

1 **The interplay between facilitation and habitat type drive spatial vegetation patterns in**
2 **global drylands**

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4 Miguel Berdugo*¹, Santiago Soliveres², Sonia Kéfi³, Fernando T. Maestre¹

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

9 ²Institute of Plant Sciences, University of Bern, Altenbergrain 21, 3013 Bern, Switzerland.

10 ³ISEM, CNRS, Université de Montpellier, IRD, EPHE, Montpellier, France.

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12 *Correspondance to: mglberdugo@gmail.com. ORCID id: 0000-0003-1053-8907

13

14 **ABSTRACT**

15 The size distribution of discrete plant patches (PSD), a common descriptor of the spatial
16 patterns of vascular vegetation, has been linked to variations in land degradation and
17 ecosystem functioning in drylands. However, most studies on PSDs conducted to date have
18 focused on a single or a few study sites within a particular region. Therefore, little is know on
19 the general typology and distribution of PSDs at the global scale, and on the relative
20 importance of biotic and abiotic factors as drivers of their variation across geographical
21 regions and habitat types. We analyzed 115 dryland plant communities from all continents
22 except Antarctica to investigate the general typology of PSDs, and to assess the relative
23 importance of biotic (plant cover, frequency of facilitation, soil amelioration, height of the
24 dominant species) and abiotic (aridity and sand content) factors as drivers of PSDs across
25 contrasting habitat types (shrublands and grasslands). We found that both power-law and
26 lognormal PSDs were generally distributed regardless of the region of the world considered.
27 The percentage of facilitated species in the community drives the emergence of power-law
28 like spatial patterns in both shrublands and grasslands, although mediated by different
29 mechanisms (soil and climatic amelioration, respectively). Other drivers of PSDs were
30 habitat-specific: height of the dominant species and total cover were particularly strong
31 drivers in shrublands and grasslands, respectively. The importance of biotic attributes as
32 drivers of PSDs declined under the most arid conditions in both habitats. We observed that
33 PSDs deviated from power law functions not only due to the loss of large, but also of small
34 patches. Our results expand our knowledge about patch formation in drylands and the habitat-

35 dependency of their drivers. They also highlight different ways in which facilitation may act
36 on ecosystem functioning through the formation of plant spatial patterns.

37

38 **KEYWORDS**

39 Aridity, functional traits, grasslands, patch-size distributions, power laws, shrublands, spatial
40 patterns.

41 INTRODUCTION

42 Vegetation in arid, semi-arid and dry-subhumid ecosystems (drylands, hereafter) is usually
43 arranged in a two-phase mosaic formed by plant patches interspersed in a matrix of open areas
44 devoid of perennial vascular vegetation (Tongway et al. 2001). The frequency of size classes
45 of these plant patches (patch-size distributions, referred to as PSD hereafter) can be
46 characterized by heavy-tail distributions, which have been linked to changes in ecosystem
47 functioning (Maestre and Escudero 2009, Berdugo et al. 2017b) and degradation status (Kéfi
48 et al. 2007a, Scanlon et al. 2007) in drylands. Mathematical models suggest that PSDs of
49 dryland vegetation follow power law functions (i.e., there are many small patches and a few
50 very large ones, (Kéfi et al. 2007a, Scanlon et al. 2007), and that increasing environmental
51 harshness (e.g. higher aridity or grazing pressure) reduces the number of large patches,
52 thereby generating truncated power laws (Kéfi et al. 2007a, Lin et al. 2010).

53 The shift from power-law to other PSDs has been observed in field sites undergoing
54 degradation (Kéfi et al. 2007a, Scanlon et al. 2007, Lin et al. 2010), but truncated power laws
55 or lognormal functions have also been found to best fit PSDs in well preserved ecosystems
56 (Maestre and Escudero 2009, von Hardenberg et al. 2010, Berdugo et al. 2017b). To explain
57 these contrasting results, we need to better understand the ecological mechanisms by which
58 PSDs shift from power law to other distributions. Plausible ecological mechanisms, such as
59 the loss of large patches or the emergence of dominant scales (i.e., overrepresentation of some
60 patch sizes) have been proposed to explain changes in PSDs (e.g., see Von Hardenberg et al.
61 2001, Xu et al. 2015). Nevertheless, we still lack empirical evaluations of the importance of

62 these ecological processes in real-world ecosystems, which precludes a complete
63 interpretation of the effects that plant spatial patterns may have on ecosystem functioning.

64 Facilitative interactions are often invoked as a major driver of PSDs in drylands, as
65 they promote the formation of large patches that underpin the creation of power-law PSDs
66 (Kéfi et al. 2007a, Scanlon et al. 2007, Xu et al. 2015, Berdugo et al. 2017b). Facilitative
67 mechanisms that can increase the size of plant patches include improvements in soil and
68 microclimatic conditions beneath nurses, which allow protégé plants to thrive under
69 environments to which they are poorly adapted (Maestre et al. 2003, Liancourt et al. 2017,
70 Berdugo et al. 2017c). Whereas soil amelioration depends on the attributes of nurses
71 (Pugnaire et al. 1996, Maestre et al. 2001) and the environmental conditions in which they
72 live (e.g., sandy soils exhibit the largest differences in fertility between nurse and open areas,
73 see Ochoa-Hueso et al. 2017), the effect of shading may be more influenced by the pool of
74 beneficiary species and their relative adaptation to climate (Soliveres and Maestre 2014,
75 Liancourt et al. 2017, Berdugo et al. 2017c). Both facilitative mechanisms could be important
76 mediators of the impact of facilitation on ecosystem functioning by creating particular spatial
77 patterns, a link that is still poorly understood (Cardinale et al. 2002, Maestre et al. 2010,
78 Wright et al. 2017). Soil amelioration directly impacts average ecosystem functioning, and
79 also increases soil heterogeneity (Dean et al. 1999, Ochoa-Hueso et al. 2017). On the other
80 hand, preserving a high diversity of species may promote ecosystem functioning through
81 niche complementarity (Tilman et al. 1997, Gross et al. 2017). Thus, disentangling the
82 relative importance of different facilitative mechanisms on spatial pattern formation may

83 inform us about how facilitation affects ecosystem functioning via complementary processes
84 (spatial pattern formation versus direct soil amelioration and increased species richness).

85 PSDs are not only affected by degradation processes or facilitation. Functional traits of
86 the dominant species (Aguiar and Sala 1999, Maestre and Cortina 2005, Borthagaray et al.
87 2012), soil attributes (Von Hardenberg et al. 2001) or plant cover (Maestre and Escudero
88 2009) can also importantly affect PSDs. For instance, high cover might promote vegetation
89 clumping due to lack of space (Abades et al. 2014, Xu et al. 2015), while sandy soils usually
90 alter the distribution of resources causing interactions with facilitation mechanisms such as
91 differential infiltration rates (Rietkerk et al. 2004). Also, tall species may influence the basal
92 patch sizes from which PSDs emerge. Importantly, the factors driving PSDs may differ across
93 habitat types (Goslee et al. 2003, Lett and Knapp 2003, Bordeu et al. 2016), although this is
94 poorly understood due to the lack of cross-habitat studies. Contrasting dominant plant types,
95 such as grasses versus shrubs, exhibit different ways of reproduction (e.g. grasses tend to
96 reproduce via rhizomatous roots) and resource uptake (grasses have shallower roots than
97 shrubs) that inherently affect spatial pattern formation (Goslee et al. 2003, Lett and Knapp
98 2003, Ravi et al. 2008). Also, grasses and shrubs differentially affect ecohydrological
99 mechanisms such as run-off, erosion or evapotranspiration, with shrubs producing higher
100 differences in water availability with adjacent bare ground areas than grasses (Huxman et al.
101 2005, Ludwig et al. 2005, Okin et al. 2009, Berdugo et al. 2014). These ecohydrological
102 effects have been previously documented to affect the way in which grasses and shrubs
103 interact with other species (Aguiar et al. 1992, Maestre et al. 2003). Therefore, differences
104 between habitat types could also influence how processes such as plant-plant interactions

105 affect PSDs. Increases in aridity have been found to be correlated with reduced vegetation
106 cover (Delgado-Baquerizo et al. 2013) and different relative dominance of grasses vs. shrubs
107 in drylands (Knapp et al. 2008). Therefore, understanding the interactions between aridity and
108 other PSD drivers is of paramount importance to better understand and forecast how dryland
109 ecosystems respond to ongoing climate change.

110 The current lack of understanding of the relative importance of biotic vs abiotic
111 drivers of PSDs in drylands restricts our ability to forecast changes in their structure in
112 response to climate change, and to use them as indicators of land degradation in these areas.
113 To contribute to filling this gap in our knowledge, we investigated the PSDs of perennial
114 vegetation in 115 drylands from all continents except Antarctica spanning a wide range of
115 environmental conditions, soil and vegetation types. This allowed us to assess: (i) the region
116 and habitat-type dependency of PSDs in drylands worldwide, (ii) the relative importance of
117 aridity and biotic (plant cover, facilitative interactions, soil amelioration, habitat type and
118 plant functional traits) factors as drivers of PSDs, and (iii) whether the importance of different
119 PSDs drivers changes depending on the habitat considered (shrublands vs. grasslands).

120

121 **MATERIAL AND METHODS**

122 **Study sites and data collection**

123 We studied 115 dryland ecosystems from 13 countries (Fig. 1), which are a subset of the 236
124 sites from Ochoa-Hueso et al. (2017). Annual mean temperature and rainfall ranged from 2.6
125 to 25.7 °C and from 67 to 801 mm, respectively. Elevation, latitude and longitude varied from

126 76 to 4524 m.a.s.l., from -41° to 40° , and from -115° to 142° , respectively. The database
127 includes three habitat types (grasslands, shrublands and open woodlands/savanna); however,
128 we did not use open woodlands/savanna because there were very few sites suitable for our
129 analyses (see details below). Grassland and shrubland sites covered a wide range in species
130 richness (2 to 39 perennial species) and total plant cover (from 4.5 to 82.8 %). See Maestre et
131 al. (2012), for full details.

132 At each site we performed a standardized field survey protocol. We established four
133 30 m long transects separated 8 m from each other and measured the cover of perennial plants
134 using the line intercept method as detailed in Maestre et al. (2012). We also collected five soil
135 samples at 0-5 cm depth under the dominant species and in bare ground areas close by. These
136 soils were sieved (2 mm mesh), air dried for one month and stored for laboratory analyses. To
137 standardize soil analyses, the samples were shipped to Spain, where they were analyzed in the
138 same laboratory.

139 **Measurement of patch-size distributions**

140 From the 236 sites available, we used for this study 115 sites from which we were able to
141 quantify their PSDs using high-resolution remote sensing data (see Berdugo et al., 2017b) for
142 details). In brief, we downloaded VirtualEarth (<http://www.bing.com/maps>) and Google Earth
143 (<https://earth.google.com>) images with resolution $\leq 30\text{cm/pixel}$. To obtain a sufficient number
144 of patches as to fit power law functions to their PSDs, we took three adjacent subplots of 50m
145 x 50m per site. The first one was placed to fit that surveyed in the field. We classified the
146 images by using automatic luminance threshold detection, and contrasted their results with

147 those from other classification methods based on expert knowledge (see Appendix 1 for
148 details). Finally, remote-sensing cover estimates from the first subplot were correlated with
149 field measurements to ensure that the classification procedure reproduced what was observed
150 on the field. The image classification analyses used fitted reasonably well observed field data
151 (see Appendix, Fig. S1).

152 For each site, we extracted all the patches and their sizes resulting from the image
153 classification analyses of the three subplots. We pooled them and fitted a power law to their
154 distributions. We used the approach of Clauset et al. (2009) to get the two main parameters of
155 power law distributions:

156
$$p(x) = \frac{\alpha-1}{x_{\min}} \left(\frac{x}{x_{\min}} \right)^{-\alpha} \quad \text{equation (1)}$$

157 where x represents the patch size and $p(x)$ describes the frequency of patches of a certain size.
158 This equation represents the probability density function of a power decay. The parameters of
159 the distribution are x_{\min} , the minimum patch size from which the fit to a power law starts
160 (below that point data are discarded from the fitting procedure) and α , the rate of decay of
161 frequency with patch sizes (see details in Berdugo et al., 2017b).

162 Sometimes the range of data remaining after discarding patch sizes lower than x_{\min} is
163 not representative of the observed PSD, especially when it is curved and best fits a lognormal
164 function. To obtain an estimation of the range of patch sizes to which a power law could be
165 fitted, we calculated the power law relative range (PLR) as:

166
$$PLR = 1 - \frac{(\log_{10}[x_{max}] - \log_{10}[x_{smallest}])}{(\log_{10}[x_{max}] - \log_{10}[x_{smallest}])} \quad \text{equation (2)}$$

167 where, $x_{smallest}$ and x_{max} are the size of the smallest and largest patch in the image,
168 respectively. PLR theoretically varies from 1 (all data fitted to a power law function) to 0 (no
169 data fits a power law function). PLR is related to the shape of the distribution and thereby to
170 the goodness of fit to a power law (Berdugo et al. 2017b), but is not exclusive to power law
171 distributions (i.e. may be used for other heavy tailed distributions as well; e.g. simulated
172 lognormal distributions fitted using this methodology had a PLR around 0.3-0.4). The use of
173 the PLR allowed us to: i) compare all PSDs among our sites, which vary from power law to
174 lognormal, using a standard methodology for all of them, and ii) produce general descriptors
175 of all the PSDs evaluated, independent of whether they fitted better to a power law or a
176 lognormal function.

177 **Assessment of biotic and environmental factors**

178 At each site, we measured biotic and environmental attributes known to influence PSDs: sand
179 content, aridity, plant cover, height of the dominant species, percentage of facilitated species
180 and soil amelioration (the increase in soil fertility under plant patches). Further rationale for
181 the selection of these variables is presented in Appendix 2.

182 We measured sand content according to Kettler et al. (2001). The aridity level for each
183 site was calculated as 1 – Aridity Index (AI). AI is precipitation/potential evapotranspiration,
184 obtained from Zomer et al. (2008), which use climatic interpolations provided by Worldclim
185 (Hijmans et al. 2005). Total perennial cover was estimated using the line-intercept method

186 along four 30-m long transects within each site, and ranged from 4% to 83% in our study
187 sites. The height of the dominant species was obtained from previous studies, local floras and
188 global databases (Kattge et al., 2011; see Soliveres et al., 2014, Le Bagousse-Pinguet et al.
189 2017, for more details on trait data acquisition). We introduced habitat type (grassland and
190 shrubland) to control for differences in the growth form of the dominant species. Habitat
191 types were identified both types depending on the dominant plant form inhabiting the sites.

192 We measured plant-plant interactions in two ways to disentangle their potential effects
193 on PSDs mediated either by their frequency or the strength of soil amelioration. First, as a
194 measure of the frequency of positive plant-plant interactions, we quantified the proportion of
195 species more associated with a given nurse than expected by chance. For doing so, we
196 compared the number of individuals found in open sites vs. those found under nurses and
197 calculated a χ^2 value for each pairwise interaction (see Soliveres et al., 2014 for full details).
198 The frequency of facilitative interactions was measured in a subset of 70 sites. Second, the
199 strength of soil amelioration may increase the survival and growth of beneficiaries by nurses.
200 We assessed it by measuring the difference in the organic carbon contents obtained in
201 vegetated and bare ground areas (Allington and Valone 2014). We measured organic carbon
202 by colorimetry after oxidation with a mixture of potassium dichromate and sulfuric acid
203 (Anderson and Ingram 1994).

204

205 **Statistical analyses**

206 *Describing the general typology of patch-size distributions*

207 The way in which PLR decrease may indicate processes of interest (e.g., decreases in PLR
208 associated with less small patches would indicate lack of recruitment, whereas a lack of large
209 patches would impede the clustering of plant patches). Thus, we attempted to explore how the
210 geometry of PSDs changed with decreasing PLR. The parameters x_{\max} and x_{\min}
211 (corresponding to the maximum patch size and the patch size of the initialization point of a
212 power law, respectively) are involved in the calculation of PLR. Hence, according to eqn 2,
213 we expect PLR to decrease with higher x_{\min} or lower x_{\max} . By relating both parameters to PLR
214 we expect to gain insights into how PLR shortening occurs in curved PSDs. It might be either
215 that: i) large patches become more infrequent with departures from power law fitting, thus
216 shrinking PLR from the right side of the PSD; ii) the size of the large patches remain constant
217 in all the study sites and that PLR is reduced because power law initializes in larger patch
218 sizes (thus x_{\min} increases while x_{\max} remain constant; iii) that PLR is diminished as a
219 consequence of both processes at the same time. To visualize the change in overall geometry
220 of PSDs with decreasing PLR, we collapsed all PSDs into a single plot.

221 *Identifying the drivers of patch-size distributions*

222 Prior to analyze the drivers of PLR, we fitted a statistical model to PLR as a function of both
223 latitude and longitude to assess whether PSDs exhibited any biogeographic trend. We also
224 compared the PLR of different zones of the world to evaluate whether these biogeographic
225 patterns were found in different study areas. To defined the zones as: North America; South
226 America, Mediterranean basin; Asia and Australia.

227 We used multi-model inference to assess how environmental and biotic drivers affect
228 observed PSDs. This analytical procedure fits all possible combinations of predictors and
229 ranks the models obtained according to their Akaike information criterion, corrected for small
230 sample size/ number of predictors ratio (AICc). Models deviating less than two units of AICc
231 from the best model, i.e. that with the lowest AICc, are not considered different from it
232 (Burnham and Anderson 2004). Between the best models selected according to this criterion,
233 a weighted average of standardized effects for each predictor is calculated (see Lukacs et al.,
234 2009). We built a model using PLR as a response variable, and sand content, aridity, habitat,
235 cover, height of the dominant species, facilitation and soil amelioration as predictors. We
236 evaluated all possible interactions of biotic attributes with aridity to assess whether the
237 deviations of PSDs from power laws that has been hypothesized when aridity increases (Kéfi
238 et al. 2007a) acts through interactions with biotic factors. To know whether different habitats
239 differ on the relative importance of other predictors as drives of PLR, we introduced all
240 possible habitat \times rest of predictors interactions. We repeated the analysis for grasslands and
241 shrublands separately to better show the interaction between habitat type and the other factors
242 evaluated. We performed this analysis with those sites for which we had all the information
243 (N=71), but analyses with the sites that did not include facilitation data (N = 111) were
244 consistent with those shown here (see Appendix, Fig. S2).

245 We performed multi-model inference analysis with the package MuMIn (Barton 2016)
246 in R (R Development Core Team 2008). Prior to model fitting, we box-cox transformed the
247 response variable to approximate normality of the residuals using the function boxcox of the

248 package MASS (Venables and Ripley 2002) in R. Primary data are available in figshare <doi:
249 10.6084/m9.figshare.5640193> (Berdugo et al. 2017a).

250 **RESULTS**

251 The PSDs of all 115 sites were heavy-tailed with varying levels of curvature (Fig. 2). We
252 found that the increase of x_{\min} and the decrease of x_{\max} acted in tandem to create deviations of
253 PSDs from a power law function (Appendix Fig. S3). As PLR decreased, PSDs tend to curve
254 by exhibiting a plateau in the first part of the distributions, thus suggesting the emergence of a
255 predominant scale (Fig. 2). A few distributions with a very low PLR showed ample curves
256 with high x_{\max} values (Fig. 2i), indicating the absence of processes forming power laws. Some
257 of the distributions with the highest PLR had spanning clusters (i.e., abnormally large patches
258 that are usually formed by vegetation merging in high covered sites, see Abades et al. 2014,
259 see Fig. 2v). In sum, the curvature of distributions with low PLR was explained mainly by a
260 loss of large patches, but also by a decrease in the relative proportion of small patches
261 compared to the distributions showing higher PLR (Fig. 2).

262 PLR values did not vary with latitude, and increased slightly with longitude (Fig. 1).
263 However, PLR maintained similar values across regions of the world (except for Africa and
264 Asia, where they were higher compared to the Mediterranean basin and South America and
265 North America, although a few points were sampled in the former regions, Appendix, Fig.
266 S4). When we analyzed all habitat types together, total cover, percentage of facilitated species
267 and the height of the dominant species were the main biotic factors driving the emergence of

268 power laws in PSDs (Fig. 3). The two latter interacted significantly with aridity, with a
269 reduced effect of plant height and facilitation under drier conditions. Aridity and sand content
270 were only significant in the models with the highest statistical power (i.e., without percentage
271 of facilitated species as a predictor, Appendix Fig. S2) and led in both cases to more curved
272 PSDs.

273 The importance of PLR drivers varied with the habitat type considered, as suggested
274 by the interactions between habitat type and soil amelioration in the overall model (Fig. 3a).
275 In grasslands, the main predictor of PLR was total cover, followed by the percentage of
276 facilitated species (Fig. 3b). In shrublands, height, percentage of facilitated species and soil
277 amelioration all promoted the emergence of power laws in PSDs (Fig. 3c). Effects of total
278 cover on the emergence of power laws were, however, dampened and even disappeared in the
279 models with more statistical power in shrublands (Appendix, Fig. S2). Soil sand content was
280 an important driver reducing the occurrence of large patches in shrublands, but not in
281 grasslands. As with facilitation and plant height, increasing aridity also dampened the effects
282 of soil amelioration on PLR.

283 **DISCUSSION**

284 **Typology of patch-size distributions**

285 Studies conducted over a few sites have shown that the PSDs of dryland vegetation
286 can be fitted to a power law function (Scanlon et al. 2007, Lin et al. 2010, Moreno de las
287 Heras et al. 2011). Our results confirmed these findings, and extended them to a wide variety
288 of dryland communities worldwide. We also showed that variations in PSDs are not driven by

289 geographical changes, but rather depend on the habitat type considered. The truncation of
290 power law patch distributions has been associated to the loss of large patches in ecosystems
291 undergoing degradation (Kéfi et al. 2007a, Lin et al. 2010). However, we also observed
292 deviations from power law functions due to the loss of not only the large, but also the small
293 patches. This is shown by the curvature observed both on the left and right parts of the PSD
294 (Fig. 2). The loss of both large and small patches is not often invoked as a major driver of
295 change in PSDs, although similar patterns to those observed here globally have been already
296 found in the field (Quets et al. 2013, Berdugo et al. 2017b), as well as in theoretical studies
297 (Marani et al. 2006, von Hardenberg et al. 2010). The loss of small patches could be
298 explained by a reduction in the number of recruited seedlings under harsh environments
299 (Weltzin and McPherson 1999), or by the lower number of isolated individuals found in
300 ecosystems dominated by facilitation (Bertness and Callaway 1994, Soliveres et al. 2014).

301 Apart from this general pattern, we found several types of distributions in the studied
302 drylands. For instance, some curved distributions (especially those with low PLR) appeared
303 without showing a plateau before x_{\min} . These distributions probably are better fitted by
304 exponential distributions than by lognormal ones. Both lognormal and exponential
305 distributions have been fitted to PSDs (Manor and Shnerb 2008, von Hardenberg et al. 2010),
306 but the former entails the emergence of a predominant scale, whereas exponential
307 distributions do not. Importantly, PSDs fitted by exponential distributions may still contain
308 large patches (Fig. 2i). This may be related with the overall scale of the system (i.e., when
309 trees are present, patches can be large and not clumped, and thus their PSDs would not exhibit

310 power laws). At the same time, we found evidence of the presence of spanning clusters (i.e.,
311 the appearance of very large patches spanning one side of the studied area to the other, see
312 highest PLR cases in Fig. 2v). Spanning clusters are formed because high cover levels can
313 increase the merging of vegetation when biomass reaches a saturating level, even if there is no
314 mechanism promoting vegetation clumping (Abades et al. 2014, Xu et al. 2015). Although the
315 formation of spanning clusters has been found to be more frequent at cover values around
316 60% in previous studies (Abades et al. 2014), we found these clusters in sites with lower
317 cover values, while some sites with cover > 60% did not exhibit them (Appendix, Fig. S5).

318 **Abiotic factors drive the shape of patch-size distributions across habitats**

319 Although aridity was not a significant driver of the change in PSDs, it strongly modulated the
320 effects of biotic attributes on PSDs in shrublands, but not in grasslands. Grasslands in our
321 dataset were particularly prevalent under moderate aridity conditions (Appendix, Fig. S6), so
322 the lack of effect of aridity interactions might be a consequence of a lower aridity range in the
323 grasslands surveyed. Our findings indicate that, in shrublands, aridity prevents biotic
324 attributes (traits of the dominant species, plant-plant interactions) to form large patches under
325 the most arid conditions. This provides empirical support to the often hypothesized
326 facilitation collapse as the mechanism underlying shifts from power law to curved PSDs
327 under extreme environments (Kéfi et al. 2007b). Some studies have observed or hypothesized
328 a diminished importance of facilitation for community assembly as aridity increases
329 (Holmgren and Scheffer 2010, Berdugo et al. 2017c). Although this pattern does not seem to
330 hold for the effect of facilitation on species richness (Soliveres and Maestre 2014), unimodal

331 facilitation-aridity relationships have been observed for the effect of facilitation on species
332 abundances (Berdugo et al. 2017c). Such a decrease in the importance of facilitation has been
333 related to community specialization to arid conditions (Berdugo et al. 2017c), and, therefore,
334 may underpin the low importance of positive plant-plant interactions under these conditions.
335 Our results link this decrease in facilitative interactions with the reduction in the frequency of
336 large patches and to the abrupt changes in PSDs observed under extreme arid conditions
337 (Berdugo et al. 2017b).

338 **Habitat-specific factors drive the shape of patch-size distributions**

339 We found large differences in the drivers of PSDs depending on the habitat type considered.
340 In grasslands, the main factor controlling the emergence of large patches was total cover. It is
341 important to note that we cannot differentiate cause from consequence (cover driving spatial
342 pattern or the other way around) from our observational study. On the one hand, some studies
343 have linked patch formation with increases in the ability of plants to maintain a high biomass
344 due to an increased resource capture efficiency (Aguiar and Sala 1999, Boer and
345 Puigdefábregas 2005). On the other hand, as we already discussed, high cover can lead to the
346 emergence of spanning clusters. In shrublands, the effect of cover on PLR was not as high as
347 in grasslands, and was not even significant in the model performed with our highest amount
348 of sites (Appendix, Fig. S2). Since total cover does not differ between habitat types ($F_{1,68} =$
349 1.14 , $P = 0.29$, in the dataset with facilitation [$N=71$]; $F_{1,109} < 0.01$, $P = 0.95$, in the full
350 dataset), this result suggests either that: i) cover is not enhanced in shrublands by spatial
351 pattern formation or ii) clumping of vegetation into large patches due to space constraints is

352 more likely in grasslands than in shrublands. In this last case, mechanisms such as the way in
353 which the different plant types compete (and thus repel each other) might be playing a
354 determinant role. In shrublands, individuals are larger, and also structure forming strata that
355 might increase competition for light that is less likely to occur between grasses. The latter is
356 supported by the significant effect of height on PLR found in shrublands, but not in
357 grasslands, thus indicating that the size of dominant individuals is important to define PSDs.
358 As a result, the formation of patches in shrublands strongly relies on the size of the dominant
359 individuals, and merging with other plants through facilitative interactions may occur in
360 different strata, thus not showing a direct link with total cover as measured in this study.

361 We found that the percentage of facilitated species was an important driver of PLR in
362 both grasslands and shrublands, whereas soil amelioration was only important in shrublands.
363 We also found that, whereas in grasslands the number of individuals that are facilitated
364 promoted the formation of large patches (as shown by the better fit of the PSDs to a power
365 law), in shrublands this number had the opposite effect (Appendix, Table S1). This result
366 suggests that, in shrublands, the number of individuals is constraining the ability of nurses to
367 increase patch sizes, probably because the more individuals in an area, the less they can grow
368 (Schöb et al. 2014). This result probably relates to the way in which grasses and shrubs
369 exploit belowground resources. Grasses allow more species to coexist by expanding the
370 niches of less-adapted species and by promoting the coexistence of understory species
371 through niche segregation (Soliveres et al. 2011, 2015, Berdugo et al. 2017c). We showed that
372 this translates into the enlargement of patches. However, grasses have shallow roots. Thus,
373 once established, beneficiaries may have problems to grow under grasses, which often
19

374 compete with neighbouring plants (Paterno et al. 2016, O'Brien et al. 2017), specially at the
375 seedling stage (Barberá et al. 2006, Soliveres et al. 2010). Therefore, the patch size would be
376 directly related to the number of beneficiaries (which are probably small), but not to their
377 size, in this case (Appendix, Table S1). Conversely, shrubs exploit deeper water sources, and
378 their beneficiaries compete with each other to grow, but not with the nurse (Paterno et al.
379 2016, O'Brien et al. 2017), so the size of the patch is more influenced by both the size the
380 beneficiaries and that of the nurse. The association between the percentage of facilitated
381 species and PLR suggest that the results of previous theoretical approaches which investigated
382 the effects of facilitation on pattern formation on models without taking into account
383 multispecific responses of facilitation (e.g. Kéfi et al. 2007a, von Hardenberg et al. 2010) may
384 be affected by incorporating several plant species interacting with each others. Our study
385 highlights the necessity of including community-specific mechanisms of facilitation in models
386 on spatial patterns. These community-specific mechanisms may depend on species pool and
387 habitat filtering, in addition to the strength of facilitation *per se* (Fukami 2015, Berdugo et al.
388 2017c).

389 Our results relate soil amelioration mechanisms to patch formation only in shrublands,
390 and niche-complementarity mechanisms in both grassland and shrublands. These important
391 differences between habitat types on how facilitation drives patch formation have been
392 previously overlooked. Both mechanisms can directly impact ecosystem functioning (through
393 the effect of the dominants on nutrients pools, see Grime, 1998, or by enhancing the diversity
394 of species, see Tilman et al., 1997, respectively) and are directly affected by facilitation
395 (Maestre et al. 2003, Le Bagousse-Pinguet et al. 2014). It remains to be identified, however, if
20

396 these two facilitation-related mechanisms only have an indirect effect, mediated by their
397 effect on plant spatial patterns, or if they also have direct effects on ecosystem functioning.
398 Future studies need to examine whether these feedbacks between more direct (soil
399 amelioration and increases in species richness) and indirect (through the formation of spatial
400 patterns) effects of facilitation on ecosystem functioning might feedback on each other, to
401 better understand the overall consequences of facilitation for ecosystem functioning.

402 Our study also informs about the structural implications of the worldwide reported
403 shifts from grasslands to shrublands, also known as shrub or woody encroachment (Eldridge
404 et al. 2011). Shrub encroachment by itself does not necessarily entail losses in ecosystem
405 diversity and/or functioning (Eldridge et al. 2011, Eldridge and Soliveres 2015). However,
406 our findings suggest that, if the dominant growth form shifts, the processes of spatial pattern
407 formation might be altered and become more dependent on soil amelioration. If accompanied
408 by increases in aridity, our results predict that shrub encroachment could be associated to
409 fewer large patches due to facilitation waning, which might be linked to functionality losses
410 (Berdugo et al. 2017b). Indeed, the effects of shrub encroachment on soil functioning change
411 throughout aridity gradients, shifting from positive to negative with aridity (Jackson et al.
412 2002, Eldridge et al. 2011, but see Knapp et al., 2008).

413

414 **CONCLUDING REMARKS**

415 By examining the typology and drivers of PSDs in drylands worldwide, we found that PSDs
416 tend to deviate from power laws by losing large, but also small patches. Our results
417 demonstrate differences in the drivers of PSDs depending on the habitat type considered. We
418 provide evidence of the importance of positive plant-plant interactions as a driver of spatial
419 pattern formation, an effect that was mainly due to the addition of new species to the patches,
420 rather than by a soil amelioration effect under the nurses (although this mechanism was also
421 important in shrublands). We also highlight the importance of plant cover and the height of
422 the dominant species as drivers of PSDs in grasslands and shrublands, respectively. All
423 together, this study constitutes a significant step forward on our understanding of how
424 vegetation spatial patterns are formed and distributed in drylands, highlighting the influence
425 of habitat-type and aridity on the relative importance of the drivers of such patterns.

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429

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439

440 **AUTHOR CONTRIBUTIONS**

441 FTM designed the study and coordinated data collection. MB analyzed the data, helped by SK
442 and SS. MB wrote the manuscript, with contributions from all authors.

443

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609

610 **FIGURE CAPTIONS**

611 **Figure 1. Map of patch-size distributions across the studied sites.** The colour switch from
612 blue to red according to the power law relative range value. A: Map of the world; B: zoom on
613 Mediterranean area; C: Zoom on North America area; D: Zoom on South America area.

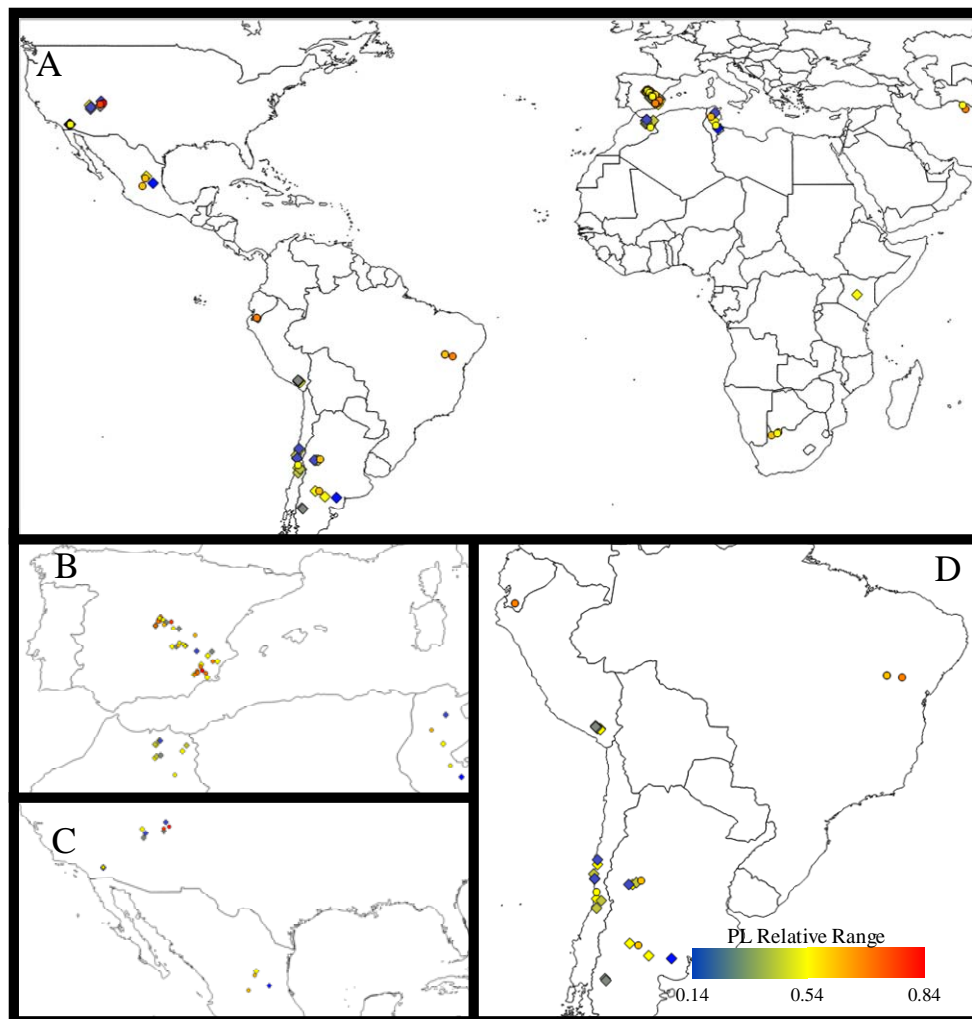
614 **Figure 2. Patch-size distributions of perennial vegetation in the drylands studied.** PSDs
615 with increasing PLR from left to right (i: 0.1-0.25; ii: 0.25-0.4; iii: 0.4-0.55; iv: 0.55-0.7 and
616 v: 0.7-0.85). Scales of both x and y axis are the same to ensure comparability. Color indicates
617 the power law relative range of distributions (PLR, according to the legend), with higher
618 values indicating a closer fit to a power law function.

619 **Figure 3. Drivers of patch-size distributions in global drylands.** Standardized effect sizes
620 of drivers of power law range for all habitat types (A; N= 70), grasslands (B; N = 37) and
621 shrublands (C; N = 33) after model averaging of the best models in multimodel inference
622 analysis (ΔAIC respect from the best model < 2). Abiotic (red) and biotic (blue) drivers, and
623 the interactions between them (dark red) and with habitat type (dark blue) are displayed.
624 Shaded areas represent 95% confidence intervals of effect sizes; the red line represents effect
625 sizes of 0 and the inner and outer dark grey lines represent effect sizes of -1 and 1,
626 respectively.

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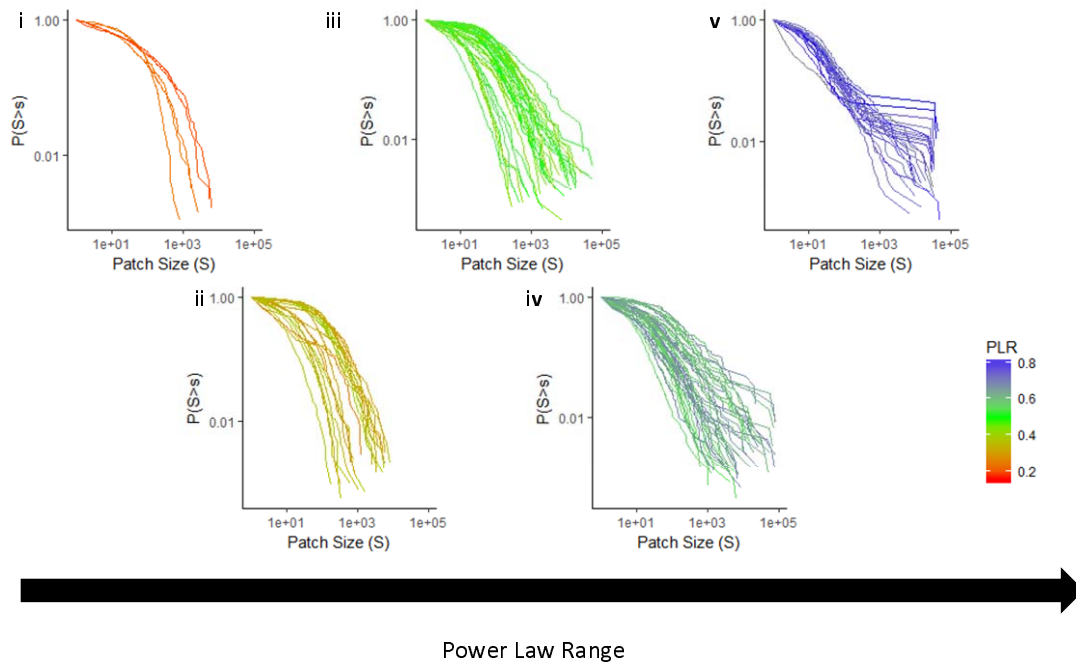
628

629 **FIGURES**



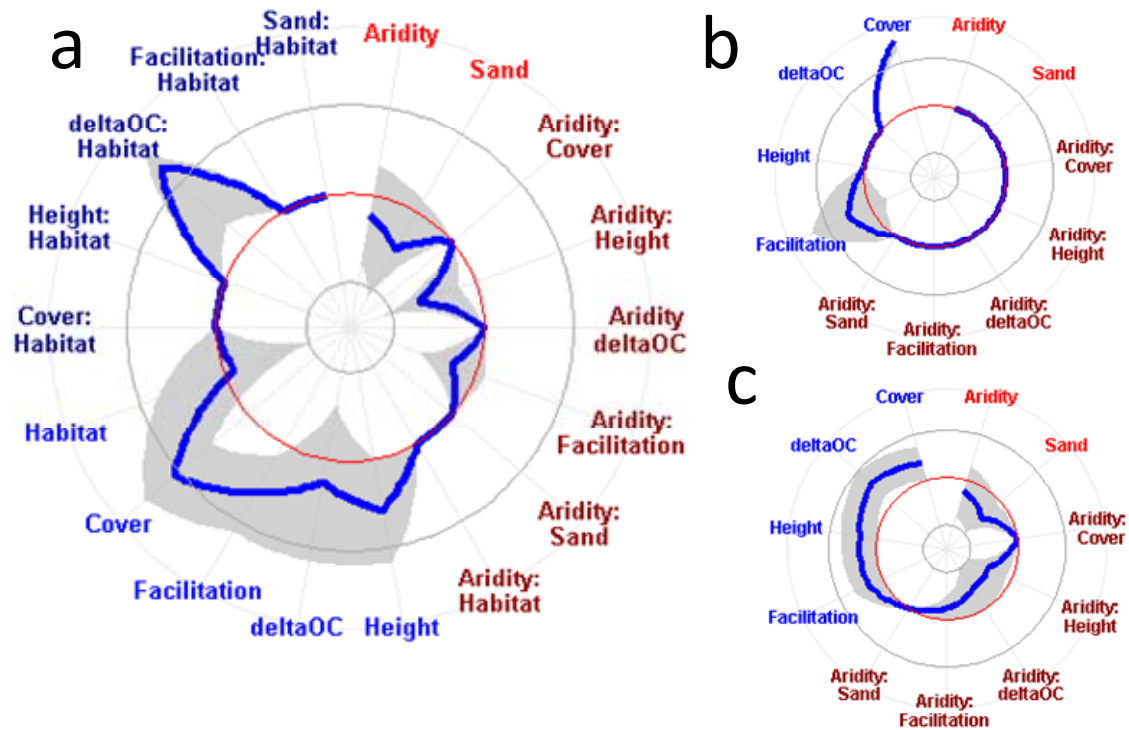
630

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