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# Phylogenetic, functional, and taxonomic richness have both positive and negative effects on ecosystem multifunctionality

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1 **Running head: biodiversity attributes and multifunctionality**

2 **Title: Phylogenetic, functional and taxonomic richness have both positive and negative**  
3 **effects on ecosystem multifunctionality**

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23 **Abstract**

24 Biodiversity encompasses multiple attributes such as the richness and abundance of species  
25 (taxonomic diversity), the presence of different evolutionary lineages (phylogenetic diversity),  
26 and the variety of growth forms and resource-use strategies (functional diversity). These  
27 biodiversity attributes do not necessarily relate to each other, and may have contrasting effects  
28 on ecosystem functioning. However, how they simultaneously influence the provision of  
29 multiple ecosystem functions related to carbon, nitrogen and phosphorus cycling  
30 (multifunctionality) remains unknown. We evaluated the effects of the taxonomic, phylogenetic  
31 and functional attributes of dominant (mass-ratio effects) and subordinate (richness effect) plant  
32 species on the multifunctionality of 123 drylands from six continents. Our results highlight the  
33 importance of the phylogenetic and functional attributes of subordinate species as key drivers  
34 of multifunctionality. In addition to a higher taxonomic richness, we found that simultaneously  
35 increasing the richness of early diverging lineages and the functional redundancy between  
36 species increased multifunctionality. In contrast, the richness of most recent evolutionary  
37 lineages and the functional and phylogenetic attributes of dominant plant species (mass-ratio  
38 effects) were weakly correlated with multifunctionality. However, they were important drivers  
39 of individual nutrient cycles. By identifying which biodiversity attributes contribute the most  
40 to multifunctionality, our results can guide restoration efforts aiming to maximize either  
41 multifunctionality or particular nutrient cycles, a critical step to combat dryland desertification  
42 worldwide.

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48 **Significance**

49 Biodiversity is declining globally, but its different taxonomic, functional and evolutionary  
50 attributes are doing so at a different pace. Understanding how these attributes influence  
51 ecosystem functioning is crucial to better predict the ecological consequences of biodiversity  
52 loss. Based on a survey of 123 drylands worldwide, our results highlight the phylogenetic and  
53 functional attributes of subordinate species as key drivers of the provision of multiple  
54 ecosystem functions simultaneously (multifunctionality). Our study expands our understanding  
55 of the relationship between biodiversity and multifunctionality by identifying the diversity of  
56 early diverging lineages and functional redundancy as important biodiversity attributes to  
57 prioritize in conservation and restoration programs aimed at promoting dryland  
58 multifunctionality worldwide.

59

60 **Key-words**

61 Functional diversity | Mass-ratio hypothesis | **Nutrient cycling** | Phylogenetic diversity |  
62 Taxonomic diversity.

63

64 \body

## 65 **Introduction**

66 Understanding the relationship between biodiversity and the capacity of ecosystems to perform  
67 multiple functions simultaneously (multifunctionality) has been a core ecological research topic  
68 in the last decade (1–4). In recent years, considerable research efforts have been devoted to  
69 explore how the biodiversity – ecosystem multifunctionality relationship (B-EMF relationship  
70 hereafter) is contingent upon the number and identity of ecosystem functions considered (e.g.,  
71 refs. (5, 6)). In contrast, how multiple attributes of biodiversity such as the richness and  
72 abundance of species (taxonomic diversity), the diversity of evolutionary lineages  
73 (phylogenetic diversity) and that of the traits related to resource-use strategy (functional  
74 diversity) simultaneously influence ecosystem functioning remains poorly investigated (7–11),  
75 particularly at the global scale. Since these biodiversity attributes do not necessarily correlate  
76 (12, 13), assessing how they simultaneously influence multifunctionality is not only crucial to  
77 expand our fundamental understanding of the B-EMF relationships, but also to prioritize  
78 relevant biodiversity attributes in global conservation programs, and to improve management  
79 actions to preserve and restore terrestrial ecosystems (12, 14).

80 While most B-EMF studies have focused on species richness (1–3), functional diversity  
81 is also a key driver of multifunctionality (15–17). Higher functional diversity could enhance  
82 multifunctionality either because co-occurring species with contrasting trait values increase the  
83 overall resource utilization (18) or by including species that strongly affect ecosystem  
84 functioning (“sampling effect”; ref. (19)). The phylogenetic diversity of plant communities can  
85 also influence ecosystem functions such as biomass production (7, 8). However, how  
86 phylogenetic diversity influences the B-EMF relationships remains unclear (20), and we do not  
87 know whether early diverging *vs.* recent evolutionary events ultimately influence ecosystem  
88 functioning (21). Phylogenetic diversity is a key biodiversity attribute when it effectively  
89 encompasses unmeasured biological traits that are relevant for ecosystem functioning (7, 22).

90 As such, considering simultaneously phylogenetic diversity, which often grasps traits that are  
91 not typically measured (e.g. those related to plant-pathogen or plant-mycorrhiza interactions  
92 (23, 24), and measured traits could better account for the many dimensions of trait diversity  
93 exhibited by plant species (7, 13). Therefore, doing so could provide greater insights on how  
94 the multidimensionality of biodiversity influences multifunctionality.

95 No matter the taxonomic, phylogenetic or functional attribute of biodiversity we look  
96 at, focusing solely on richness ignores the overwhelming effect that dominant species may have  
97 on ecosystem functioning (25, 26). According to the mass-ratio hypothesis (25), the effect of  
98 plant species on ecosystem functioning is directly proportional to their biomass (mass-ratio  
99 effects), and thus is relatively insensitive to the richness of subordinate species (25). This  
100 hypothesis was originally framed for individual functions related to biomass production and  
101 carbon cycling (25–27). However, the importance of the dominant species seems less clear  
102 when focusing on multifunctionality (28, 29), as it may depend on the attribute of biodiversity  
103 or the function considered.

104 To better understand the functional consequences of biodiversity changes occurring  
105 worldwide, we gathered data from 123 dryland ecosystems from six continents, including  
106 steppes, savannas and shrublands (*SI Appendix*, Fig. S1), to investigate how multiple plant  
107 diversity attributes simultaneously influence multifunctionality. We used eight complementary  
108 biodiversity metrics that account for changes in the taxonomic, phylogenetic (early diverging  
109 and recent lineages) and functional diversity of plant communities (see methods; *SI Appendix*,  
110 Fig. S2, Tables S1 and S2). Within this framework, our selection included metrics that were  
111 weighted and non-weighted by species abundance to disentangle the effect of dominant (mass-  
112 ratio effects) vs. that of subordinate (richness effects) plant species on multifunctionality. After  
113 controlling for important climatic, soil and geographic variables, we related multiple  
114 biodiversity metrics to four indices of multifunctionality using the multiple thresholds approach

115 (30). The four indices were: 1) multifunctionality (based on 11 weakly correlated functions), 2)  
116 carbon cycling (C; including organic carbon concentration; pentose content and aboveground  
117 plant productivity), 3) nitrogen cycling (N; including nitrate concentration, dissolved organic  
118 nitrogen, protein content and potential nitrification) and 4) phosphorus cycling (P; including  
119 available, inorganic and total phosphorus, and phosphatase enzymatic activity) (*SI Appendix*,  
120 Table S3). We tested the core hypothesis that considering multiple biodiversity attributes  
121 simultaneously increases the strength of biodiversity effects on multifunctionality.

122

## 123 **Results**

124 The biodiversity metrics studied were strongly related to multifunctionality, **even after**  
125 **accounting for the strong influence of geographic, climate and soil properties on ecosystem**  
126 **functioning** (Fig. 1). Biodiversity attributes explained up to 18% of multifunctionality (total  
127 variance), and up to 25%, 22% and 27% of the variation in the indices derived for C, N and P  
128 cycling, respectively. While species richness alone explained on average ~ 5% of variation in  
129 multifunctionality and up to 8% for C cycling, the inclusion of multiple biodiversity attributes  
130 enhanced the effect of biodiversity on multifunctionality by three-fold. Functional,  
131 phylogenetic and taxonomic biodiversity attributes were all selected in the most parsimonious  
132 models as significant predictors of multifunctionality, indicating that they have complementary  
133 effects on C, N and P cycling.

134 Richness effects [the sum of explained variance of species richness and of non-weighted  
135 functional (FDIS) and phylogenetic (PSV, MNTD) metrics] explained between 76-100% of the  
136 biotic effects on multifunctionality (Fig. 2a). In contrast, the importance of dominant species  
137 through mass-ratio effects (i.e. the metrics weighted by the abundance of the species) increased  
138 when considering each nutrient cycle individually (Fig. 2b, c, d). Mass-ratio effects contributed,  
139 on average, to 51%, 41% and 63% of the explained variance for C, N and P cycling,

140 respectively. Mass-ratio effects were mostly related to the functional identity (CWM-SLA and  
141 CWM-H) of dominant species rather than to their functional/phylogenetic diversities. In  
142 summary, richness effects due to subordinate species were the strongest predictors of  
143 multifunctionality, while mass-ratio effects better explained C, N and P cycling separately.

144 The net relationship between biodiversity and multifunctionality was generally positive,  
145 although weak, and even null when high multifunctionality thresholds were considered (Fig.  
146 3a). This result was consistent regardless of the number of biodiversity attributes considered  
147 (Fig. 4) but varied with the nutrient studied. Thus, despite the larger amount of variance  
148 explained (Fig. 1), the net effect of biodiversity on ecosystem functioning was not stronger  
149 when multiple biodiversity attributes were included (Fig. 4). The inconsistency between  
150 variance explained and the net effect observed was mainly caused by contrasting effects of  
151 individual biodiversity attributes on different nutrient cycles taken separately and on overall  
152 multifunctionality.

153 When evaluating the sets of functions separately, we observed positive relationships  
154 between biodiversity and C and P cycling (Fig. 3b and d), which turned negative in the case of  
155 N cycling (Fig. 3c). In addition, we observed contrasting relationships depending on the  
156 biodiversity attribute considered (Fig. 5). Species richness and phylogenetic diversity (PSV)  
157 were positively related to multifunctionality (Fig. 5a), and to C, N and P cycling (Fig. 5b, c, d).  
158 However, FDIS (describing the dispersion of functional trait values observed within  
159 communities) was negatively related to multifunctionality, C and N cycling. These results  
160 highlight that particular combinations of biodiversity attributes are needed to maximize either  
161 targeted nutrient cycles or overall multifunctionality.

162

## 163 **Discussion**



164 We investigated how multiple biodiversity attributes (taxonomic, phylogenetic and functional  
165 richness and mass-ratio effects) simultaneously influenced the multifunctionality of 123  
166 drylands worldwide. Together, these attributes explained up to 27% of variation in  
167 multifunctionality **across a wide range of geographic contexts, climatic and soil conditions**. The  
168 simultaneous effect of multiple biodiversity attributes on multifunctionality stresses the need to  
169 move from a single taxonomic to a more multidimensional perspective of biodiversity to better  
170 grasp its complex effects on the functioning of terrestrial ecosystems. The importance of  
171 considering multiple biodiversity attributes has been recently shown for biomass production  
172 and its temporal variability, or for N availability (9–11, 31). Our results expand this research  
173 by highlighting how multiple biodiversity attributes differentially impact both  
174 multifunctionality and major nutrient cycles at the global scale.

175 Our study helps to reconcile two influential hypotheses on the effects of biodiversity on  
176 ecosystem functioning (19, 25). Mass-ratio effects (i.e., the abundance-weighted metrics  
177 considered, accounting for the effect of the most dominant species) were the strongest  
178 predictors related to individual nutrient cycles, but were weakly correlated with  
179 multifunctionality. As such, the Mass-ratio hypothesis may not apply when considering  
180 multiple functions simultaneously (see also ref. (28)). In contrast, richness effects (those mainly  
181 driven by subordinate species) were the almost exclusive biotic drivers of multifunctionality in  
182 the drylands studied. Our results show that richness effects increase in importance when aiming  
183 at maximizing multiple ecosystem functions simultaneously. This matches the common view  
184 that species are unique, i.e. that a high number of co-occurring subordinate species can promote  
185 different functions at different times and places, therefore maximising the performance of  
186 multiple functions simultaneously (1, 2, 5, 6). Our study extends the view of taxonomic  
187 diversity to the phylogenetic and functional attributes of subordinate species as important  
188 predictors of multifunctionality in terrestrial ecosystems.

189 Biodiversity had an overall positive effect on multifunctionality when considering  
190 multiple biodiversity attributes simultaneously. However, and contrarily as hypothesized, this  
191 effect was relatively weak (Fig. 3a; Fig. 4). The observed weak B-EMF relationship resulted  
192 first from contrasting relationships among the sets of functions relating to different  
193 biogeochemical cycles (Fig. 3b, c and d). Also, we observed contrasting effects among the  
194 studied biodiversity attributes (Fig. 5). As a result, biodiversity effects on multifunctionality  
195 did not increase when considering multiple biodiversity attributes simultaneously (Fig. 4).  
196 These contrasting effects match with recent evidences reporting the occurrence of diverse  
197 (positive, neutral and negative) biodiversity – ecosystem functioning relationships in real world  
198 ecosystems, especially when considering ecosystem functions other than plant biomass (4, 11,  
199 32, 33). Our findings highlight that B-EMF relationships do not only depend on the combination  
200 of functions studied (e.g., ref. (6)), but also on the identity of biodiversity attributes considered.  
201 Therefore, ignoring the variety of attributes that biodiversity encompasses, such as taxonomic,  
202 phylogenetic and functional diversity, or the influence of subordinate vs. dominant species may  
203 largely bias our ability to predict the consequences of biodiversity loss for the functioning of  
204 terrestrial ecosystems.

205 In opposition to the positive effect of species richness on multifunctionality and on C,  
206 N and P cycling, functional richness (FDIS: the trait dispersion within communities) was  
207 negatively related to multifunctionality, C and N cycling (Fig. 5). This negative effect of FDIS  
208 is in line with previous observed negative effects of trait dispersion on dryland  
209 multifunctionality (17), as well as on the production and stability of biomass in several  
210 ecosystems (7, 10, 31). The contrasting effect between species richness and FDIS highlights  
211 the importance of functional redundancy within the studied communities to maintain high  
212 multifunctionality levels. This may be particularly true for communities experiencing strong  
213 abiotic stress such as dryland plant communities. Maximizing functional redundancy between

214 species in drylands (31) may limit the inclusion of mal-adapted plant strategies particularly  
215 under drier conditions, which in turn may alter plant-soil feedbacks and accelerate land  
216 degradation and desertification processes (16, 17, 34).

217         Phylogenetic diversity played a significant role as driver of multifunctionality even after  
218 controlling for taxonomic and functional diversity, confirming the importance to consider this  
219 attribute in future B-EMF research. Phylogenetic diversity may reflect additional axes of  
220 functional specialization that are neither captured by maximum plant height nor by SLA, two  
221 fundamental traits reflecting plant resource-use strategies (35). Phylogenetic diversity may  
222 effectively take into account “hidden traits” that are particularly relevant for the functioning of  
223 drylands (e.g. traits related to pathogen infection, pollination rates or mycorrhizal associations  
224 (23) or to plant demographic strategies (36)) and thus are required to properly model B-EMF  
225 relationships. Dryland multifunctionality increased with a higher diversity of evolutionary  
226 lineages (PSV). The coexistence of species from both quaternary and tertiary periods are  
227 commonly observed in arid regions as a consequence of facilitative interactions (37). Also, PSV  
228 had opposite effects on multifunctionality compared to FDIS, indicating that maximizing both  
229 the phylogenetic distinctiveness and functional redundancy within species-rich communities  
230 are complementary drivers of higher ecosystem multifunctionality. Our results also reflect that  
231 evolutionary distinct lineages shared similar maximum plant height and SLA attributes (see  
232 also (38)). This pattern may arise from both species filtering with suitable trait values and the  
233 adaptive evolution of traits in local lineages. A deeper understanding of the role of these  
234 processes could shed light on the importance of natural selection and convergent evolution as  
235 key evolutionary processes involved in the functioning of dryland ecosystems.

236         To further understand the linkages between the diversity of evolutionary lineages and  
237 multifunctionality, we investigated such relationships both at the most recent evolutionary  
238 events (tip level: MNTD) and across the whole tree (PSV). This approach revealed that both

239 MNTD and PSV are related to ecosystem functioning in drylands worldwide (Figs. 1 and 5).  
240 While we observed exclusive effects of PSV on multifunctionality, those of MNTD were even  
241 stronger when considering individual nutrient cycles (positive and negative for C and N cycling,  
242 respectively). These B-EMF patterns indicate an increase in the importance of early diverging  
243 lineages with increasing the number of functions considered, i.e. that the diversity of more  
244 ancient lineages increases present-day multifunctionality. Alongside, recent evolutionary  
245 events might reflect recent innovations promoting C cycling and productivity (Fig. 5, *SI*  
246 *Appendix*, Tables S4 and S5) without altering the level of multifunctionality. Our study was not  
247 designed to specifically investigate the changes in B-EMF relationships over evolutionary  
248 times. Nonetheless, the contrasted B-EMF patterns observed at two phylogenetic scales open  
249 new horizons on the importance of species evolutionary history for the emergence of  
250 “multifunctional” ecosystems, e.g. for tracking when biodiversity became an important  
251 multifunctionality driver.

252 Our results emphasize the need to consider the multidimensionality of biodiversity to  
253 better understand B-EMF relationships. The biodiversity attributes involved in individual  
254 nutrient cycles were mostly related to mass-ratio effects. In contrast, richness effects enhanced  
255 multifunctionality through the diversity of early diverging lineages and functional redundancy  
256 within species-rich communities. In an era of global biodiversity crisis, our results can  
257 contribute to shape conservation, restoration and management efforts based on species  
258 attributes to prioritize targeted nutrient cycles or overall multifunctionality, and therefore  
259 optimizing the limited budgets allocated to maintain ecosystem functioning and associated  
260 services in drylands, the Earth’s largest biome.

261

262 **Methods**

263 **Characteristics of the study sites.** We obtained field data from 123 sites located in 13 countries  
264 (*SI Appendix*, Fig. S1). These sites (30 m x 30 m) are representative from the major vegetation  
265 types found in drylands and differ widely in plant species richness and environmental  
266 conditions (see further details in *SI Appendix*, Fig. S1).

267 **Ecosystem multifunctionality.** We assessed ecosystem functioning at each site using 11  
268 variables that provide a comprehensive and balanced design of C (organic C, pentose, plant  
269 productivity), N (nitrate, dissolved organic N, proteins, potential N transformation rate) and P  
270 (total and available P, activity of phosphatase and inorganic P) cycling and storage. These  
271 variables (hereafter functions) are uncorrelated with each other (see details in *SI Appendix*,  
272 Table S3), and together constitute a good proxy for nutrient cycling, biological productivity,  
273 and build-up of nutrient pools (3, 39–41).

274 We calculated four indices based either on all measured functions (multifunctionality)  
275 or on different set of functions representing C (three functions), N (four functions) and P (four  
276 functions) cycling (*SI Appendix*, Table S3). We standardized separately the 11 functions  
277 measured ( $F$ ) using the Z-score transformation:

$$278 \quad Z - score_{ij} = \frac{F_{ij} - Mean F_i}{SD F_i} \quad \text{Equation (2);}$$

279 where  $F_{ij}$  is the value of a function  $i$  in the community  $j$ ,  $Mean F_i$  and  $SD F_i$  are the mean and  
280 the standard deviation of the function  $F_i$  calculated for the 123 studied communities,  
281 respectively. We used a multiple threshold approach to evaluate whether multiple functions are  
282 simultaneously performing at high levels (30). In short, this approach counts the number of  
283 functions that reach a given threshold (as the % of the maximum value of each of the functions  
284 observed in the dataset). This maximum is taken as the top 5% values for each function  
285 observed across all study sites (42). Considering multiple thresholds allows a better  
286 understanding of how biodiversity affects ecosystem functioning, and to account for potential  
287 trade-offs between the functions evaluated (30). We considered thresholds between 20% and

288 80% (every 5%), since care should be taken to avoid over-interpreting results at very high or  
289 low thresholds (43). Each calculated threshold (T) was smoothed by using a moving average  
290 with intervals [T-10%, T+10%]. We used this approach for all functions together, and also for  
291 those that only relate to the C, N and P cycling. We also calculated multifunctionality as the  
292 average of the standardized values across all functions (3, 15), obtaining results similar to those  
293 presented in the main text (*SI Appendix*, Fig. S3).

294 **Plant diversity attributes and biodiversity metrics.** Biodiversity effects on ecosystem  
295 functioning can arise from 1) dominant plant species through mass-ratio effects (25), and 2)  
296 subordinate species through richness effects (19). Both mass-ratio and richness effects can  
297 encompass taxonomic, phylogenetic and functional attributes (*SI Appendix*, Fig. S2). To  
298 account for all these possible biodiversity effects, we included eight metrics that reflect the full  
299 spectrum of the attributes considered in our framework (*SI Appendix*, Figs. S2 and S4, and  
300 Table S1). These metrics were weakly correlated among themselves (Spearman's correlation  
301 coefficient < 0.6) and did not induce multicollinearity issues in our analyses (*SI Appendix*, Table  
302 S2). Studied metrics included taxonomic (species richness), functional [community-weighted  
303 mean for height and SLA (CWM.H and CWM.SLA), weighted and non-weighted functional  
304 dispersion (w.FDIS and FDIS)] and phylogenetic [phylogenetic species variability (PSV),  
305 weighted and non-weighted Mean Nearest Taxon Distance (w.MNTD and MNTD)] diversity  
306 (full methodological details in *SI Appendix*, Figs. S2 and S4).

307 The use of these metrics also allowed us to assess mass-ratio (i.e. the functional identity  
308 and diversity of dominant species; *sensu* ref. (25)) vs. richness effects by comparing abundance-  
309 weighted vs. non-weighted metrics. Considering MNTD and PSV allowed us to investigate  
310 whether ecosystem functioning relates to recent vs. early diverging evolutionary events,  
311 respectively (44). Finally, we must note that species evenness was not included in the present  
312 study due to its strong correlation with w.FDIS ( $r > 0.8$ , *SI Appendix*, Table S1).

313 **Environmental and spatial variables considered.** Mean annual temperature (MAT), mean  
314 annual precipitation (MAP) and precipitation seasonality (PS: coefficient of variation of 12  
315 monthly rainfall totals) were obtained from Worldclim (www.worldclim.org), a high resolution  
316 (30 arc seconds or ~ 1km at equator) global database (45). These variables are major  
317 determinants of ecosystem structure and functioning in drylands worldwide (see (46) for a  
318 review), were not highly correlated between them in our sites and provide a comprehensive  
319 representation of climatic conditions.

320 We summarized local edaphic parameters at each site using soil sand content and pH.  
321 These variables, measured as described in Maestre et al. (3), play key roles in the availability  
322 of water and nutrients in drylands (47), and are major drivers of the composition and diversity  
323 of plant and microbial communities (41, 48). Clay and silt contents were not used in our  
324 analyses due to their correlation with sand content ( $r = -0.52$  and  $-0.55$ , respectively). By doing  
325 so we avoided over-parameterizing our models and kept the number of environmental and biotic  
326 predictors of multifunctionality balanced in our analyses. We also considered the latitude and  
327 longitude of the study sites in our analyses to account for spatial autocorrelation in our data (3,  
328 17, 31, 48) (see also *SI Appendix*, Fig. S5).

329 **Statistical analyses.** Relationships between biodiversity attributes and the four indices of  
330 ecosystem functioning used were assessed using multiple linear regression models and  
331 sequentially repeated across multifunctionality thresholds ranging from 20% to 80%. The  
332 models included the following predictors: (i) **geographic variables [Latitude, Longitude (sin)**  
333 **and Longitude (cos)]**, abiotic variables (MAT, MAP, PS, soil sand content and pH) and  
334 biodiversity metrics (species richness, CWM-SLA, CWM-H, FDIS, w.FDIS, PSV, MNTD,  
335 w.MNTD). After inspecting the data, a quadratic term was allocated to soil pH to properly  
336 model non-linear responses.

337 We used a model selection procedure for each threshold separately, based on minimizing  
338 the corrected Akaike information criterion (AICc), to select the best predictors of the four  
339 indices of ecosystem functioning. In a first step, we performed a model simplification using a  
340 backward regression procedure with the *stepAICc* function in *R*. We subsequently removed  
341 non-significant quadratic and interaction terms that did not impact the predictive ability of the  
342 model. Then, a model selection procedure based on AICc selection ( $\Delta\text{AICc} < 2$ ) was applied  
343 on the resulting models to select the best predictors supported by the data. This procedure was  
344 performed using the *dredge* function in the R package *MuMIn* (49). Model residuals were  
345 inspected to ensure homoscedasticity and normality. All predictors and response variables were  
346 standardized before analyses using the Z-score to interpret parameter estimates on a comparable  
347 scale.

348 We evaluated the importance of the predictors under consideration as drivers of  
349 multifunctionality and sets of functions related to C, N and P cycling. For doing so, we  
350 expressed the importance of predictors as the percentage of variance they explain, based on the  
351 comparison between the absolute values of their standardized regression coefficients and the  
352 sum of all standardized regression coefficients from all predictors in the models. This method  
353 is similar to a variance partition analysis because we previously transformed all predictors to  
354 Z-scores. The following identifiable variance fractions were then examined: i) geography, ii)  
355 climate, iii) soil, and iv) each of the different biodiversity metrics considered. We repeated this  
356 analysis to identify three variance fractions: the mass-ratio effects through i) the identity  
357 (CWM-H and CWM-SLA) and ii) diversity of dominant species (w.FDIS and w.MNTD); and  
358 iii) richness effects (all non-weighted metrics).

359 Net biodiversity effects were calculated as the sum of the standardized regression  
360 coefficients of all metrics of biodiversity selected during the model selection procedures.

361



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## 377 **References**

- 378 1. Gamfeldt L, Hillebrand H, Jonsson PR (2008) Multiple functions increase the  
379 importance of biodiversity for overall ecosystem functioning. *Ecology* 89(5):1223–31.
- 380 2. Isbell F, et al. (2011) High plant diversity is needed to maintain ecosystem services.  
381 *Nature* 477(7363):199–202.
- 382 3. Maestre FT, et al. (2012) Plant species richness and ecosystem multifunctionality in  
383 global drylands. *Science* (80- ) 335(6065):214–218.
- 384 4. Soliveres S, et al. (2016) Biodiversity at multiple trophic levels is needed for ecosystem  
385 multifunctionality. *Nature* 536(7617):456–459.
- 386 5. Meyer ST, et al. (2018) Biodiversity-multifunctionality relationships depend on identity

- 387 and number of measured functions. *Nat Ecol Evol* 2(1):44–49.
- 388 6. Gamfeldt L, Roger F (2017) Revisiting the biodiversity-ecosystem multifunctionality  
389 relationship. *Nat Ecol Evol* 1(7):1–7.
- 390 7. Flynn DFB, Mirotchnick N, Jain M, Palmer MI, Naeem S (2011) Functional and  
391 phylogenetic diversity as predictors of biodiversity--ecosystem-function relationships.  
392 *Ecology* 92(8):1573–1581.
- 393 8. Cadotte MW, Dinnage R, Tilman D (2012) Phylogenetic diversity promotes ecosystem  
394 stability. *Ecology* 93(8):223–233.
- 395 9. Naeem S, et al. (2016) Biodiversity as a multidimensional construct: a review ,  
396 framework and case study of herbivory ' s impact on plant biodiversity. *Proc R Soc B*  
397 *Biol Sci* 283:20153005.
- 398 10. Craven D, et al. (2018) Multiple facets of biodiversity drive the diversity–stability  
399 relationship. *Nat Ecol Evol* 2:1579–1587.
- 400 11. Roger F, Bertilsson S, Langenheder S, Osman OA, Gamfeldt L (2016) Effects of  
401 multiple dimensions of bacterial diversity on functioning, stability and  
402 multifunctionality. *Ecology* 97(10):2716–2728.
- 403 12. Brum FT, et al. (2017) Global priorities for conservation across multiple dimensions of  
404 mammalian diversity. *Proc Natl Acad Sci* 114(29):7641–7646.
- 405 13. Tucker CM, Davies TJ, Cadotte MW, Pearse WD (2018) On the relationship between  
406 phylogenetic diversity and trait diversity. *Ecology* 99(6):1473–1479.
- 407 14. Balvanera P, et al. (2014) Linking biodiversity and ecosystem services: Current  
408 uncertainties and the necessary next steps. *Bioscience* 64(1):49–57.
- 409 15. Mouillot D, Villéger S, Scherer-Lorenzen M, Mason NWH (2011) Functional structure  
410 of biological communities predicts ecosystem multifunctionality. *PLoS One*  
411 6(3):e17476.

- 412 16. Valencia E, et al. (2015) Functional diversity enhances the resistance of ecosystem  
413 multifunctionality to aridity in Mediterranean drylands. *New Phytol* 206(2):660–671.
- 414 17. Gross N, et al. (2017) Functional trait diversity maximizes ecosystem multifunctionality.  
415 *Nat Ecol Evol* 1(5):1–9.
- 416 18. Naeem S, Thompson LJ, Lawler SP, Lawton JH, Woodfin RM (1994) Declining  
417 biodiversity can alter the performance of ecosystems. *Nature* 368:734–737.
- 418 19. Tilman D, Lehman CL, Thomson KD (1997) Plant diversity and ecosystem productivity.  
419 *Proc Natl Acad Sci USA* 94:1857–1861.
- 420 20. Cadotte MW, et al. (2017) Explaining ecosystem multifunction with evolutionary  
421 models. *Ecology* 98(12):3175–3187.
- 422 21. Harmon LJ, et al. (2009) Evolutionary diversification in stickleback affects ecosystem  
423 functioning. *Nature* 458(7242):1167–1170.
- 424 22. Venail P, et al. (2015) Species richness, but not phylogenetic diversity, influences  
425 community biomass production and temporal stability in a re-examination of 16  
426 grassland biodiversity studies. *Funct Ecol* 29(5):615–626.
- 427 23. Gilbert GS, Webb CO (2007) Phylogenetic signal in plant pathogen-host range. *Proc*  
428 *Natl Acad Sci* 104(12):4979–4983.
- 429 24. Montesinos-Navarro A, Segarra-Moragues JG, Valiente-Banuet A, Verdú M (2015)  
430 Evidence for phylogenetic correlation of plant-AMF assemblages? *Ann Bot* 115(2):171–  
431 177.
- 432 25. Grime JP (1998) Benefits of plant diversity to ecosystems: Immediate, filter and founder  
433 effects. *J Ecol* 86(6):902–910.
- 434 26. Garnier ERIC, Ortiz JAC, Ille GEB (2004) Plant Functional Markers Capture Ecosystem  
435 Properties. 85(9):2630–2637.
- 436 27. Smith MD, Knapp a K (2003) Dominant species maintain ecosystem function with non-

- 437 random species loss. *Ecol Lett* 6:509–517.
- 438 28. Lyons KG, Brigham CA, Traut BH, Schwartz MW (2005) Rare species and ecosystem  
439 functioning. *Conserv Biol* 19(4):1019–1024.
- 440 29. Soliveres S, et al. (2016) Locally rare species influence grassland ecosystem  
441 multifunctionality Locally rare species influence grassland ecosystem  
442 multifunctionality. *Philos Trans R Soc B Trans R Soc B* 371(1694):20150269.
- 443 30. Byrnes JEK, et al. (2014) Investigating the relationship between biodiversity and  
444 ecosystem multifunctionality: Challenges and solutions. *Methods Ecol Evol* 5(2):111–  
445 124.
- 446 31. García-Palacios P, Gross N, Gaitán J, Maestre FT (2018) Climate mediates the  
447 biodiversity–ecosystem stability relationship globally. *Proc Natl Acad Sci*:201800425.
- 448 32. Cardinale BJ, et al. (2012) Biodiversity loss and its impact on humanity. *Nature*  
449 486(7401):59–67.
- 450 33. Jiang L, Pu Z, Nemergut DR (2008) On the importance of the negative selection effect  
451 for the relationship between biodiversity and ecosystem functioning. *Oikos* 117(4):488–  
452 493.
- 453 34. Ochoa-Hueso R, et al. (2018) Soil fungal abundance and plant functional traits drive  
454 fertile island formation in global drylands. *J Ecol* 106:242–253.
- 455 35. Díaz S, et al. (2016) The global spectrum of plant form and function. *Nature*  
456 529(7585):167–171.
- 457 36. Salguero-Gómez R, et al. (2015) The compadre Plant Matrix Database: An open online  
458 repository for plant demography. *J Ecol* 103(1):202–218.
- 459 37. Valiente-Banuet A, Verdú M (2007) Facilitation can increase the phylogenetic diversity  
460 of plant communities. *Ecol Lett* 10(11):1029–1036.
- 461 38. Cornwell WK, et al. (2014) Functional distinctiveness of major plant lineages. *J Ecol*

- 462 102(2):345–356.
- 463 39. Whitford WG (2002) *Ecology of desert systems* (Academic Press).
- 464 40. Reynolds JF, et al. (2007) Global desertification: building a science for dryland  
465 development. *Science* (80- ) 316(5826):847–851.
- 466 41. Delgado-Baquerizo M, et al. (2016) Microbial diversity drives multifunctionality in  
467 terrestrial ecosystems. *Nat Commun* 7.
- 468 42. Zavaleta ES, Pasari JR, Hulvey KB, Tilman GD (2010) Sustaining multiple ecosystem  
469 functions in grassland communities requires higher biodiversity. *Proc Natl Acad Sci*  
470 107(4):1443–1446.
- 471 43. Lefcheck JS, et al. (2015) Biodiversity enhances ecosystem multifunctionality across  
472 trophic levels and habitats. *Nat Commun* 6:1–7.
- 473 44. Graham CH, Storch D, Machac A (2018) Phylogenetic scale in ecology and evolution.  
474 *Glob Ecol Biogeogr* 27(2):175–187.
- 475 45. Hijmans RJ, Cameron SE, Parra JL, Jones PG, Jarvis A (2005) Very high resolution  
476 interpolated climate surfaces for global land areas. *Int J Climatol Int J Clim* 25:1965–  
477 1978.
- 478 46. Maestre FT, Salguero-Gómez R, Quero JL (2012) It is getting hotter in here:  
479 Determining and projecting the impacts of global environmental change on drylands.  
480 *Philos Trans R Soc B Biol Sci* 367(1606):3062–3075.
- 481 47. Loik ME, Breshears DD, Lauenroth WK, Belnap J (2004) A multi-scale perspective of  
482 water pulses in dryland ecosystems: climatology and ecohydrology of the western USA.  
483 *Oecologia* 141(2):269–281.
- 484 48. Le Bagousse-Pinguet Y, et al. (2017) Testing the environmental filtering concept in  
485 global drylands. *J Ecol* 105(4):1058–1069.
- 486 49. Bartoń K (2017) MuMIn: Multi-model inference. Version 1.40.0. Available at:

487 <http://CRANR-project.org/package=MuMIn>.

488

## 489 **Figure legends**

490 **Figure 1.** Relative importance of eight uncorrelated biodiversity metrics, geographical, climatic  
491 and soil predictors across multiple thresholds of multifunctionality (a) and sets of functions  
492 related to C, N and P cycling (b, c, d). The relative importance of predictors is expressed as the  
493 percentage of variance they explain, and is based on **the absolute value of their** standardized  
494 regression coefficients. CWM.H and CWM.SLA: community-weighted mean for height and  
495 SLA; PSV: phylogenetic species variability; w.FDIS and FDIS: abundance-weighted and non-  
496 weighted functional dispersion; w.MNTD and MNTD: weighted and non-weighted Mean  
497 Nearest Taxon Distance.

498

499 **Figure 2.** Relative importance of mass-ratio vs. richness effects across multiple  
500 multifunctionality (a) and sets of functions related to C, N and P cycles (b, c, d) thresholds. The  
501 importance of predictors is expressed as the percentage of variance they explain, and is based  
502 on **the absolute value of their** standardized regression coefficients. Mass-ratio effects were  
503 calculated as the sum of the variances explained by the abundance-weighted metrics [CWM.H,  
504 CWM.SLA, w.FDIS, w.MNTD)]. Richness effects were calculated as the explained variances  
505 of non-weighted metrics (Species richness, FDIS, PSV and MNTD). Abbreviations as in Fig.  
506 1.

507

508 **Figure 3.** Net effects of biodiversity attributes on multifunctionality (a), and on carbon (b),  
509 nitrogen (c) and phosphorus (d) cycling indices. The net effect was calculated as the sum of the  
510 standardized regression coefficients of all biodiversity metrics selected during the model  
511 selection procedures.

512

513 **Figure 4.** Net effects of biodiversity on multifunctionality depending on the number of  
514 biodiversity attributes and multifunctionality thresholds considered. These effects are presented  
515 at 30%, 50% and 70% thresholds, and are based on the number of plant diversity attributes  
516 retained in all models after the backward model selection procedure. The net effect was  
517 calculated as the sum of the standardized regression coefficients of all biodiversity attributes  
518 selected during the model selection procedures. **Note that we used a violin function to highlight**  
519 **the density of points and a jitter function to visualize the data distribution.**

520

521 **Figure 5.** Standardized regression coefficients of model predictors and associated 95%  
522 confidence intervals for a) multifunctionality and C, N and P cycling (b, c, d) indices.  
523 Standardized regression coefficients result from model averaging procedures and are averaged  
524 across the entire spectrum of thresholds (20-80%) evaluated. Confidence intervals that do not  
525 cross the zero line indicate that the predictors under consideration are associated with a  
526 statistically significant ( $P < 0.05$ ) change in multifunctionality. See *SI Appendix*, Table S4 for  
527 the variation of standardized regression coefficients of each predictor along the threshold  
528 gradient evaluated.