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Temperature and aridity regulate spatial variability of soil multifunctionality in drylands across the globe

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Abstract:	The relationship between the spatial variability of soil multifunctionality (i.e. the capacity of soils to conduct multiple functions; SVM) and major climatic drivers, such as temperature and aridity, has never been assessed globally in terrestrial ecosystems. We surveyed 236 dryland ecosystems from six continents to evaluate the relative importance of aridity and mean annual temperature, and of other abiotic (e.g., texture) and biotic (e.g., plant cover) variables as drivers of SVM, calculated as the averaged coefficient of variation for multiple soil variables linked to nutrient stocks and cycling. We found that increases in temperature and aridity were globally correlated to increases in SVM. Some of these climatic effects on SVM were direct, but others were indirectly driven through reductions in the number of vegetation patches and increases in soil sand content. The predictive capacity of our structural equation modelling was clearly higher for the spatial variability of N- than for C- and P- related soil variables. In the case of N cycling, the effects of temperature and aridity were both

	<p>direct and indirect via changes in soil properties. For C and P, the effect of climate was mainly indirect via changes in plant attributes. These results suggest that future changes in climate may decouple the spatial availability of these elements for plants and microbes in dryland soils. Our findings significantly advance our understanding of the patterns and mechanisms driving SVM in drylands across the globe, which is critical for predicting changes in ecosystem functioning in response to climate change.</p>

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Soil spatial variability in drylands

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Temperature and aridity regulate spatial variability of soil multifunctionality in drylands across the globe

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1 **Abstract**

2 The relationship between the spatial variability of soil multifunctionality (i.e. the
3 capacity of soils to conduct multiple functions; SVM) and major climatic drivers, such
4 as temperature and aridity, has never been assessed globally in terrestrial ecosystems.
5 We surveyed 236 dryland ecosystems from six continents to evaluate the relative
6 importance of aridity and mean annual temperature, and of other abiotic (e.g., texture)
7 and biotic (e.g., plant cover) variables as drivers of SVM, calculated as the averaged
8 coefficient of variation for multiple soil variables linked to nutrient stocks and cycling.
9 We found that increases in temperature and aridity were globally correlated to increases
10 in SVM. Some of these climatic effects on SVM were direct, but others were indirectly
11 driven through reductions in the number of vegetation patches and increases in soil sand
12 content. The predictive capacity of our structural equation modelling was clearly higher
13 for the spatial variability of N- than for C- and P- related soil variables. In the case of N
14 cycling, the effects of temperature and aridity were both direct and indirect via changes
15 in soil properties. For C and P, the effect of climate was mainly indirect via changes in
16 plant attributes. These results suggest that future changes in climate may decouple the
17 spatial availability of these elements for plants and microbes in dryland soils. Our
18 findings significantly advance our understanding of the patterns and mechanisms
19 driving SVM in drylands across the globe, which is critical for predicting changes in
20 ecosystem functioning in response to climate change.

21

22

23 **Keywords:** Multifunctionality; carbon cycling; nitrogen cycling; phosphorous cycling;
24 spatial heterogeneity; climate change.

25

26 **Introduction**

27 The uneven distribution of soil characteristics is a ubiquitous feature of most terrestrial
28 ecosystems, and is known to regulate a wide range of ecosystem processes including
29 individual plant performance and competitive ability (Day et al. 2003), community-
30 level productivity (Maestre and Reynolds 2006), trophic interactions (Tsunoda et al.
31 2014), and nutrient cycling (Schlesinger et al. 1990, Ochoa-Hueso et al. 2018). This
32 spatial variability in soil variables (SV hereafter) is largely controlled by the interaction
33 of multiple biological, chemical and physical processes acting simultaneously at
34 multiple scales (Jackson and Caldwell 1993, Farley and Fitter 1999, Zuo et al. 2010).
35 While the environmental drivers of SV have been studied on individual functions and at
36 local scales (e.g. N availability), the role of environment in driving multiple ecosystem
37 functions simultaneously still needs to be considered to achieve an integrative
38 understanding on the drivers of within-site SV (Byrnes et al. 2014).

39 Given the ubiquitous nature of SV and its role as a modulator of plant and soil
40 fauna responses to climate change (García-Palacios et al. 2012), a deeper understanding
41 of the major drivers of the spatial variability in multiple soil functions (i.e. soil
42 multifunctionality, SVM) across the globe is of paramount importance to anticipate
43 changes in ecosystem functioning under global change scenarios (Fraterrigo and Rusak
44 2008, IPCC 2013). Remarkably, a relatively large body of literature has explored the
45 effects of SV locally or in regional comparisons (Linstädter et al. 2014, Guuroh et al.
46 2018), but no study has yet assessed the major environmental drivers of SVM in
47 terrestrial ecosystems across the globe, which remains largely unexplored and poorly
48 understood. This is particularly relevant for dryland ecosystems (i.e. arid, semi-arid and
49 dry-subhumid ecosystems), where SVM is a widespread phenomenon (Schlesinger et al.
50 1990, Ochoa-Hueso et al. 2018). In drylands, which typically have a patchy plant
51 distribution, SVM likely arises from the strong functional differences between vegetated
52 patches, where plants largely drive biological processes such as litter decomposition or
53 N fixation, and unvegetated areas, with higher importance of physical processes such as
54 erosion by wind or water (Li et al. 2007). Drylands cover about 45% of Earth's land
55 surface and support more than 38% of the global human population (Právělie 2016), and
56 their global extent may increase by up to 23% by the end of this century due to
57 forecasted increases in aridity (Huang et al. 2016). These areas are particularly sensitive
58 to the effects of climate change, so expected increases in aridity and temperature (up to
59 2-4 °C, depending on projections, IPCC 2013) will promote changes in vegetation and

60 soil properties that could have significant consequences for SVM in drylands
61 worldwide. For instance, recent field surveys have found that increases in aridity are
62 linked to decreases in plant cover and to increases in the encroachment rate of woody
63 vegetation across the globe (Dougill and Thomas 2004, Vicente-Serrano et al. 2012,
64 Delgado-Baquerizo et al. 2013), phenomena that would likely lead to parallel increases
65 in SVM. However, to date, no study has considered the multiple direct and indirect (e.g.
66 via plant and soil features) effects of temperature or aridity on SVM. The likely
67 influence of climate on SVM, together with the well-known influence of SVM on
68 ecosystem functioning, anticipate changes in the ability of dryland ecosystems to
69 provide goods and services under ongoing climate change. This, together with the
70 global importance of drylands and their particular sensitivity to climatic changes, justify
71 efforts to better understand the role of major climate change drivers, such as
72 temperature and aridity, in determining SVM globally directly and indirectly via plant
73 and soil attributes.

74 Here, we used a database including 236 dryland sites from six continents (Fig.
75 S1) to evaluate the role and relative importance of aridity and mean annual temperature,
76 together with other key environmental factors (soil properties and plant attributes), as
77 drivers of SVM in drylands worldwide. We hypothesized that increases in aridity and
78 temperature will promote SVM directly, but also indirectly via reductions in plant cover
79 and shifts in soil properties, as plant community composition and structure are largely
80 known to be major drivers of soil spatial variability in drylands (Schlesinger et al.
81 1990).

82

83 **Methods**

84 We used data from a global field survey conducted in 236 dryland sites from 19
85 countries (Fig. S1; Argentina, Australia, Botswana, Brazil, Burkina Faso, Chile, China,
86 Ecuador, Ghana, Iran, Israel, Kenya, Mexico, Morocco, Peru, Spain, Tunisia, USA, and
87 Venezuela). These sites include the 224 drylands used in Maestre et al. (2012) plus 12
88 additional sites from Botswana, Ghana and Burkina Faso surveyed in 2012 and 2013.
89 All sites surveyed were restricted to dryland ecosystems [defined as regions with an
90 aridity index ($AI = \text{mean precipitation}/\text{mean potential evapotranspiration}$) between 0.05
91 and 0.65 (Gao and Giorgi 2008)] and encompassed a wide variety of dryland vegetation
92 types, including grasslands, shrublands, savannas, dry seasonal forests and open, tree-

93 dominated woodlands. Mean annual precipitation and temperature of the study sites
94 ranged from 66 mm to 1219 mm, and from -1.8 °C to 27.8 °C.

95 Data collection was carried out between February 2006 and December 2013,
96 focusing on 30 m x 30 m plots representative of the vegetation at each site, and using a
97 standardized sampling protocol (Maestre et al. 2012). Soils were sampled during the dry
98 season in most of the sites using a stratified random procedure. At each plot, five 50 cm
99 × 50 cm quadrats were randomly placed under the canopy of the dominant perennial
100 species and in open areas devoid of perennial vegetation. A composite sample
101 consisting of five 145 cm³ soil cores (0 - 7.5 cm depth) was collected from each
102 quadrat, bulked, and homogenized in the field. When more than one dominant plant
103 species was present, samples were also collected under the canopies of five randomly
104 selected individuals of the co-dominant species. Thus, the number of soil samples
105 varied between 10 and 15 per site. Soil samples were taken to the laboratory, sieved (2
106 mm mesh), air-dried for one month and stored for laboratory analyses. In drylands, soil
107 properties remain largely similar after air-drying (the most common status for these
108 soils), so we did not expect large changes in soil properties after air-drying (Zornoza et
109 al. 2006, 2009). To facilitate the comparison of results across sites, dried soil samples
110 from all sites were shipped to Spain for laboratory analyses.

111 We measured the cover and number of perennial plant patches at each site using
112 the line-intercept method along four 30 m long transects separated 8 m from each other
113 (Brun and Box 2006). At each transect, we also surveyed 20 contiguous 1.5 m × 1.5 m
114 quadrats (80 quadrats per site). Within these quadrats, we counted the number of species
115 present to estimate species richness. Soil pH was measured with a pH meter, in a 1:2.5
116 (mass:volume, soil:water) suspension. Soil sand content was estimated according to
117 (Kettler et al. 2001). Mean annual temperature (MAT) and aridity (1-aridity index [ratio
118 of precipitation to potential evapotranspiration]) were obtained from Zomer et al.
119 (2008), who used interpolations from the Worldclim global database (Hijmans et al.
120 2005).

121 We measured 14 variables closely related to C, N and P cycling and storage.
122 Total N was determined using a CN analyzer (Leco CHN628 Series, Leco Corporation,
123 St Joseph, MI, USA). Total organic C was determined by colorimetry after oxidation
124 with a mixture of potassium dichromate and sulfuric acid (Anderson and Ingram 1993).
125 Soil pentoses and hexoses, as well as soil ammonium and nitrate were measured
126 colorimetrically from soil extracts as described in Delgado-Baquerizo et al. (2015). Soil

127 samples (2.5 g of soil) were extracted with 0.5 M K_2SO_4 in a ratio 1:5. Extracts were
128 shaken in an orbital shaker at 200 r.p.m. for 1 h at 20°C and filtered to pass a 0.45- μ m
129 Millipore filter (Jones and Willett 2006). Potential net N mineralization rate was
130 estimated as the difference between initial and final inorganic N (sum of ammonium
131 and nitrate) before and after incubation under potential conditions (Allen et al. 1986).
132 Phosphatase activity was measured by determination of the amount of p-nitrophenol
133 released from 0.5 g soil after incubation at 37°C for 1 h with the substrate p-nitrophenyl
134 phosphate in MUB buffer (Tabatabai and Bremner 1969). The activity of b-glucosidase
135 was assayed following the procedure for phosphatase, but using p-nitrophenyl-b-D-
136 glucopyranoside as substrate and trishydroxymethyl aminomethane instead of NaOH
137 when preparing the buffer (Tabatabai 1982). Available phosphorus was determined
138 colorimetrically from sodium bicarbonate extracts (Moir and Tiessen 2007). Soil
139 proteins, phenols and aromatic compounds were evaluated as detailed in Maestre et al.
140 (2012). These variables were selected because they are considered good proxies of key
141 ecosystem processes linked to soil fertility, nutrient cycling, biological productivity, and
142 the build-up of nutrient pools.

143 To estimate SVM, we first calculated the variability within each site of the
144 different soil variables measured. To do so, we calculated the site-level coefficient of
145 variation (CV) using the composite soil samples obtained at each site (n per site varied
146 between 10 and 15; see above). The CV is a relative measure of heterogeneity that can
147 accommodate variance-mean scaling, avoiding the tendency for variance to increase
148 with the mean (Duarte 1991). Therefore, it has been shown to be more useful than
149 absolute measures of variability such as the standard deviation for comparing variability
150 within biological properties (Schlesinger et al. 1990, Fraterrigo and Rusak 2008). We
151 calculated SVM as the arithmetic mean for all individual site-level CVs of all soil
152 variables. We also calculated the SVM of C-, N-, and P- related variables separately
153 (hereafter C-SVM, N-SVM, and P-SVM) by calculating the arithmetic mean of
154 individual site-level CVs of soil variables related to the C (i.e. total organic C, activity
155 of b-glucosidase, phenols, aromatic compounds, hexoses and pentoses), N (total
156 nitrogen, ammonium, nitrate, proteins, potential nitrification rate, and amino acids), and
157 P (available phosphorus, and phosphatase activity) cycles.

158 To evaluate the effects of biotic and abiotic factors on SVM, we first explored
159 the relationships between MAT, aridity and SVM using regression analysis. Then, we
160 used random forest modelling (Breiman 2001) to identify the most important predictors

161 of SVM among the following: latitude, longitude, mean annual temperature, aridity,
162 plant species richness, plant cover, number of plant patches, the ratio between woody
163 and herbaceous cover, soil sand, and soil pH. Finally, to achieve a system-level
164 understanding of the major drivers of SVM, we used structural equation modelling
165 (SEM, (Grace 2006)). In particular, we used SEM to evaluate the multiple direct and
166 indirect effects of biotic and abiotic drivers on SVM (our *a priori* model based on our
167 current knowledge is available in Fig. S2). Structural equation modelling is particularly
168 useful in large-scale correlative studies because it allows us to partition causal
169 influences among multiple variables, and to separate the direct and indirect effects of
170 the predictors included in the model (Grace 2006). Variables were log- or square root-
171 transformed, when necessary, to improve linearity in the relationships in our SEM
172 models. There is no single universally accepted test of overall goodness of fit for SEM,
173 applicable in all situations regardless of sample size or data distribution. Here we used
174 the chi-squared test (χ^2 ; the model has a good fit when χ^2 is low, i.e., $c. \leq 2$, and P is
175 high, traditionally > 0.05); and the root-mean-square error of approximation (RMSEA;
176 the model has a good fit when RMSEA is low, i.e., $c. \leq 0.05$, and P is high,
177 traditionally > 0.05) (Schermelleh-Engel et al. 2003). After verifying the adequate fit of
178 our model, we were free to interpret the path coefficients of the model and their
179 associated P -values. A path coefficient is analogous to the partial correlation
180 coefficient, and describes the strength and sign of the relationships between two
181 variables (Grace 2006). The probability that a path coefficient differs from zero was
182 tested using bootstrap tests (Schermelleh-Engel et al. 2003). We calculated the
183 standardized total effects of all biotic and abiotic drivers on the selected heterogeneity
184 metrics (Grace 2006). The net influence that one variable had upon another was
185 calculated by summing all direct and indirect pathways (effects) between two variables.
186 Then we parameterized the model using our dataset and tested its overall goodness of
187 fit. All SEM and regression analyses were conducted using AMOS 20 (IBM SPSS Inc.,
188 Chicago, IL, USA) and Sigma Plot 12, respectively (Systat Software Inc., San José, CA,
189 USA). Random forest modelling was performed with R 3.3.2 using the rfPermute
190 package (R Core Team, Vienna, Austria).

191

192

193 Results

194 Regression analyses showed a positive quadratic relationship between SVM and mean
195 annual temperature (MAT; Fig. 1a) and aridity (Fig. 1b). The random forest models
196 indicated that all explored environmental factors were significant predictors of SVM, N-
197 SVM, C-SVM, and P-SVM, except plant cover and plant richness in the case of P-SVM
198 (Fig. 2). These models identified, in this order, (i) soil sand content, MAT, the number
199 of plant patches per plot, soil pH, and aridity as the major individual predictors of SVM
200 (Fig. 2a); (ii) MAT, soil pH and sand content, and aridity for N-SVM (Fig. 2b); (iii) soil
201 sand content, the number of plant patches, MAT, and aridity for C-SVM (Fig. 2c); and
202 (iv) the number of plant patches, MAT, soil sand content and aridity for P-SVM (Fig.
203 2d).

204 Our SEM explained around 22% of the variation in SVM (Fig. 3a). We found
205 direct effects from both MAT and aridity on SVM (Fig. 3a). Moreover, we found
206 multiple indirect effects of MAT and aridity on SVM via reductions in number of plant
207 patches (Fig. 3a). Aridity also promoted SVM indirectly via positive effects on sand
208 content. The standardized total effects (sum of direct and indirect effects from SEM)
209 indicated that MAT and aridity were important predictors of SVM, with strong positive
210 effects on SVM in both cases (Fig. 3b). Sand content (positive) and the number of plant
211 patches and soil pH (negative) were also important drivers of SVM.

212 The element-specific SEMs explained 26%, 14% and 12% of the variation
213 observed in N-, C-, and P-SVM, respectively (Fig. 4). The models showed that N-SVM
214 was positively and significantly related to MAT and soil sand content, but negatively
215 related to soil pH (Fig. 4a), whereas C-SVM and P-SVM were only negatively
216 influenced by the number of plant patches (Figs. 4c, 4e). The standardized total effects
217 indicated that N-SVM was positively influenced by MAT and soil sand content, but
218 negatively by soil pH (Fig. 4b); C-SVM was positively regulated by aridity and plant
219 cover, but negatively by the number of plant patches and soil pH (Fig. 4d); and P-SVM
220 was mainly positively related to aridity and MAT, but strongly and negatively related to
221 the number of plant patches (Fig. 4f).

222

223

224 **Discussion**

225 Our work represents the first global assessment of the major environmental predictors
226 of the spatial variability of multiple surrogates of ecosystem functions (SVM). More
227 importantly, we provide new mechanistic insights indicating that increases in aridity
228 and mean annual temperature are linked to overall increases in the SVM of drylands
229 across the globe both directly and indirectly (via reductions in plant patches and
230 increases in sand content). This study builds on the seminal article from Schlesinger et
231 al. (1990) that illustrated how the loss of vegetation cover due to human-driven
232 disturbances can lead to changes in the heterogeneity of soil resources at the local scale.
233 Although the amount of variance explained by our models is relatively low ($R^2 < 0.25$),
234 this is a common outcome in global surveys in which the variability of sampled sites is
235 inevitably high (Moles et al. 2009). Furthermore, it is inherently challenging to
236 characterize the heterogeneity of soil resources, as it can be affected simultaneously by
237 different sources of variability that can operate and affect SVM at different temporal
238 and spatial scales (Fraterrigo and Rusak 2008).

239 Our results demonstrate that changes in temperature and aridity are not only
240 directly related to SVM, but also emerge from the influence of these climatic variables
241 on vegetation and/or soil features. For instance, increases in aridity enhanced SVM
242 mainly through increases in soil sand content and through reductions in the number of
243 plant patches. On the other hand, increases in MAT were negatively related to SVM
244 through decreases in soil sand content. However, this effect was clearly overcome by
245 both the negative effect of MAT on the number of plant patches (which further
246 decreases SVM) and the direct effects of temperature on SVM, resulting in a net
247 positive and strong effect of increasing temperature on SVM. Results from previous
248 studies conducted at the local scale suggest that any disturbance leading to decreases in
249 vegetation cover (e.g. overgrazing) and increases in woody plant encroachment should
250 increase SV (Schlesinger et al. 1990, Dougill and Thomas 2004) through the
251 development of high fertility areas under and around plant canopies (characterized by
252 higher production of above- and below-ground litter, leachates, and exudates and lower
253 erosion rates), and low fertility areas in the zones devoid of perennial vascular
254 vegetation (Schlesinger et al. 1990, Hook et al. 1991, Ochoa-Hueso et al. 2018). Our
255 results provide partial empirical support for this hypothesis at a global scale in dryland
256 ecosystems, and confirm that any impact of climatic variation on vegetation spatial
257 variability might also have significant consequences for SVM globally.

258 Our mechanistic model suggests that total plant cover has limited direct effects
259 on SVM (Fig. 3). However, a higher number of plant patches in our plots was strongly
260 and directly linked to lower levels of SVM. Thus, it seems that more even inputs of
261 litter and a higher capacity to redistribute soil nutrients spatially, as a result of a more
262 homogeneous distribution of plant patches, are more important than the total area
263 covered by plants to maintain lower levels of soil spatial variability, at least at the scale
264 evaluated in this study. Previous studies show that increases in aridity, or other
265 disturbances such as overgrazing, are tightly linked to plant cover losses and to
266 increases in the percentage of sand-sized particles in the soil (Schlesinger et al. 1990, Li
267 et al. 2007). Here, we show that increases in temperature and aridity such as those
268 forecasted with climate change, and the likely concomitant decreases in total plant cover
269 and increases in the amount of sand in the soil might result in a general increase in the
270 spatial variability of soil resources and functionality in drylands worldwide (Vicente-
271 Serrano et al. 2012, Delgado-Baquerizo et al. 2013). Perennial plants modify soil
272 texture by decreasing losses (or increasing the accumulation) of fine soil particles, thus
273 decreasing the relative abundance of sand-sized grains in the soil (Linstädter and
274 Baumann 2013). This process is likely to increase the functional differences between
275 vegetated areas (where plants typically drive soil biological processes and promote soil
276 nutrient redistribution via roots and microorganisms; Schlesinger et al. 1990, Hook et
277 al. 1991), and open areas between plant patches dominated by physical processes such
278 as wind and water erosion (Li et al. 2007).

279 Soil heterogeneity drives many key ecosystem processes (Farley and Fitter 1999,
280 Day et al. 2003, Maestre and Reynolds 2006, Zuo et al. 2010, Tsunoda et al. 2014), but
281 predicting the effects of the observed changes in SVM is not trivial. According to the
282 traditional view of spatial heterogeneity as a driver of species diversity, increased SVM
283 should promote plant and soil biota diversity (Bakker et al. 2003, Davies et al. 2005).
284 Recent studies suggest that, more likely, SVM can both increase and decrease not only
285 diversity, but also ecosystem function, depending on factors such as the scale of the
286 heterogeneity, the environmental conditions, as well as species identity and composition
287 (Hutchings et al. 2003). Increases in SVM in low productivity systems such as drylands
288 could change the size symmetry of belowground competition, favouring larger (in the
289 case of plants) or more mobile (in the case of soil biota) species, which are more
290 capable of rapidly exploiting nutrient patches than smaller species (Rajaniemi 2007,
291 Reynolds and Haubensak 2009). On the other hand, changes in SVM typically promote

292 multiple plant morphological and physiological responses, such as changes in nutrient
293 uptake kinetics, biomass allocation, and root production and morphology (Robinson
294 1994, García-Palacios et al. 2012). Thus, the ability of individual species (and
295 individuals within species) to adapt to the forecasted increase (with climate change) in
296 soil spatial variability will likely determine their establishment (Maestre et al. 2003),
297 competitive ability (Robinson et al. 1999, Hodge 2004), productivity (Dougill and
298 Thomas 2004), and survival rate (Wijesinghe et al. 2005).

299 Of particular interest were the different responses of the element-specific N-, C-,
300 and P-SVM to the environmental predictors. The predictive capacity of our model was
301 clearly higher for N-SVM than for C- and P-SVM. While we also found strong direct
302 effects of aridity on N-SVM, the fate of C- and P-SVM was mainly indirectly driven by
303 reductions in number of plant patches. Different ecosystem compartments or processes
304 may have different sensitivities to the direct or indirect effects of aridity (Evans and
305 Burke 2012), and past studies have shown asymmetrical responses of N, C, and P cycles
306 to climate change, with N cycling being consistently the most susceptible among them
307 (Durán et al. 2013). Several mechanisms linked to increases in aridity and temperature
308 could be behind this different sensitivity of the spatial variability of N, C and P in soils.
309 For instance, different microbial communities have different sensitivities to warming
310 and drought, leading to the accumulation of different soil nutrient pools (Sheik et al.
311 2011). Also, unlike P and C, whose availabilities are principally linked to the parent
312 material and the decomposition of litter from plant communities, respectively, soil N is
313 fixed from the atmosphere by soil microbial communities (e.g., most cyanobacteria),
314 which are common in many dryland soils (Schlesinger and Bernhardt 2012). Increases
315 in aridity will increase the amount of potential habitat available for biocrust
316 communities, which spread in the open areas between plant patches and form mosaics
317 of multiple species (Delgado-Baquerizo et al. 2016a). Similarly, increases in aridity
318 promote the abundance of autotrophic communities tightly linked to the N cycle (e.g.
319 archaeal nitrifiers; Delgado-Baquerizo et al. 2016b). Thus, the strong links between
320 aridity and the spatial distribution of N cycling-related microbial communities might
321 help explain the strong direct effect of climate on N-SVM, not observed for P- or C-
322 SVM. On the contrary, the strong indirect effects of aridity on C- and P-SVM via
323 reductions in number of plant patches might be related to reduced litter decomposition,
324 as our C- and P-SVM indexes include the activities of enzymes, such as beta-
325 glucosidase and phosphatase, that are involved in the degradation of organic matter into

326 simpler C and P components.

327 The biogeochemical cycles of N, C, and P are tightly interlinked in terrestrial
328 ecosystems by processes such as photosynthesis, atmospheric N fixation, respiration,
329 decomposition and microbial mineralization (Vitousek 2004, Schlesinger and Bernhardt
330 2012). However, as these processes are likely to be altered, perhaps in different ways,
331 by anthropogenic disturbances such as climate change, it has been suggested that N, C,
332 and P cycles can become decoupled (Schlesinger et al. 1990, Peñuelas et al. 2012,
333 Vicente-Serrano et al. 2012, Delgado-Baquerizo et al. 2013). Here we show that
334 increasing aridity and temperature had stronger effects on the heterogeneity of N- than
335 C-, and P-related variables. These results suggest expected changes in climate, by
336 compromising the essential co-occurrence of areas with similar N, C and P contents,
337 might lead to a decoupling of the spatial availability of these elements for plants and
338 microbes in dryland soils across the globe. Heterogeneity is rarely employed as a
339 response variable to assess the effects of human impacts on ecosystems, but recent
340 studies indicate that it can be a sensitive metric *per se*, capturing effects and differences
341 sometimes not detected by averaging (Underwood 1991, Callaghan and Holloway 1999,
342 Fraterrigo and Rusak 2008). Indeed, whereas a recent study using our same database
343 showed that C and N cycles are likely to become uncoupled from the P cycle in coming
344 decades due to increasing aridity (Delgado-Baquerizo et al. 2013), our explicit
345 consideration of SVM unveiled an additional (spatial) C-N-P decoupling mechanism
346 that could have important consequences for ecosystem functioning (Schimel 2010, Finzi
347 et al. 2011, Peñuelas et al. 2012, Delgado-Baquerizo et al. 2013).

348 Together, our work provides the first empirical evidence that changes in
349 temperature and aridity are linked to alterations of the SVM in drylands across the
350 globe. Our results also confirm that the direction of these effects is maintained when
351 analyzing the spatial variability of N-, C-, and P-variables independently. However, the
352 spatial variability of N-cycling processes was more sensitive to changes in temperature
353 and aridity than that of C-, and P-cycling. Whereas the effects of aridity and temperature
354 on N-SVM were mainly direct, in the case of C-SVM and P-SVM these effects were
355 indirectly driven by reductions in the number of plant patches promoted by aridity.
356 These findings significantly advance our understanding of the patterns and mechanisms
357 driving the spatial heterogeneity of soil multifunctionality across the globe, which is
358 critical for understanding the responses of terrestrial ecosystems to ongoing climate
359 change.

360

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372

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582 **Figures**

583 Figure 1. Relationships between mean annual temperature and aridity [defined as 1-
584 aridity index (ratio of precipitation to potential evapotranspiration)] and the variability
585 (coefficient of variation) of soil multifunctionality (SVM). The solid lines represent the
586 fitted regressions. R^2 shows the proportion of variance explained.

587

588 Figure 2. Random forest mean predictor importance (% of increase of MSE) of biotic
589 and abiotic drivers on the spatial variability (coefficient of variation) of soil
590 multifunctionality (SVM, a), N-related variables (SVM-N, b), C-related variables
591 (SVM-C, c), and P-related variables (P-SVM, d). Significance levels of each predictor
592 are as follows: * $P < 0.05$, ** $P < 0.01$, and *** $P < 0.001$.

593

594 Figure 3. (a) Effects of mean annual temperature, aridity, soil variables (pH and sand
595 content), biotic attributes (plant cover and richness, number of plant patches and woody
596 to herbaceous cover ratio [W/H]) and geographical coordinates (longitude and latitude)
597 on the spatial variability (coefficient of variation) of soil multifunctionality (SVM).
598 Numbers adjacent to arrows are standardized path coefficients, analogous to relative
599 regression weights, and indicative of the effect size of the relationship. * $P < 0.05$ and
600 ** $P < 0.01$. Only significant relationships ($P < 0.05$) are shown. Arrow widths are
601 proportional to the strength of the relationship. Squares are observable variables. The
602 proportion of variance explained (R^2) appears alongside the response variable in the
603 model. Goodness-of-fit statistics for each model are shown in the bottom (d.f.= degrees
604 of freedom; RMSEA = root mean squared error of approximation). The components
605 within spatial geolocation, climate, soil (properties) and plant attributes are included as
606 independent observable variables in the model, however we group them in the same box
607 in the model for graphical simplicity. (b) Standardized total effects (direct plus indirect
608 effects derived from the structural equation models) of SVM predictors.

609

610 Figure 4. Effects of mean annual temperature, aridity, soil variables (pH and sand
611 content), biotic attributes (plant cover and richness, number of plant patches, and woody
612 to herbaceous cover ratio [W/H]) and geographical coordinates (longitude and latitude)
613 on the spatial variability (coefficient of variation) of the soil multifunctionality of N-
614 (a), C- (c), and P-(d) related variables (N-SVM, C-SVM, and P-SVM, respectively).
615 Numbers adjacent to arrows are standardized path coefficients, analogous to relative

616 regression weights, and indicative of the effect size of the relationship. * $P < 0.05$ and
617 ** $P < 0.01$. Only significant relationships ($P < 0.05$) are shown. Arrow widths are proportional
618 to the strength of the relationship. Squares are observable variables. The proportion of
619 variance explained (R^2) appears alongside the response variable in the model.
620 Goodness-of-fit statistics for each model are shown in the bottom (d.f.= degrees of
621 freedom; RMSEA = root mean squared error of approximation). The components within
622 spatial geolocation, climate, soil (properties) and plant attributes are included as
623 independent observable variables in the model, however we group them in the same box
624 in the model for graphical simplicity. Plots (b), (d) and (f) show the standardized total
625 effects (direct plus indirect effects derived from the structural equation models) of N-
626 SVM, C-SVM, and P-SVM predictors, respectively.

627

628 Extended data Figure 1: Map of the location of the sites used in this study.

629

630 Extended data Figure 2: A-priori structural equation model used in this study. We
631 included spatial coordinates (latitude and longitude), climate (aridity and mean annual
632 temperature), soil characteristics (sand content and pH), and biotic attributes (cover,
633 richness, number of plant patches, and woody: herbaceous cover ratio) as potential
634 drivers of the spatial variability of soil multifunctionality (SVM). We built our
635 structural equation model by considering all these relationships, as explained in the
636 Methods section of the manuscript.

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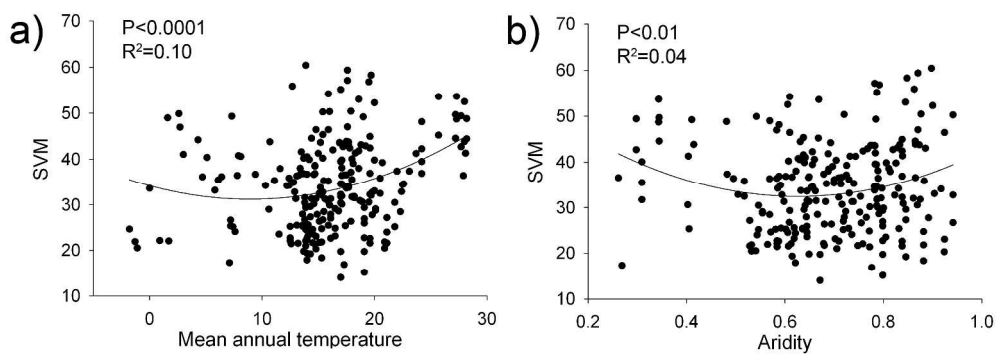


Figure 1

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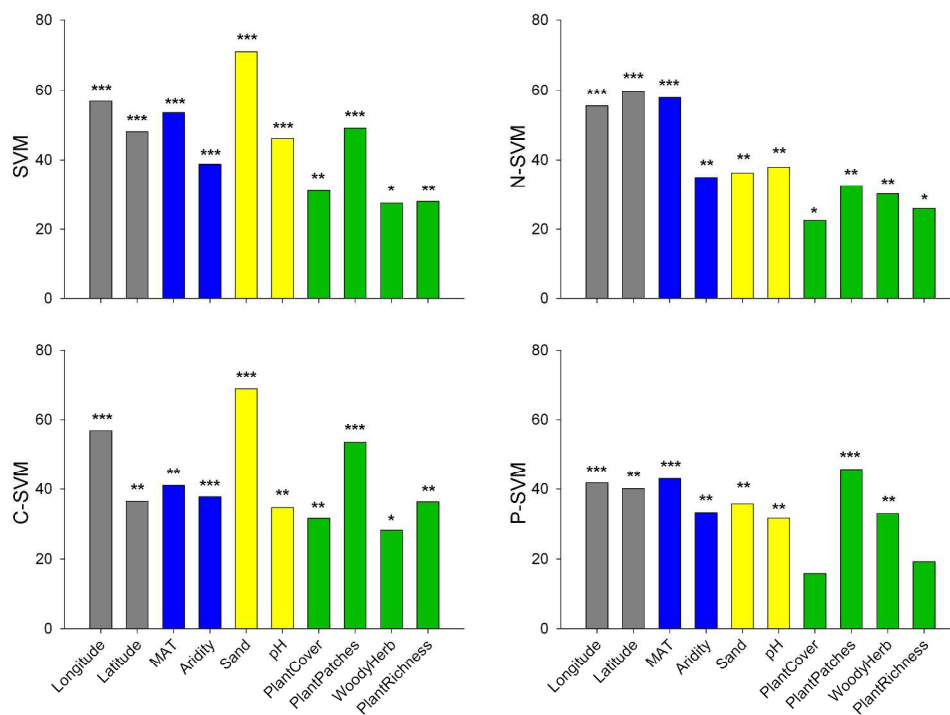


Figure 2

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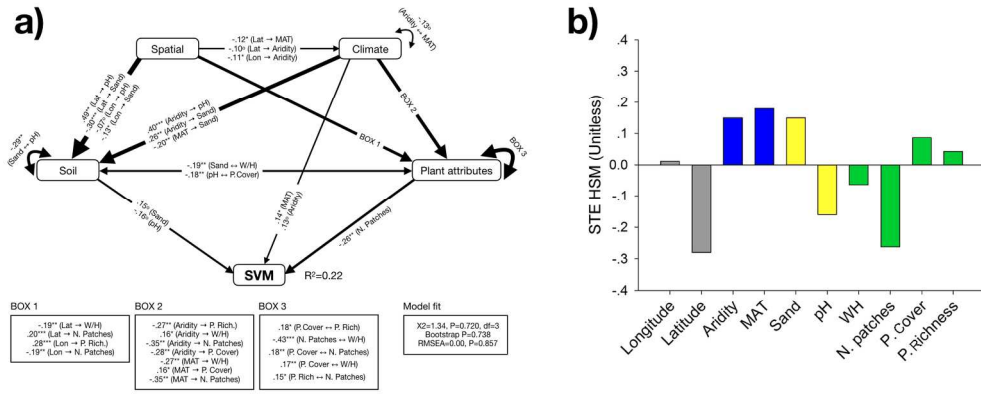


Figure 3

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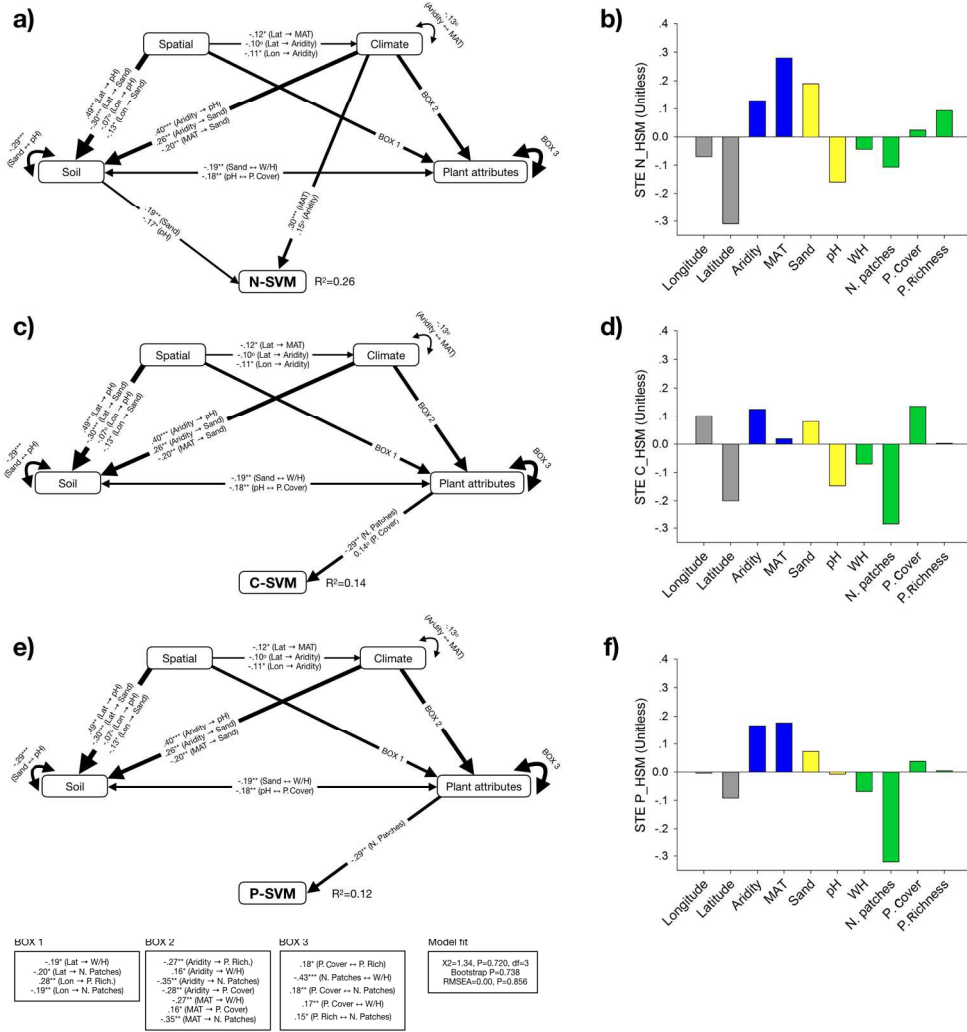
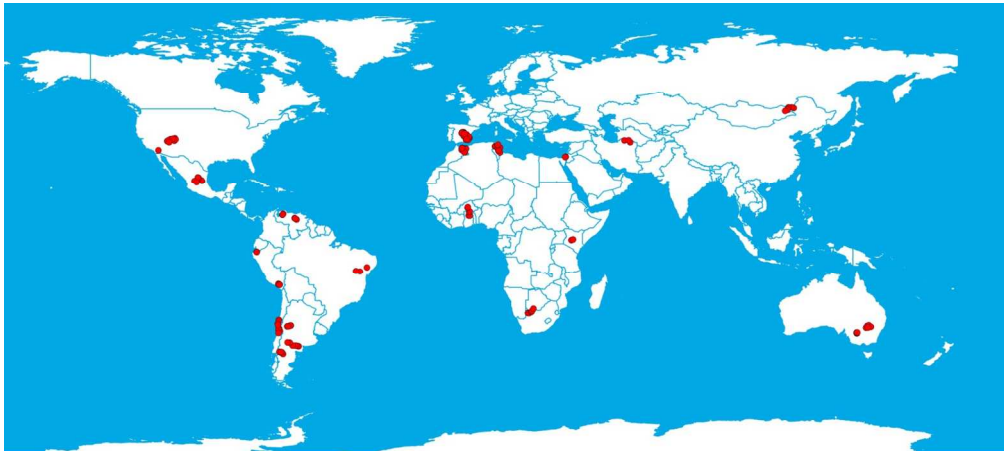
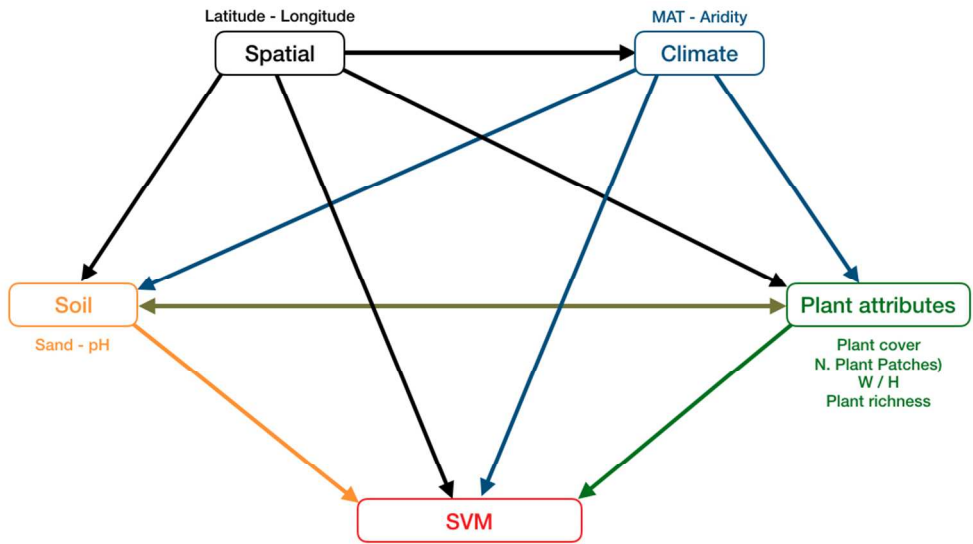


Figure 4



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