences for
384 multifunctionality. Increasing the abundance of non-sprouting shrubs augmented CW-
385 leaf traits, and strongly decreased multifunctionality, along the aridity gradient (green
386 line, Fig. 5). Finally, in scenario 3 we fixed the abundance of sprouting shrubs to 30%
387 to maintain high values of functional diversity along the aridity gradient and to model
388 its effects on multifunctionality. In this scenario, multifunctionality values remained
389 high for most of the aridity gradient, declining only under high aridity conditions (red
390 line, Fig. 5).

391

392 **DISCUSSION**

393 Our study represents a first attempt to evaluate how multiple traits mediated dryland
394 multifunctionality responses to two major global change drivers, i.e. aridity and shrub
395 encroachments. Dryland multifunctionality largely depends on the functional structure
396 of the plant communities. Our results indicate that mass ratio and niche
397 complementarity processes, as reflected by CWM and FD, respectively, were equally
398 important as drivers of multifunctionality responses to both aridity and shrub
399 encroachment (Fig. 3). Specifically, the two key findings from our study are: (i) high
400 FD improved the resistance of multifunctionality (i.e., the ability not to be affected by
401 something, especially adversely; Oxford Dictionaries, 2014) to increases in aridity; (ii)

402 two sets of simple plant functional traits (size traits like VH and leaf traits like SLA or
403 LDMC) can capture the effect of shrub encroachment on multifunctionality with a
404 relative high accuracy. Thus, this set of traits can be particularly helpful to identify
405 when and where shrub species affect multifunctionality positively or negatively, and to
406 clarify the contrasted results previously found in the literature regarding the effects of
407 shrub encroachment on ecosystem functioning (Eldridge *et al.*, 2011).

408

409 **Functional diversity enhances multifunctionality in drylands**

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

421 In temperate ecosystems, the effect of high FD on ecosystem functioning has
422 been generally associated to higher resource acquisition rates (Van Ruijven & Berendse,
423 2005) and resource use efficiency (Gross *et al.*, 2007a), temporal niche variability
424 (Maire *et al.*, 2012) and plant soil feedbacks (Van der Heijden *et al.*, 2008). While
425 future experiments are needed to identify the underlying mechanisms supporting the
426 positive relationship between FD and ecosystem multifunctionality reported here, our

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

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

436 (ii) High leaf trait diversity indicates the occurrence of contrasting leaf strategies
437 (Westoby *et al.*, 2002) commonly found in Mediterranean systems (e.g., stress
438 avoidance vs. tolerance; Ackerly *et al.*, 2002; Freschet *et al.*, 2011). Differences in
439 the leaf strategy of co-occurring species may have strong positive effects on
440 ecosystem processes such as productivity (Gross *et al.*, 2007a), carbon cycling
441 (Milcu *et al.*, 2014), and litter decomposition rates (Bardgett & Shine, 1999;
442 Cornwell *et al.*, 2008). For instance, some studies have shown that increasing the
443 FD of litter positively influences microbial communities (Zak *et al.*, 2003) and litter
444 decomposition rates (Vos *et al.*, 2013), two potentially important factors for
445 maintaining and improving dryland multifunctionality.

446

447 **Multiple traits mediate the impact of mass ratio processes on multifunctionality**

448 By considering multiple traits, our study showed that the outcomes of shrub
449 encroachment can be explained by size-related and leaf traits. Shrub encroachment by
450 sprouting shrubs species (such as *Q. coccifera*) had a positive cascading effect on
451 multifunctionality, which was mediated by increasing CW-size trait values (Fig. 3), in

452 accordance with Maestre *et al.* (2009). Increasing plant size in dryland communities has
453 been shown to be strongly associated with an increase in FD size traits locally, and with
454 a high spatial heterogeneity of plant biomass within communities (Gross *et al.*, 2013),
455 two features that can have potential positive effects on ecosystem functioning as
456 discussed above. Maestre *et al.* (2009) showed how large *Quercus* species can increase
457 the availability of local soil resources under their canopy in semi-arid *S. tenacissima*
458 grasslands. The positive effects of these shrubs on local resources have been shown to
459 increase species diversity of the whole community (Maestre *et al.*, 2009; Soliveres *et*
460 *al.*, 2011), an important parameter reinforcing the positive effect of sprouting shrubs on
461 multifunctionality (Quero *et al.*, 2013). Our results complement previous findings by
462 illustrating how sprouting shrubs can enhance functional diversity within dryland
463 communities, ultimately affecting multifunctionality.

464 CW-leaf trait values increased with an increase in the abundance of non-
465 sprouting shrubs (Table 1). This had a negative impact on multifunctionality,
466 particularly in the most arid part of the gradient. The negative effect of fast growing
467 species on multifunctionality can be explained by a negative plant soil feedback, as
468 suggested by Garnier *et al.* (2004). Negative relationships between SLA and soil
469 nutrient contents have previously been found in Mediterranean French grasslands
470 (Garnier *et al.*, 2004) and along successional vegetation stages, where fast-growing
471 species are replaced by slow-growing species (Berendse, 1990). Higher growth and
472 nutrient acquisition rates may accelerate nutrient uptake from the soil (Lavorel &
473 Garnier, 2002). At the same time, plants with higher SLA may produce litter with
474 higher decomposition rates (Kazakou *et al.*, 2006). Together with the reduction of litter
475 accumulation per unit of soil surface, these effects may accelerate nutrient loss at the
476 scale of the whole ecosystem (Garnier *et al.*, 2004). This may be particularly true in the

477 most arid part of the aridity gradient, where the typical characteristics of the semi-arid
478 Mediterranean climate are worsened. For instance, the high variability of interannual
479 precipitation distribution promotes increases in water runoff during short periods
480 (Martínez-Mena *et al.*, 2001) and increases soil erosion that might accelerate nutrient
481 loss (Martínez-Mena *et al.*, 2002). In addition, the negative effect of fast growing
482 summer deciduous species on multifunctionality can be amplified via **an effect on FD**
483 **size traits (e.g. the negative link between CW-leaf traits and FD-size traits in Fig. 3).**
484 Summer deciduous species with a stress avoidance strategy can outcompete the more
485 stress-tolerant grass and shrub species (Gross *et al.*, 2013) **by producing allelopathic**
486 **compounds (as has been found for species such as *Artemisia herba-alba*, Escudero *et***
487 ***al.*, 2000).** Competition between fast- and slow-growing species may decrease the
488 abundance of **slow-growing** sprouting shrubs and modify the size and spatial
489 distribution of plant biomass within communities (Gross *et al.*, 2013). This situation
490 may decrease the positive effects of sprouting shrubs on functional diversity,
491 accelerating species loss and affecting the functioning of the whole ecosystem (Maestre
492 *et al.*, 2009).

493

494 **Importance of functional diversity for ecosystem resistance to increasing aridity**

495 **The sensitivity analysis allowed us to explore how aridity interplays with plant**
496 **functional community structure to determine multifunctionality (Fig. 5). While aridity**
497 **had a direct detrimental effect on multifunctionality (scenario 1, Fig.5, Delgado-**
498 **Baquerizo *et al.*, 2013), this negative effect was further reinforced by the increase in**
499 **abundance of non-sprouting shrubs, as favoured by increasing aridity (scenario 2, Fig.**
500 **5). Moreover, we found an interactive effect of aridity and FD-leaf traits on**
501 **multifunctionality (Fig. 3), suggesting that the effects FD-leaf traits shifted from**

502 positive to negative as aridity increased. At low aridity levels, high FD-leaf traits may
503 reflect the coexistence between fast growing species characterized by perennial leaves
504 (e.g. *Brachypodium retusum*), and stress-tolerant shrub or grass species (Frenette-
505 Dussault *et al.*, 2012) that maximised ecosystem multifunctionality. In contrast, under
506 high aridity conditions, the increase in FD-leaf traits observed reflected the increasing in
507 abundance of non-sprouting shrubs (see selection effect in Loreau & Hector, 2001),
508 characterized by high value of leaf traits (i.e. fast growing species with summer
509 deciduous, Gross *et al.*, 2013) that may negatively affect ecosystem functioning.

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

525 We standardized our sampling design by selecting sites with similar soil, slopes
526 and aspect (south-facing slopes). Local variation in topo-edaphic conditions could

527 however alter plant community structure (Fonseca *et al.*, 2000; Gross *et al.*, 2008) and
528 multifunctionality. For instance, while we did not find any significant effect of slope on
529 multifunctionality, other local factors such as slope aspect, soil texture or bedrock type
530 could affect water availability (Fonseca *et al.*, 2000; Gomez-plaza *et al.*, 2001; Delgado-
531 Baquerizo *et al.*, 2013). Evaluating how local topo-edaphic factors interplay with
532 climatic/land use factors to determine the functional structure of dryland communities
533 and their effect on multifunctionality represents an important research front for the
534 future.

535

536 **Concluding remarks**

537 Our work suggests that the functional traits of dominant species and their diversity
538 within communities modulate changes in multifunctionality in Mediterranean
539 ecosystems along gradients of aridity and shrub encroachment. We showed that
540 maintaining and enhancing FD (promoted by sprouting shrubs) in these ecosystems may
541 help to buffer negative effects of climate change on multifunctionality. We also
542 identified key traits that can predict accurately the outcome of shrub encroachment. Our
543 results contribute to resolve the existing debate in the literature on the contrasted effects
544 of shrub encroachment in drylands worldwide (e.g. Schlesinger *et al.*, 1990; Maestre *et*
545 *al.*, 2009). On the one hand, traits related to the size of the plant species reflected the
546 abundance of sprouting shrubs, which positively feedback on multifunctionality via
547 their positive effect of FD. On the other hand, leaf traits such as SLA were related to the
548 abundance of non-sprouting shrubs, which negatively impacted multifunctionality
549 (particularly at the driest part of the aridity gradient studied). These results suggest that
550 high values of SLA may typify those shrub species that are commonly associated to
551 advance land degradation and desertification in drylands (Eldridge *et al.* 2011).

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

559

560 **Acknowledgements**

561 We thank M. D. Puche, V. Ochoa, B. Gozalo, M. Delgado-Baquerizo, M. Berdugo, A.
562 Gallardo and A. Prado-Comesaña for their help with the soil analyses, and four
563 reviewers and the editor for the multiple and constructive comments provided on earlier
564 versions of our article. This research was funded by the European Research Council
565 under the European Community's Seventh Framework Programme (FP7/2007-
566 2013)/ERC Grant agreement 242658 (BIOCOM). Y.L.B.P is supported by the project
567 Postdoc USB (reg.no. CZ.1.07/2.3.00/30.0006) realized through EU Education for
568 Competitiveness Operational Programme and funded by the European Social Fund and
569 Czech State Budget.

570

571 **References**

- 572 **Ackerly D, Knight C, Weiss S, Barton K, Starmer, K. 2002.** Leaf size, specific leaf
573 area and microhabitat distribution of chaparral woody plants: contrasting patterns in
574 species level and community level analysis. *Oecologia* **130**: 449-457.
- 575 **Akaike, H. 1973.** Information theory and an extension of the maximum likelihood
576 principle. In *Second international symposium on information theory*. Akademiai
577 Kiado, 267-281.
- 578 **Asner GP, DeFries RS, Houghton R. 2004.** *Typological responses of ecosystems to*
579 *land use change*. American Geophysical Union.
- 580 **Austin AT, Yahdjian L, Stark JM, Belnap J, Porporato A, Norton U, Ravetta DA,**
581 **Schaeffer SM. 2004.** Water pulses and biogeochemical cycles in arid and semiarid
582 ecosystems. *Oecologia* **141**: 221–235.
- 583 **Bardgett RD, Shine A. 1999.** Linkages between plant litter diversity, soil microbial
584 biomass and ecosystem function in temperate grasslands. *Soil Biology and Biochemistry*
585 **31**: 317-321.
- 586 **Berendse F. 1990.** Organic matter accumulation and nitrogen mineralization during
587 secondary succession in heathland ecosystems. *Journal of Ecology* **78**: 413–427.
- 588 **Bradford MA, Wood SA, Bardgett RD, Black HI, Bonkowski M, Eggers T,**
589 **Graystong SJ, Kandelerh E, Manningi P, Setäläjä H, et al. 2014.** Discontinuity in the
590 responses of ecosystem processes and multifunctionality to altered soil community
591 composition. *Proceedings of the National Academy of Sciences* **111**: 14478-14483.
- 592 **Byrnes JEK, Gamfeld L, Isbell F, Lefcheck JS, Griffin JN, Hector A, Cardinale**
593 **BJ, Hooper DU, Dee LE, Duffy JE. 2014.** Investigating the relationship between
594 biodiversity and ecosystem multifunctionality: Challenges and solutions. *Methods in*
595 *Ecology and Evolution*, doi: 10.1111/2041–210X.12143.

- 596 **Cardinale BJ, Duffy JE, Gonzalez A, Hooper DU, Perrings C, Venail P, Narwani**
597 **A, Mace GM, Tilman D, Wardle DA, et al. 2012.** Biodiversity loss and its impact on
598 humanity. *Nature* **486**: 59-67.
- 599 **Chapin FS, Zavaleta ES, Eviner VT, Naylor RL, Vitousek PM, Reynolds HL,**
600 **Hooper DU, Lavorel S, Sala OE, Hobbie SE et al. 2000.** Consequences of changing
601 biodiversity. *Nature* **405**: 234–242.
- 602 **Cornelissen JHC, Lavorel S, Garnier E, Diaz S, Buchmann N, Gurvich DE, Reich**
603 **PB, Steege H, Morgan HD, Van Der Heijden MGA, et al. 2003.** A handbook of
604 protocols for standardised and easy measurement of plant functional traits worldwide.
605 *Australian Journal of Botany* **51**: 335–380.
- 606 **Cornwell WK, Cornelissen JH, Amatangelo K, Dorrepaal E, Eviner VT, Godoy O,**
607 **Hobbie SE, Hoorens B, Kurokawa H, Pérez-Harguindeguy N et al. 2008.** Plant
608 species traits are the predominant control on litter decomposition rates within biomes
609 worldwide. *Ecology Letters* **11**: 1065-1071.
- 610 **De Bello F, Lavorel S, Díaz S, Harrington R, Cornelissen JH, Bardgett RD, Berg**
611 **MP, Cipriotti P, Feld CK, Hering D et al. 2010.** Towards an assessment of multiple
612 ecosystem processes and services via functional traits. *Biodiversity and Conservation*
613 **19**: 2873-2893.
- 614 **Delgado-Baquerizo M, Maestre FT, Gallardo A, Bowker MA, Wallenstein M,**
615 **Quero JL, Soliveres S, Ochoa V, Gozalo B, García-Gómez M et al. 2013.**
616 Decoupling of soil nutrient cycles as a function of aridity in global
617 drylands. *Nature* **502**: 672-676.
- 618 **Díaz S, Cabido M. 2001.** Vive la difference: plant functional diversity matters to
619 ecosystem processes. *Trends in Ecology & Evolution* **16**: 646-655.

- 620 **Díaz S, Lavorel S, de Bello F, Quérier F, Grigulis K, Robson TM. 2007.**
621 Incorporating plant functional diversity effects in ecosystem services assessments.
622 *Proceedings of the National Academy of Sciences* **104**: 20684-20689.
- 623 **Eldridge DJ, Bowker MA, Maestre FT, Roger E, Reynolds JF, Whitford WG.**
624 **2011.** Impacts of shrub encroachment on ecosystem structure and functioning: towards
625 a global synthesis. *Ecology Letters* **14**: 709–722.
- 626 **Escudero A, Albert MJ, Pita JM, Pérez-García F. 2000.** Inhibitory effects of
627 *Artemisia herba-alba* on the germination of the gypsophyta *Helianthemum squamatum*.
628 *Plant Ecology* **148**: 71-80.
- 629 **Feng S, Fu Q. 2013.** Expansion of global drylands under a warming climate.
630 *Atmospheric Chemistry & Physics*, **13**: 10081-10094.
- 631 **Fonseca CR, Overton JM, Collins B, Westoby M. 2000.** Shifts in trait-combinations
632 along rainfall and phosphorus gradients. *Journal of Ecology* **88**: 964-977.
- 633 **Fowler N. 1986.** The role of competition in plant communities in arid and semiarid
634 regions. *Annual Review of Ecology and Systematics* **17**: 89-110.
- 635 **Frenette-Dussault C, Shipley B, Meziane D, Hingrat Y. 2012.** Trait-based climate
636 change predictions of plant community structure in arid steppes. *Journal of*
637 *ecology*, **101**: 484-492.
- 638 **Freschet GT, Dias AT, Ackerly DD, Aerts R, van Bodegom PM, Cornwell WK,**
639 **Dong M, Kurokawa H, Liu G, Onipchenko VG et al. 2011.** Global to community
640 scale differences in the prevalence of convergent over divergent leaf trait distributions
641 in plant assemblages. *Global Ecology and Biogeography*, **20**: 755-765.
- 642 **Gaitán JJ, Oliva G, Bran D, Maestre FT, Aguiar MR, Jobbágy EG, Buono G,**
643 **Ferrante D, Nakamatsu V, Ciari G, et al. 2014.** Vegetation structure is as important

- 644 as climate to explain ecosystem function across Patagonian rangelands. *Journal of*
645 *Ecology* **102**: 1419–1428.
- 646 **Gamfeldt L, Hillebrand H, Jonsson PR. 2008.** Multiple functions increase the
647 importance of biodiversity for overall ecosystem functioning. *Ecology* **89**: 1223-1231.
- 648 **García-Gómez M, Maestre FT. 2011.** Remote sensing data predict indicators of soil
649 functioning in semi-arid steppes, central Spain. *Ecological Indicators* **11**: 1476-1481.
- 650 **Garnier E, Cortez J, Billes G, Navas ML, Roumet C, Debussche M, Laurent G,**
651 **Blanchard A, Aubry D, Bellmann A, Neill C, Toussaint J.P. 2004.** Plant functional
652 markers capture ecosystem properties during secondary succession. *Ecology* **85**: 2630–
653 2637.
- 654 **Gómez-Plaza A, Martinez-Mena M, Albaladejo J, Castillo VM. 2001.** Factors
655 regulating spatial distribution of soil water content in small semiarid catchments.
656 *Journal of hydrology* **253**: 211-226.
- 657 **Gotelli NJ, Ulrich W, Maestre FT. 2011.** Randomization tests for quantifying species
658 importance to ecosystem function. *Methods in Ecology and Evolution* **2**: 634-642.
- 659 **Grace JB, Bollen KA. 2005.** Interpreting the Results from Multiple Regression and
660 Structural Equation Models. *Bulletin of the Ecological Society of America* **86**: 283–
661 295.
- 662 **Grace JB. 2006.** *Structural equation modeling and natural systems*. Cambridge
663 University Press, Cambridge, UK.
- 664 **Grime JP. 1998.** Benefits of plant diversity to ecosystems: immediate, filter and
665 founder effects. *Journal of Ecology* **86**: 902–910.
- 666 **Gross N, Suding KN, Lavorel S. 2007a.** Leaf dry matter content and lateral spread
667 predict response to land use change for six subalpine grassland species. *Journal of*
668 *Vegetation Science* **18**: 289–300.

- 669 **Gross N, Suding KN, Lavorel S, Roumet C. 2007b.** Complementarity as a mechanism
670 of coexistence between functional groups of grasses. *Journal of Ecology* **95**: 1296-1305.
- 671 **Gross N, Robson TM, Lavorel S, Albert C, Bagousse-Pinguet L, Guillemin R. 2008.**
672 Plant response traits mediate the effects of subalpine grasslands on soil moisture. *New*
673 *Phytologist* **180**: 652-662.
- 674 **Gross N, Börger L, Soriano-Morales SI, Le Bagousse-Pinguet Y, Quero JL,**
675 **García-Gómez M, Valencia-Gómez E, Maestre FT. 2013.** Uncovering multiscale
676 effects of aridity and biotic interactions on the functional structure of Mediterranean
677 shrublands. *Journal of Ecology* **101**: 637-649.
- 678 **Hector A, Bagchi R. 2007.** Biodiversity and ecosystem multifunctionality. *Nature* **448**:
679 188-190.
- 680 **Hijmans RJ, Cameron SE, Parra JL, Jones PG, Jarvis A. 2005.** Very high resolution
681 interpolated climate surfaces for global land areas. *International journal of climatology*
682 **25**: 1965–1978.
- 683 **Hooper DU, Chapin FS, Ewel JJ, Hector A, Inchausti P, Lavorel S, Lawton JH,**
684 **Lodge D, Loreau M, Naeem S et al. 2005.** Effects of biodiversity on ecosystem
685 functioning: A consensus of current knowledge. *Ecological Monographs* **75**: 3–35.
- 686 **Isbell F, Calcagno V, Hector A, Connolly J, Harpole WS, Reich PB, Scherer-**
687 **Lorenzen M, Schmid B, Tilman D, van Ruijven J. 2011.** High plant diversity is
688 needed to maintain ecosystem services. *Nature* **477**: 199-202.
- 689 **Kazakou E, Vile D, Shipley B, Gallet C, Garnier E. 2006.** Co-variations in litter
690 decomposition, leaf traits and plant growth in species from a Mediterranean old-field
691 succession. *Functional Ecology* **20**: 21-30.
- 692 **Knapp AK, Briggs JM, Collins SL, Archer SR, Bret-Harte MS, Ewers BE, Peters**
693 **DP, Young DR, Shaver GR, Pendall E et al. 2008.** Shrub encroachment in North

- 694 American grasslands: shifts in growth form dominance rapidly alters control of
695 ecosystem carbon inputs. *Global Change Biology* **14**: 615-623.
- 696 **Kazakou E, Vile D, Shipley B, Gallet C, Garnier E. 2006.** Co-variations in litter
697 decomposition, leaf traits and plant growth in species from a Mediterranean old-field
698 succession. *Functional Ecology* **20**: 21-30.
- 699 **Laliberté E, Legendre P. 2010.** A distance-based framework for measuring functional
700 diversity from multiple traits. *Ecology* **91**: 299–305.
- 701 **Laliberté E, Tylianakis JM. 2012.** Cascading effects of long-term land-use changes on
702 plant traits and ecosystem functioning. *Ecology* **93**: 145-155.
- 703 **Laughlin DC. 2014.** Applying trait-based models to achieve functional targets for
704 theory-driven ecological restoration. *Ecology Letters* **17**: 771–784.
- 705 **Lavorel S, Garnier E. 2002.** Predicting changes in community composition and
706 ecosystem functioning from plant traits: revisiting the Holy Grail. *Functional Ecology*
707 **16**: 545–556.
- 708 **Li XY, Zhang SY, Peng HY, Hu X, Ma YJ. 2013.** Soil water and temperature
709 dynamics in shrub-encroached grasslands and climatic implications: results from Inner
710 Mongolia steppe ecosystem of north China. *Agricultural and Forest Meteorology* **171**:
711 20-30.
- 712 **Loreau M, Hector A. 2001.** Partitioning selection and complementarity in biodiversity
713 experiments. *Nature* **412**: 72-76.
- 714 **Maestre FT, Escudero A. 2009.** Is the patch-size distribution of vegetation a suitable
715 indicator of desertification processes? *Ecology* **90**: 1729-1735.
- 716 **Maestre FT, Puche MD, Bowker MA, Hinojosa MB, Martínez I, García-Palacios**
717 **P, Castillo AP, Soliveres S, Luzuriaga AL, Sánchez AM et al. 2009.** Shrub

- 718 encroachment can reverse desertification in Mediterranean semiarid grasslands. *Ecology*
719 *Letters* **12**: 930–941.
- 720 **Maestre FT, Quero JL, Gotelli NJ, Escudero A., Ochoa V, Delgado-Baquerizo,**
721 **García-Gómez M, Bowker MA, Soliveres S, Escolar C et al. 2012a.** Plant species
722 richness and ecosystem multifunctionality in global drylands. *Science* **335**: 214-218.
- 723 **Maestre FT, Salguero-Gómez R, Quero JL. 2012b.** It is getting hotter in here:
724 determining and projecting the impacts of global environmental change on drylands.
725 *Philosophical Transactions of the Royal Society Biological Sciences* **367**: 3062-3075.
- 726 **Maire V, Gross N, Börger L, Proulx R, Wirth C, Pontes LDS, Soussana JF,**
727 **Louault F. 2012.** Habitat filtering and niche differentiation jointly explain species
728 relative abundance within grassland communities along fertility and disturbance
729 gradients. *New Phytologist* **196**: 497-509.
- 730 **Martínez-Mena M, Castillo V, Albaladejo J. 2001.** Hydrological and erosional
731 response to natural rainfall in a semi-arid area of south-east Spain. *Hydrological*
732 *Processes* **15**: 557-571.
- 733 **Martínez-Mena M, Rogel JA, Castillo V, Albaladejo J. 2002.** Organic carbon and
734 nitrogen losses influenced by vegetation removal in a semi-arid soil. *Biogeochemistry*
735 **61**: 309–321
- 736 **Milcu A, Roscher C, Gessler A, Bachmann D, Gockele A, Guderle M, Landais D,**
737 **Piel C, Escape C, Devidal S et al. 2014.** Functional diversity of leaf nitrogen
738 concentrations drives grassland carbon fluxes. *Ecology letters* **17**: 435–444.
- 739 **Millennium Ecosystem Assessment (MEA). 2005.** *Ecosystems and human well-being.*
740 Washington, DC: Island Press, 2005.
- 741 **Mitchley J, Ispikoudis I. 1999.** Grassland and shrubland in Europe: biodiversity and
742 conservation. *Grassland Science in Europe* **4**: 239–251.

- 743 **Mokany K, Ash J, Roxburgh S. 2008.** Functional identity is more important than
744 diversity in influencing ecosystem processes in a temperate native grassland. *Journal of*
745 *Ecology* **96**: 884–893.
- 746 **Mouillot D, Vileger S, Scherer-Lorenzen M, Mason NWH. 2011.** Functional
747 Structure of Biological Communities Predicts Ecosystem Multifunctionality. *Plos one*
748 **6**: e17476.
- 749 **Oxford Dictionaries. 2014.** Oxford University Press.
750 <http://www.oxforddictionaries.com>
- 751 **Pendleton RM, Hoetinghaus DJ, Gomes LC, Agostinho AA. 2014.** Loss of Rare Fish
752 Species from Tropical Floodplain Food Webs Affects Community Structure and
753 Ecosystem Multifunctionality in a Mesocosm Experiment. *Plos one* **9**: e84568.
- 754 **Puigdefábregas J, Sole A, Gutierrez L, Del Barrio G, Boer M. 1999.** Scales and
755 processes of water and sediment redistribution in drylands: results from the Rambla
756 Honda field site in Southeast Spain. *Earth-Science Reviews* **48**: 39-70.
- 757 **Quero JL, Maestre FT, Ochoa V, García-Gómez M, Delgado-Baquerizo M. 2013.**
758 On the Importance of Shrub Encroachment by Sprouters, Climate, Species Richness and
759 Anthropic Factors for Ecosystem Multifunctionality in Semi-arid Mediterranean
760 Ecosystems. *Ecosystems* **16**: 1248-1261.
- 761 **R Development Core Team. 2012** *R: A language and environment for statistical*
762 *computing*. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-
763 07-0, URL <http://www.R-project.org/>.
- 764 **Reiss J, Bridle JR, Montoya JM, Woodward G. 2009.** Emerging horizons in
765 biodiversity and ecosystem functioning research. *Trends in Ecology & Evolution* **24**:
766 505-514.

- 767 **Sandel B, Corbin JD, Krupa M. 2011.** Using plant functional traits to guide
768 restoration: a case study in California coastal grassland. *Ecosphere* **2**: art23.
- 769 **Schlesinger WH, Reynolds JF, Cunningham GL, Huenneke LF, Jarrell WM,**
770 **Virginia R, Whitford WG. 1990.** Biological feedbacks in global desertification.
771 *Science* **247**: 1043–1048.
- 772 **Shipley B. 2009.** Confirmatory path analysis in a generalized multilevel context.
773 *Ecology* **90**: 363–368.
- 774 **Shipley B. 2013.** The AIC model selection method applied to path analytic models
775 compared using a d-separation test. *Ecology* **94**: 560-564.
- 776 **Soil Survey Staff, 1994.** *Keys to Soil Taxonomy, 6th edn.* USDA Soil Conservation
777 Service, Pocahontas Press, Blacksburg.
- 778 **Soliveres S, Eldridge DJ, Maestre FT, Bowker MA, Tighe M, Escudero A. 2011.**
779 Microhabitat amelioration and reduced competition among understory plants as drivers
780 of facilitation across environmental gradients: Towards a unifying framework.
781 *Perspectives in Plant Ecology, Evolution and Systematics* **13**: 247–258.
- 782 **Suding KN, Lavorel S, Chapin FS, Cornelissen JH, Diaz S, Garnier E, Goldberg D,**
783 **Hooper DU, Jackson ST, Navas ML. 2008.** Scaling environmental change through the
784 community-level: a trait-based response-and-effect framework for plants. *Global*
785 *Change Biology* **14**: 1125-1140.
- 786 **Trabucco A, Zomer RJ. 2009.** Global Aridity Index (Global-Aridity) and Global
787 Potential Evapo-Transpiration (Global-PET) Geospatial Database. CGIAR Consortium
788 for Spatial Information. Published online, available from the CGIAR-CSI GeoPortal at:
789 <http://www.csi.cgiar.org>
- 790 **Valentin C, d’Herbes JM, Poesen J. 1999.** Soil and water components of banded
791 vegetation patterns. *Catena* **37**: 1–24.

- 792 **Van Ruijven J, Berendse F. 2005.** Diversity–productivity relationships: initial effects,
793 long-term patterns, and underlying mechanisms. *Proceedings of the National Academy*
794 *of Sciences of the United States of America* **102**: 695-700.
- 795 **Van Der Heijden MG, Bardgett RD, Van Straalen NM. 2008.** The unseen majority:
796 soil microbes as drivers of plant diversity and productivity in terrestrial ecosystems.
797 *Ecology Letters* **11**: 296-310.
- 798 **Violle C, Navas ML, Vile D, Kazakou E, Fortunel C, Hummel I, Garnier E. 2007.**
799 Let the concept of trait be functional! *Oikos* **116**: 882–892.
- 800 **Vitousek PM, Mooney HA, Lubchenco J, Melillo JM. 1997.** Human domination of
801 Earth's ecosystems. *Science* **277**: 494-499.
- 802 **Volaire F, Barkaoui K, Norton M. 2014.** Designing resilient and sustainable
803 grasslands for a drier future: Adaptive strategies, functional traits and biotic
804 interactions. *European Journal of Agronomy* **52**: 81-89.
- 805 **Vos VC, van Ruijven J, Berg MP, Peeters ET, Berendse F. 2013.** Leaf litter quality
806 drives litter mixing effects through complementary resource use among detritivores.
807 *Oecologia* **173**: 269-280.
- 808 **Wagg C, Bender SF, Widmer F, van der Heijden MG. 2014.** Soil biodiversity and
809 soil community composition determine ecosystem multifunctionality. *Proceedings of*
810 *the National Academy of Sciences* **111**: 5266-5270.
- 811 **Westoby M, Falster DS, Moles AT, Vesk PA, Wright IJ. 2002.** Plant ecological
812 strategies: come leading dimensions of variation between species. *Annual Review of*
813 *Ecology and Systematics* **33**: 125–159.
- 814 **Whitford WG. 2002.** Ecology of desert systems. Academic Press, London, UK.

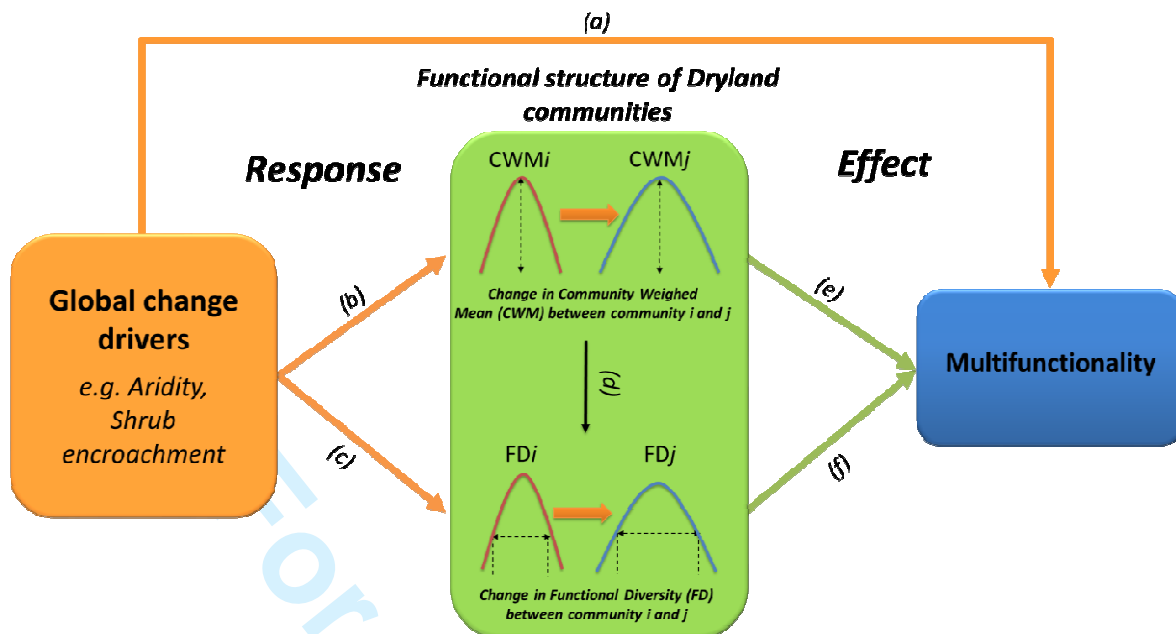
- 815 **Wright IJ, Reich PB, Westoby M, Ackerly DD, Baruch Z, Bongers F, Cavender-**
816 **Bares J, Chapin T, Cornelissen JHC, Diemer M *et al.* 2004.** The worldwide leaf
817 economics spectrum. *Nature* **428**: 821–827.
- 818 **Zak DR, Holmes WE, White DC, Peacock AD, Tilman D. 2003.** Plant diversity, soil
819 microbial communities, and ecosystem function: are there any links?. *Ecology* **84**:
820 2042-2050.
- 821 **Zavaleta ES, Pasari JR, Hulvey KB, Tilman GD. 2010.** Sustaining multiple
822 ecosystem functions in grassland communities requires higher biodiversity. *Proceedings*
823 *of the National Academy of Sciences* **107**: 1443-1446.
- 824 **Zepp RG, Erickson DJ, Paul ND, Sulzberger B. 2007.** Interactive effects of solar UV
825 radiation and climate change on biogeochemical cycling. *Photochemical &*
826 *Photobiological Sciences* **6**: 286-300.

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

832

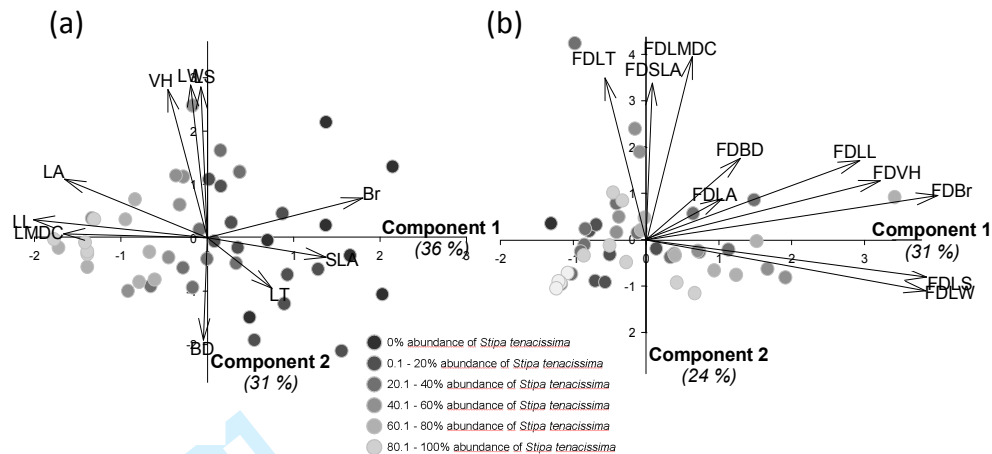
Model r^2	CW-leaf traits					CW-size traits					FD-leaf traits					
	est	DF	Fratio	Pvalue	% of r^2	est	DF	Fratio	Pvalue	% of r^2	est	DF	Fratio	Pvalue	% of r^2	est
			0.9					0.63						0.32		
Aridity	-6.842	1	28.08	<0.0001	6.5						-7.755	1	5.39	0.0255	21.1	
Aridity ²	65.8141	1	8.35	0.0063	1.9					113.7509	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				

833



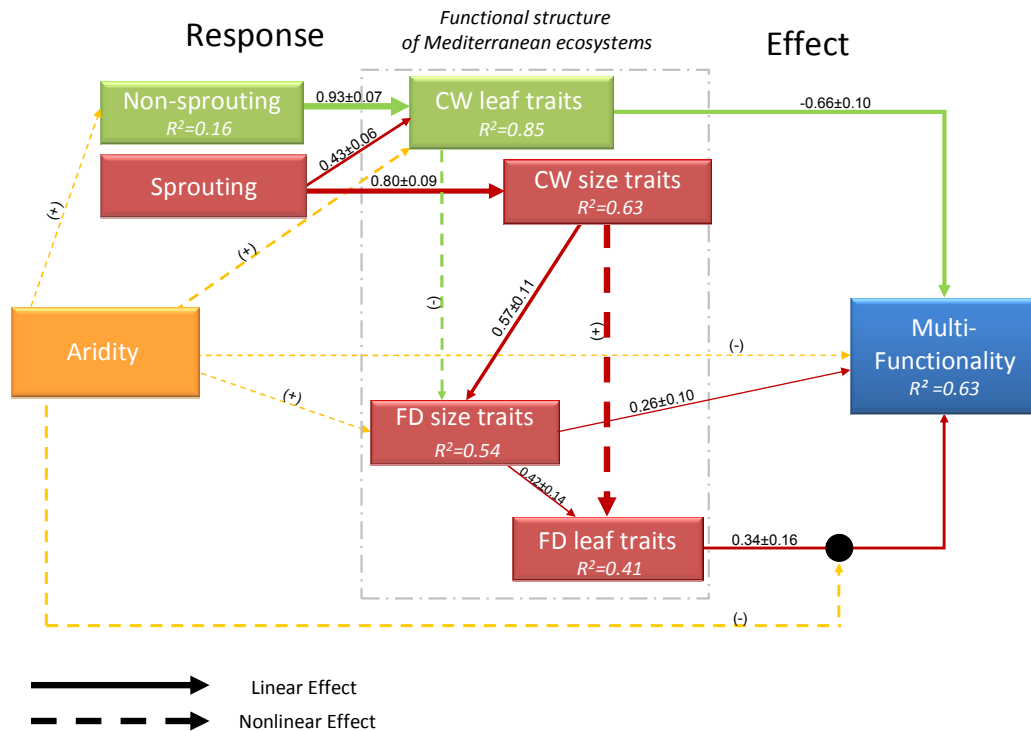
834

835 **Fig. 1.** Hypothetical relationships between aridity, shrub encroachment and the
 836 functional structure and multifunctionality of dryland communities. Aridity and shrub
 837 encroachment directly impact multifunctionality (a). The left part of the figure
 838 represents the response of the plant community to both variables (CWM: mean trait
 839 distribution [b]; FD: functional diversity [c]; and co-variation between CWT and FD
 840 [d]). Changes in community functional structure promote effects on multifunctionality
 841 via two non-exclusive mechanisms, mass-ratio process (e) and niche complementary (f).
 842 The red unimodal distributions represent a hypothetical trait distribution within a
 843 community *i* in a given environmental condition. The blue distributions represent the
 844 impact on trait distribution produced by contrasted levels of aridity and shrub
 845 encroachment in a community *j* compared to community *i*. See Appendix S1 for a
 846 detailed rationale of the different relationships depicted in the figure.



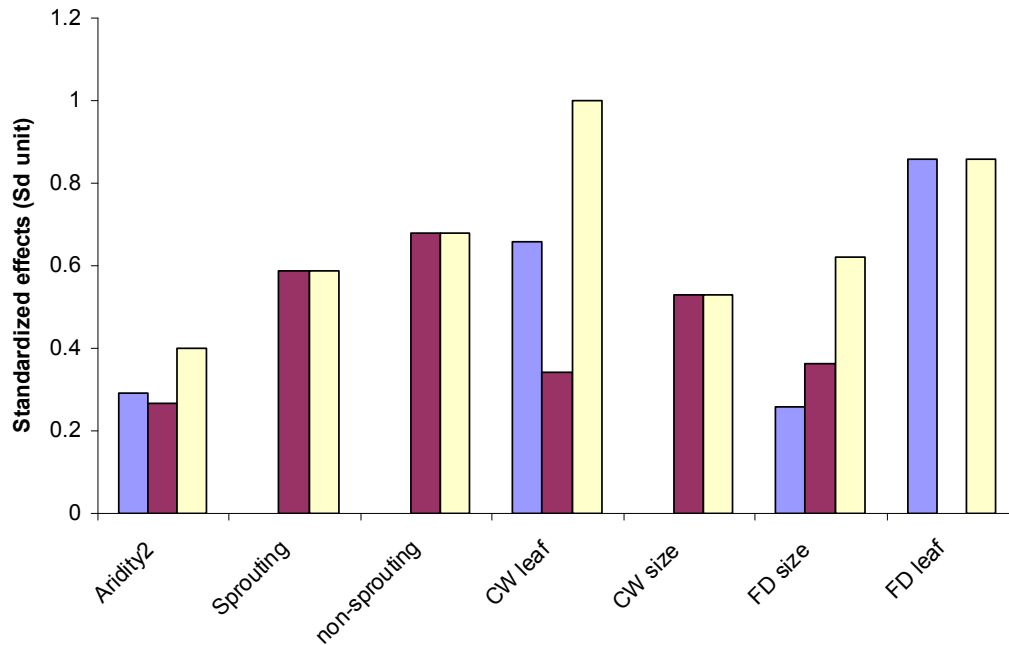
847

848 **Fig. 2.** Principal component analysis (PCA) of Community-Weighted Mean Trait (a)
 849 and Functional Diversity values (b). Light grey dots represent communities dominated
 850 by grass species, dark dots are communities dominated by shrub species. BD =
 851 branching density (number of main stems); Br = number of ramifications per stem; LA
 852 = leaf area; LDMC = leaf dry matter content; LL = leaf length; LS = lateral spread; LT
 853 = leaf thickness; LW = leaf width; SLA = specific leaf area; VH = vegetative height.
 854 For each component we indicate the % of variance explained. See Table S5a for
 855 correlations among Community-Weighted Trait values and Table S5b for correlations
 856 among Functional Diversity Trait values. Furthermore, see Table S6a for correlation
 857 between Community-Weighted Traits values and two mean components of a PCA (a)
 858 and Table S6b for the different Functional Diversity Traits value traits values and two
 859 mean components of the PCA (b).



860

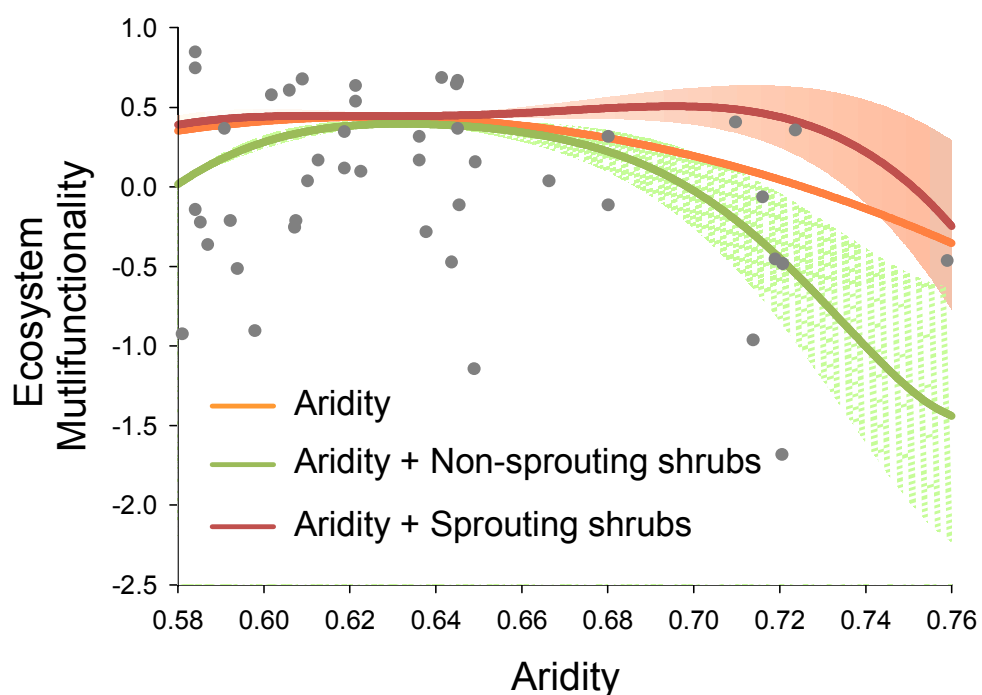
861 **Fig. 3.** Directed acyclic graph depicting the causal relationships between aridity (1-
 862 aridity index [precipitation/potential evapotranspiration]), the abundance of sprouting
 863 and non-sprouting shrubs, the functional structure of communities and
 864 multifunctionality. The width of each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



871

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

877



878

879 **Fig. 5.** Results of the sensitivity analysis carried out to evaluate the relationships
 880 between multifunctionality and aridity (1- aridity index [precipitation/potential
 881 evapotranspiration]) under different scenarios varying the abundance of shrub species.
 882 Scenario 1 (orange line) = grassland multifunctionality responses to aridity without
 883 shrubs; Scenario 2 (green line) = the abundance of non-sprouting shrubs is increased in
 884 grasslands and the abundance of sprouting shrubs is fixed at 0%; and Scenario 3 (red
 885 line) = the abundance of sprouting and non-sprouting shrubs is fixed at 30% and 0%,
 886 respectively. The shaded areas surrounding the lines are the 95% confidence intervals.
 887 The grey dots represent the position of the communities sampled around the aridity
 888 gradient.

889

890 **SUPPORTING INFORMATION**

891 The following Supporting Information is available for this article:

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

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

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

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

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

899 **Table S1.** Main characteristics of the study sites.

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

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

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

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

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

915

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

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

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

933 **RESPONSE**

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

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

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

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

959

960 **EFFECT**

961 *Arrow d*: in contrast, sprouting shrubs have been shown to increase multifunctionality
962 because their particular functional traits maximize multiple processes such as water
963 acquisition, water use efficiency, litter accumulation, and carbon storage (Maestre *et al.*,
964 2009; Eldridge *et al.*, 2011). Non-sprouting shrubs have been shown to decrease
965 multifunctionality, and in some cases accelerate desertification processes (Kefi *et al.*,

966 2007; Quero *et al.*, 2013). However, which traits mediate these effects is currently
967 unknown.

968 *Arrow e*: recent studies have shown that species diversity may increase ecosystem
969 multifunctionality (e.g. Gamfeldt *et al.*, 2008; Zavaleta *et al.*, 2010; Maestre *et al.*,
970 2012; Vos *et al.*, 2013). Mediterranean ecosystem are generally characterized by high
971 functional diversity respective to other biomes (Freschet *et al.*, 2011) which, together
972 with the fact that functional diversity may increase ecosystem multifunctionality,
973 suggests that functional diversity might be important in driving multiple ecosystem
974 processes in drylands.

975

976 **Literature Cited**

977 **Amat B, Cortina J, Zubcoff JJ. 2014.** Community attributes determine facilitation
978 potential in a semi-arid steppe. *Perspectives in Plant Ecology, Evolution and*
979 *Systematics*. doi:10.1016/j.ppees.2014.10.001

980 **Butterfield BJ, Briggs JM. 2011.** Regeneration niche differentiates functional
981 strategies of desert woody plant species. *Oecologia* **165**: 477-487.

982 **Cornwell WK, Ackerly DD. 2009.** Community assembly and shifts in plant trait
983 distributions across an environmental gradient in coastal California. *Ecological*
984 *Monographs* **79**: 109–126.

985 **Delgado-Baquerizo M, Maestre FT, Gallardo A, Bowker MA, Wallenstein M,**
986 **Quero JL, Soliveres S, Ochoa V, Gozalo B, García-Gómez M *et al.* 2013.**
987 Decoupling of soil nutrient cycles as a function of aridity in global
988 drylands. *Nature* **502**: 672-676.

- 989 **Díaz S, Lavorel S, de Bello F, Quétier F, Grigulis K, Robson TM. 2007.**
990 Incorporating plant functional diversity effects in ecosystem services assessments.
991 *Proceedings of the National Academy of Sciences* **104**: 20684-20689.
- 992 **Eldridge DJ, Bowker MA, Maestre FT, Roger E, Reynolds JF, Whitford WG.**
993 **2011.** Impacts of shrub encroachment on ecosystem structure and functioning: towards
994 a global synthesis. *Ecology Letters* **14**: 709–722.
- 995 **Ferran A, Delitti W, Vallejo VR. 2005.** Effects of fire recurrence in *Quercus coccifera*
996 L. shrublands of the Valencia Region (Spain): II plant and soil nutrients. *Plant Ecology*
997 **177**: 71–83.
- 998 **Freschet GT, Dias AT, Ackerly DD, Aerts R, van Bodegom PM, Cornwell WK,**
999 **Dong M, Kurokawa H, Liu G, Onipchenko VG et al. 2011.** Global to community
1000 scale differences in the prevalence of convergent over divergent leaf trait distributions
1001 in plant assemblages. *Global Ecology and Biogeography* **20**: 755-765.
- 1002 **Gamfeldt L, Hillebrand H, Jonsson PR. 2008.** Multiple functions increase the
1003 importance of biodiversity for overall ecosystem functioning. *Ecology* **89**: 1223-1231.
- 1004 **García-Fayos P, Gasque M. 2002.** Consequences of a severe drought on spatial
1005 patterns of woody plants in a two-phase mosaic steppe of *Stipa tenacissima* L. *Journal*
1006 *of Arid Environments* **52**: 199-208.
- 1007 **Gross N, Kunstler G, Liancourt P, de Bello F, Suding KN, Lavorel S. 2009.** Linking
1008 individual response to biotic interactions with community structure: a trait-based
1009 framework. *Functional Ecology* **23**: 1167–1178.
- 1010 **Gross N, Börger L, Soriano-Morales SI, Bagousse-Pinguet YL, Quero JL, García-**
1011 **Gómez M, Valencia-Gómez E, Maestre FT. 2013.** Uncovering multiscale effects of
1012 aridity and biotic interactions on the functional structure of Mediterranean
1013 shrublands. *Journal of Ecology* **101**: 637-649.

- 1014 **Keddy PA. 1992.** Assembly and response rules: two goals for predictive community
1015 ecology. *Journal of Vegetation Science* **3**: 157–164.
- 1016 **Kéfi S, Rietkerk M, Alados CL, Pueyo Y, Papanastasis VP, ElAich A, De Ruiter,**
1017 **PC. 2007.** Spatial vegetation patterns and imminent desertification in Mediterranean
1018 arid ecosystems. *Nature* **449**: 213-217.
- 1019 **Lavorel S, Garnier E. 2002.** Predicting changes in community composition and
1020 ecosystem functioning from plant traits: revisiting the Holy Grail. *Functional Ecology*
1021 **16**: 545–556.
- 1022 **Maestre FT, Bautista S, Cortina J, Bellot J. 2001.** Potential for using facilitation by
1023 grasses to establish shrubs on a semiarid degraded steppe. *Ecological Applications* **11**:
1024 1641-1655.
- 1025 **Maestre FT, Puche MD, Bowker MA, Hinojosa MB, Martínez I, García-Palacios**
1026 **P, Castillo AP, Soliveres S, Luzuriaga AL, Sánchez AM et al. 2009.** Shrub
1027 encroachment can reverse desertification in Mediterranean semiarid grasslands. *Ecology*
1028 *Letters* **12**: 930–941.
- 1029 **Maestre FT, Quero JL, Gotelli NJ, Escudero A., Ochoa V, Delgado-Baquerizo,**
1030 **García-Gómez M, Bowker MA, Soliveres S, Escolar C et al. 2012.** Plant species
1031 richness and ecosystem multifunctionality in global drylands. *Science* **335**: 214-2188.
- 1032 **Maire V, Gross N, Börger L, Proulx R, Wirth C, Pontes LdaS, Soussana JF,**
1033 **Louault F. 2012.** Habitat filtering and niche differentiation jointly explain species
1034 relative abundance within grassland communities along fertility and disturbance
1035 gradients. *New Phytologist* **196**: 497-509.
- 1036 **Quero JL, Maestre FT, Ochoa V, García-Gómez M, Delgado-Baquerizo M. 2013.**
1037 **On the Importance of Shrub Encroachment by Sprouters, Climate, Species Richness and**

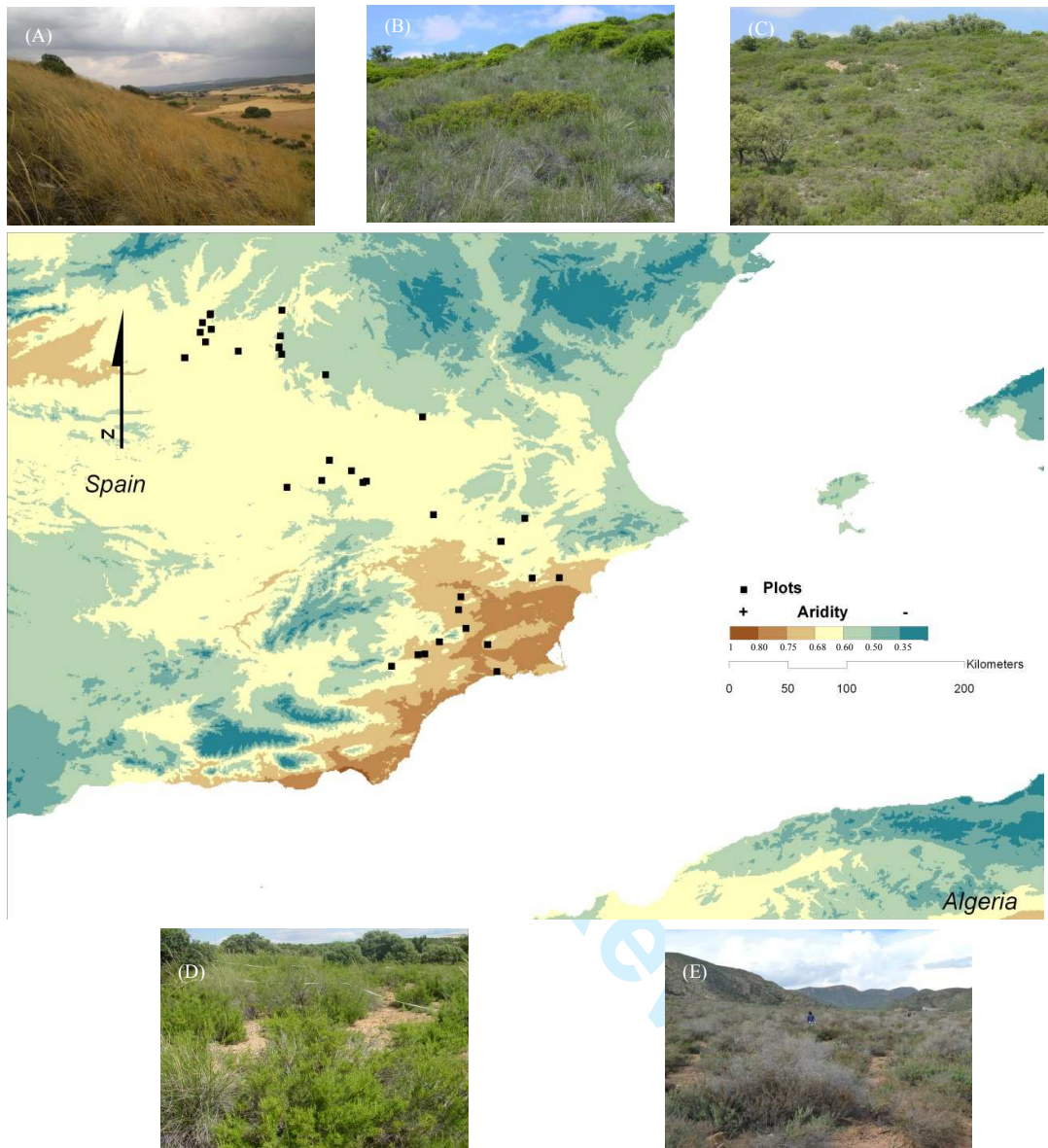
- 1038 Anthropoc Factors for Ecosystem Multifunctionality in Semi-arid Mediterranean
1039 Ecosystems. *Ecosystems* **16**: 1248-1261.
- 1040 **Soliveres S, Eldridge DJ, Maestre FT, Bowker MA, Tighe M, Escudero A. 2011.**
1041 Microhabitat amelioration and reduced competition among understorey plants as drivers
1042 of facilitation across environmental gradients: Towards a unifying framework.
1043 *Perspectives in Plant Ecology, Evolution and Systematics* **13**: 247–258.
- 1044 **Suding KN, Lavorel S, Chapin FS, Cornelissen JH, Diaz S, Garnier E, Goldberg D,**
1045 **Hooper DU, Jackson ST, Navas ML. 2008.** Scaling environmental change through the
1046 community-level: a trait-based response-and-effect framework for plants. *Global*
1047 *Change Biology* **14**: 1125-1140.
- 1048 **Valiente-Banuet A, Rumebe AV, VerdúM, Callaway RM. 2006.** Quaternary Plant
1049 lineages sustain global diversity by facilitating Tertiary lineages. *Proceedings of the*
1050 *National Academy of Sciences* **103**: 16812-16817.
- 1051 **Vos VC, van Ruijven J, Berg MP, Peeters ET, Berendse F. 2013.** Leaf litter quality
1052 drives litter mixing effects through complementary resource use among detritivores.
1053 *Oecologia* **173**: 269-280.
- 1054 **Zavaleta ES, Pasari JR, Hulvey KB, Tilman GD. 2010.** Sustaining multiple
1055 ecosystem functions in grassland communities requires higher biodiversity. *Proceedings*
1056 *of the National Academy of Sciences* **107**: 1443-1446.
- 1057

1058

1059

1060

1061



1062

1063

1064

1065

1066

1067 **Figure S1.** Map with the location of the study sites along the aridity gradient evaluated.

1068 Pictures indicate examples of the different types of communities along the aridity



1069 gradient (1- aridity index [precipitation/potential evapotranspiration]): (A) Grassland

1070 dominated by *Stipa tenacissima*; (B) Grassland with sprouting shrubs; (C) Shrublands

1071 dominated by *Rosmarinus officinalis* with sprouting shrubs; (D) Shrublands dominated

1072 by *Rosmarinus officinalis* with *Stipa tenacissima*; (E) Shrublands dominated by summer

1073 deciduous shrubs species.

<p>Sprouting shrubs:</p> <ul style="list-style-type: none"> - Resprout after a fire - Long-lived species - They have a well-developed root system because they occupy the same space for a long time. <p>Examples of species: <i>Quercus coccifera</i>, <i>Juniperus oxycedrus</i> <i>Pistacia lentiscus</i> and <i>Rhamnus lycioides</i></p>  <p><i>Quercus coccifera</i></p>	<p>Non-sprouting shrubs:</p> <ul style="list-style-type: none"> -Obligate seeders (survive fire as a dormant seed pool in the soil) -Suffer mortality after fires - Do not have a well-developed root system <p>Examples of species: <i>Rosmarinus officinalis</i>, <i>Artemisia herba-alba</i> and <i>Globularia alypum</i></p>  <p><i>Rosmarinus officinalis</i></p>
--	--

1074

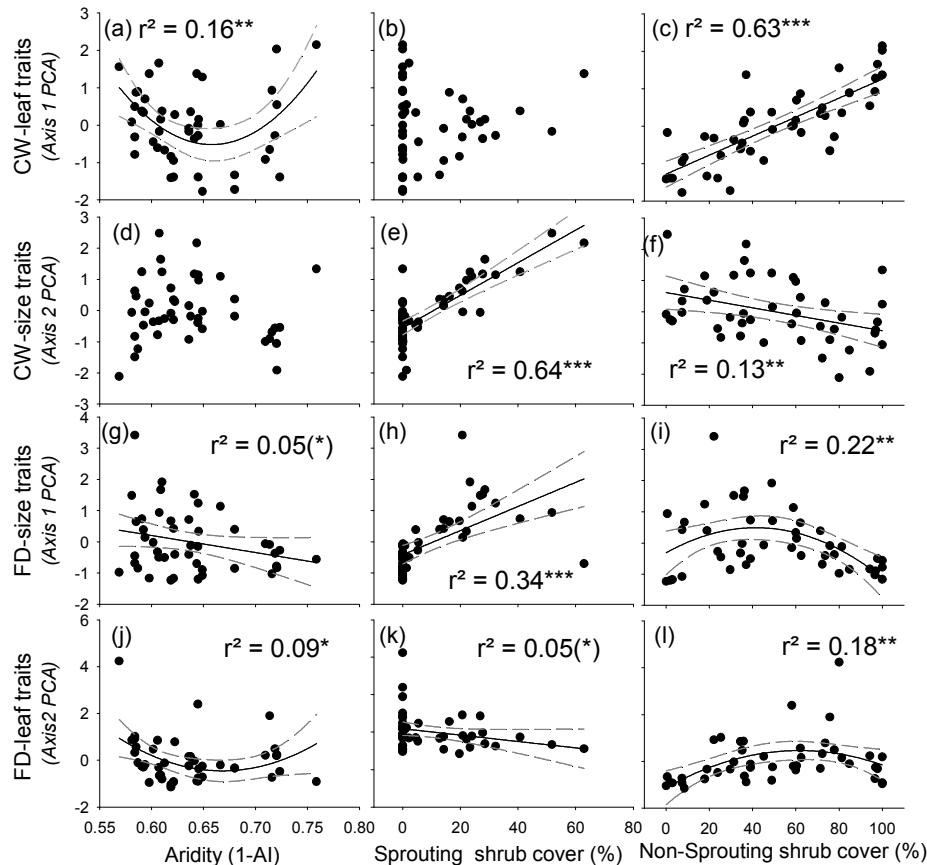
1075 **Figure S2.** Differences between non-sprouting and sprouting shrubs (based on Keeley
1076 & Zedler 1978).

1077

1078 **Literature Cited**

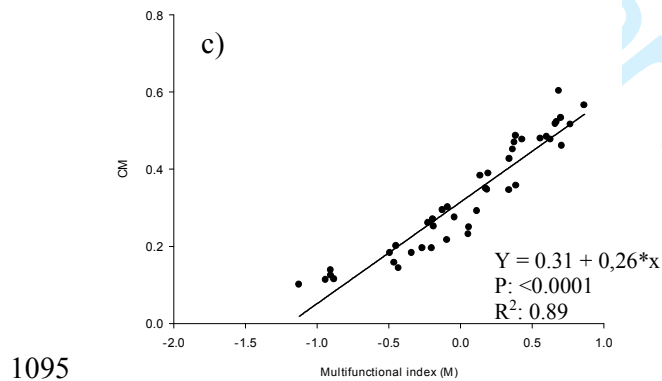
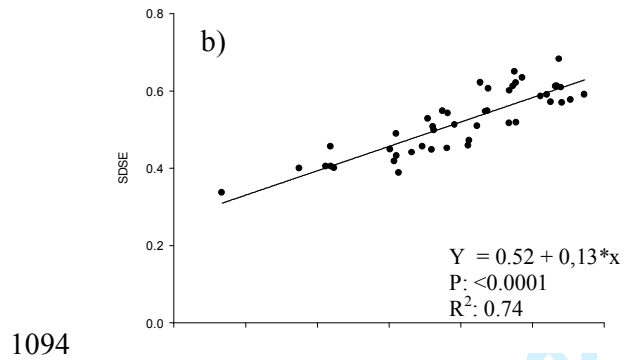
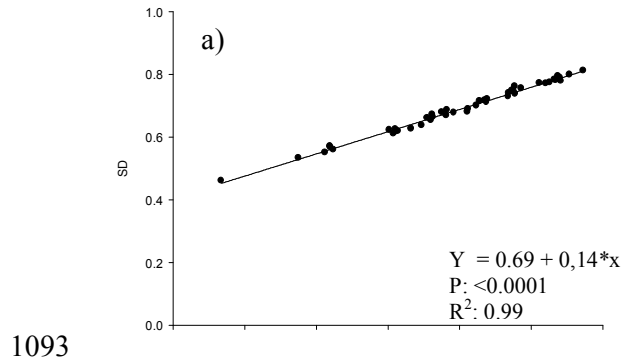
1079 **Keeley JE, Zedler PH. 1978.** Reproduction of chaparral shrubs after fire: a comparison
1080 of sprouting and seeding strategies. *American Midland Naturalist* **99**: 142-161.

1081



1082

1083 **Figure S3.** Responses to aridity (1- aridity index [precipitation/potential
 1084 evapotranspiration]) and shrub encroachment of community weighed traits (CWT) and
 1085 functional diversity (FD) evaluated with leaf and size related traits. Co-variations
 1086 among traits are shown in Fig. 2 for CWT and FD. Community responses to: aridity (1-
 1087 Aridity Index [AI]) are shown in panels (a, d, g, j); responses to shrub encroachment
 1088 separating sprouting shrub and non-sprouting shrub are shown in panels (b, e, h, k) and
 1089 (c, f, i, l) respectively. The black solid line indicates significant ($P < 0.05$) relationships;
 1090 the grey dash lines show 95% confidence intervals in these cases. We provided the R^2 of
 1091 the linear regression in each panel. (*) $P < 0.09$; * $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$.
 1092



1096 **Figure S4.** Relationships between our multifunctionality index based on the average of
 1097 Z-scores of ecosystem functions and other multifunctionality indices: a) the average of
 1098 multiple functions, previously standardized by dividing by the maximum (SD, Mouillot
 1099 *et al.*, 2011); b) this average minus the standard deviation (SDSE, Pasari *et al.*, 2011);
 1100 and (c) the cross-multiplied ten soil variables previously standardized by dividing by the
 1101 maximum (CM, Bowker *et al.*, 2013).

1102

1103

1104 **Literature Cited**

1105 **Bowker MA, Maestre FT, Mau RL. 2013.** Diversity and patch-size distributions of
1106 biological soil crusts regulate dryland ecosystem multifunctionality. *Ecosystems* **16:**
1107 923-933.

1108 **Mouillot D, Vileger S, Scherer-Lorenzen M, Mason NWH. 2011.** Funcional
1109 Structure of Biological Communities Predicts Ecosystem Multifunctionality. *Plos one*
1110 **6:** e17476.

1111 **Pasari JR, Levi T, Zavaleta ES, Tilman D. 2013.** Several scales of biodiversity affect
1112 ecosystem multifunctionality. *Proceedings of the National Academy of Sciences* **110:**
1113 10219-10222.

1114

1115 **Table S1.** Main characteristics of the study sites. Climate variables were extracted from
 1116 the Worldclim global database (www.worldclim.org) and Global Aridity Index
 1117 (Trabucco and Zomer, 2009).

COD	LAT	LON	ELE	SLO	AMT	RAI	AI	ARIDITY	CBA	TCT	NSS	SS
1	37°35'35.04"N	1°13'56.57"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	38°09'54.31"N	1°30'32.36"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

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

1118 COD = Code of the plot, LAT = latitude (WGS84 datum), LON = longitude (WGS84
1119 datum), ELE = elevation (m), SLO = slope (°), AMT = annual mean temperature, RAI =
1120 annual precipitation, AI = Aridity index (precipitation/potential evapotranspiration),
1121 ARIDITY = 1-AI, CBA= Cover of bare areas (%), TCT = total perennial cover (%),
1122 NSS= Relative cover of non-sprouting shrubs (%), SS= Relative cover of sprouting
1123 shrubs (%).

1124

1125

1126

1127

1128 **Literature Cited**

1129 **Hijmans RJ, Cameron SE, Parra JL, Jones PG, Jarvis A. 2005.** Very high resolution
1130 interpolated climate surfaces for global land areas. *International journal of climatology*
1131 **25:** 1965–1978.

1132 **Trabucco A, Zomer RJ. 2009.** Global Aridity Index (Global-Aridity) and Global
1133 Potential Evapo-Transpiration (Global-PET) Geospatial Database. CGIAR Consortium
1134 for Spatial Information. Published online, available from the CGIAR-CSI GeoPortal at:
1135 <http://www.csi.cgiar.org>

1136

1137 **Table S2.** Stepwise procedure to evaluate the responses of community weighed mean
 1138 (CWM) and functional diversity (FD) evaluated with leaf and size related traits to
 1139 aridity (1- aridity index [precipitation/potential evapotranspiration]) and shrub
 1140 encroachment. We evaluated a quadratic term when it was significant. **We also assessed**
 1141 **the effect of slope on multifunctionality; this variable was not selected in any *a priori***
 1142 **models (data not shown) and thus was removed from the final analyses.** Est: direction of
 1143 relationship; DF: degree of freedom; % of r^2 : variance decomposition analysis based on
 1144 the sum of squares.

	model mass ratio				model niche complementary				model combined hypothesis			
	(hypothesis i)				(hypothesis ii)				(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		

1145

1146 **Table S3.** Conditional independence tests applied in the different hypothesis of the d-
 1147 sep model implied by the hypothesized path models.

D-sep claim of Independence	Model formula S	Ho	P	C	P of C
				statistic	(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) {∅}	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		

(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) {∅}	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) {∅}	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*FD2) + (AI ² *FD2)	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

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

1148 *Notes:* Key to variables: NSS = non-sprouting shrubs, SS = sprouting shrubs, ARI = (1-
1149 aridity index [precipitation/potential evapotranspiration]), CWM1 = community
1150 weighted leaf trait, CWM2 = community weighted size trait, FD1 = functional
1151 dispersion size trait, FD2 = functional dispersion leaf trait, M = Multifunctionality
1152 index. \$ = The associated mixed model regression for each d-sep claim using the lm
1153 function in R to test the independence claims. The *P* value is obtained by comparing the
1154 value of the C statistic for each hypothesis to a chi-square distribution with the same
1155 degrees of freedom – note that a model is rejected if the C statistic is significantly
1156 different from the χ^2 value.
1157

1158 **Table S4.** Results of Pearson correlation coefficients between the different soil
 1159 variables (our surrogates of ecosystem functions) used to calculate the
 1160 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

1161

1162 Significance levels are as follows: * $p < 0.05$ and ** and $p < 0.01$.

1163 ORC: organic carbon; HEX: hexoses; PEN: pentoses; BGL: β -glucosidase extracellular
 1164 activity; TP: total phosphate; P_HCL: Olsen phosphate (inorganic P – HCL 1M); AVP:
 1165 available inorganic phosphate; FOS: phosphatase activity; TON: total nitrogen; AVN:
 1166 total available nitrogen; AMI: aminoacids; PRO: proteins and MIN: net potential
 1167 mineralization rate.

1168

1169 **Table S5.** Results of Pearson correlation coefficients among a) community-weighted
 1170 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

1171

b)	FDSL	FDVH	FDLA	FDLT	FDLW	FDLMDC	FDBr	FDBD	FDLS
FDSL									
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

1172 Significance levels are as follows: * $p < 0.05$ and ** and $p < 0.01$.

1173 SLA = specific leaf area; VH = vegetative height; LA = leaf area; LT = leaf thickness;

1174 LW = leaf width; LDMC = leaf dry matter content; Br = number of ramifications per

1175 stem; BD = branching density (number of main stems); LS = lateral spread; LL = leaf

1176 length.

1177

1178 **Table S6.** Results of Pearson correlation coefficients between a) different community-
 1179 weighted (CW) traits values and two mean components of a Principal Component
 1180 Analysis (component 1: CW-leaf traits and component 2: CW-size traits); b) different
 1181 functional diversity (FD) traits values and two mean components of a Principal
 1182 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**
LDMC	-0.85**	0.02
Br	0.84**	0.23
BD	-0.02	-0.64**
LS	-0.01	0.89**
LL	-0.94**	0.08

1183

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

1184 Significance levels are as follows: * $p < 0.05$ and ** and $p < 0.01$.

1185 SLA = specific leaf area; VH = vegetative height; LA = leaf area; LT = leaf thickness;

1186 LW = leaf width; LDMC = leaf dry matter content; Br = number of ramifications per

1187 stem; BD = branching density (number of main stems); LS = lateral spread; LL = leaf

1188 length.