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2 **Self-organization as a mechanism of resilience in dryland**
3 **ecosystems**
4

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Abstract

Self-organized spatial patterns are a common feature of complex systems, ranging from microbial communities to mussel beds and drylands. While the theoretical implications of these patterns for ecosystem-level processes, such as functioning and resilience, have been extensively studied, empirical evidence remains scarce. To address this gap, we analyzed global drylands along an aridity gradient using remote sensing, field data and modeling. We found that the spatial structure of the vegetation strengthens as aridity increases, which is associated with the maintenance of a high level of soil multifunctionality, even as aridity levels rise up to a certain threshold. The combination of these results with those of two individual-based models indicate that self-organized vegetation patterns not only form in response to stressful environmental conditions but also provide drylands with the ability to adapt to changing conditions while maintaining their functioning, an adaptive capacity which is lost in degraded ecosystems. Self-organization thereby plays a vital role in enhancing the resilience of drylands. Overall, our findings contribute to a deeper understanding of the relationship between spatial vegetation patterns and dryland resilience. They also represent a significant step forward in the development of indicators for ecosystem resilience, which are critical tools for managing and preserving these valuable ecosystems in a warmer and more arid world.

71 **Significance Statement**

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The spatial structure of vegetation in dryland ecosystems has long fascinated scientists due to its striking appearance. Through a combination of global field surveys, mathematical models, and remote sensing, we show that the mechanisms responsible for these patterns enable healthy dryland ecosystems to adapt to changing environmental conditions, including water shortages, by adjusting their spatial structure. Conversely, degraded ecosystems do not have this ability. Our findings underscore the critical role of spatial pattern formation in promoting resilience in dryland ecosystems. Moreover, these spatial patterns could serve as valuable indicators of ecosystem health under a changing climate, opening important perspectives for future research in this field.

83 **Main Text**

84

85 **Introduction**

86

87 Abrupt, irreversible changes in ecosystems are a serious concern given the forecasts for future
88 environmental changes and their expected pace (1). Urgently needed tools are being developed to
89 characterize and anticipate shifts in ecosystem functioning and stability. While many of these tools
90 rely on analyzing temporal changes in ecosystem properties, the spatial structure of some
91 ecosystems can also teach us about the way these ecosystems cope with stressors such as
92 changes in climate (2–5). Indeed, interactions between species and their environment can generate
93 emergent spatial patterns even in the absence of underlying heterogeneity, referred to as ‘self-
94 organized’ patterns (3, 6, 7). Drylands are one of the textbook examples of ecosystems showing
95 such patterns, as their vegetation cover presents a striking spatial structure that displays well-
96 defined statistical properties across large spatial scales (2, 8–10). One of the most commonly
97 hypothesized underlying mechanisms is that, in the harsh environmental conditions of drylands,
98 established vegetation improves the local environmental conditions and alters the redistribution of
99 resources – in particular water – from bare areas to vegetation patches, which promotes the spatial
100 aggregation of plants (3, 7, 8, 11–14).

101

102 Theoretical studies have long suggested that self-organized spatial patterns could increase overall
103 ecosystem function and resilience (3, 4, 6, 11, 13). Indeed, the capacity of drylands to spatially self-
104 organize is predicted to allow them to maintain a higher productivity than what would be expected
105 in the absence of spatial structure (3, 7, 11, 13). These self-organized patterns may change with
106 environmental conditions, such as water shortage, giving drylands the ability to adapt and maintain
107 productivity by adjusting their spatial structure (3, 11, 13). This is expected to lead to relatively
108 stable levels of ecosystem functioning despite increasing stress, allowed by changes in spatial
109 patterns. However, empirical support for this hypothesis is still elusive. Furthermore, spatial
110 vegetation patterns can also hold the key to another generic phenomenon of interest: critical
111 slowing down (5). Indeed, theoretical models have shown that self-organized spatial patterns could
112 also be used as indicators of resilience loss because they reflect the speed required by the system
113 to recover from perturbations (15): as a dynamical system approaches a point at which its stability
114 changes drastically, it takes a longer time to recover from small perturbations, which leaves traces
115 both in the temporal and in the spatial dynamics of the system (15, 16). As a consequence, spatial
116 structure is expected to show increasing variance and auto-correlation (referred to as ‘spatial early
117 warnings’) as the ecosystem loses resilience (meaning as its recovery capacity decreases) (5, 17).

118

119 Previous empirical studies have analyzed changes in vegetation patterns along local gradients (2,
120 18, 19) or in specific aspects of the vegetation patches across large spatial scales (9, 10, 20).
121 However, building a robust predictive framework for dryland ecosystems requires going a step
122 further by confronting theoretical predictions from mechanistic models to empirical observations
123 covering large geographical scales and stress gradients. Doing so is essential to validate with
124 confidence the causality of theoretical predictions about vegetation spatial patterns, their
125 importance in maintaining dryland ecosystem resilience, and to evaluate whether and how spatial
126 patterns can be used as early warning signals for the onset of desertification and abrupt ecosystem
127 shifts (2–5, 11).

128

129 Here, we provide novel empirical support for the hypothesis that changes in the spatial structure of
130 vegetation lead to relatively stable levels of dryland ecosystem functioning despite increasing
131 stress. We used a global data set of 115 dryland sites (Fig. 1), for which field and remotely-sensed
132 data about their soil and vegetation features were gathered (21). After classifying the high
133 resolution remote sensing images of our data set into presence/absence of vegetation, we
134 estimated vegetation cover and quantified its spatial structure using relevant spatial metrics based
135 on theoretical studies (5): patch-based metrics (number and size of the vegetation patches),
136 hydrological connectivity (connectivity of the bare-soil area reflecting the overall potential of the
137 landscape to redistribute or lose resources by runoff), and spatial early warnings (quantifying the
138 resilience of the ecosystem) (see Materials and Methods). At the global scales, we directly

139 compared the observed trends in these metrics along an aridity gradient to those produced by two
140 different theoretical models previously used to investigate the emergence of spatial patterns in
141 drylands (8, 13). These models describe the spatio-temporal dynamics of the vegetation assuming
142 local facilitation (i.e., plants improve their local environment thereby facilitating the recruitment of
143 others in their direct neighborhood) and global competition for limiting resources such as water (see
144 Materials and Methods).

145 146 **Results**

147
148 A two-dimensional clustering analysis of the vegetation cover and soil multifunctionality (i.e., an
149 index derived from field measurements of carbon, nitrogen and phosphorus in the soil) of the field
150 sites surveyed revealed that our dryland sites could be split into two distinct groups of relatively
151 'healthier' (those with relatively high cover and soil multifunctionality) vs 'degraded' sites (those with
152 relatively low cover and soil multifunctionality; Figs. 2 and S11). These two groups of sites differ
153 significantly in all spatial metrics measured on vegetation cover but spatial auto-correlation (i.e.,
154 *Spectral Density Ratio*; Fig. 3). Compared to degraded sites, healthier sites have larger patches,
155 less connected bare areas (i.e., lower *flowlength*) and an overall less fragmented vegetation cover
156 (i.e., steeper slope of the patch size distribution) (Figs. 3 and 4).

157
158 Across all the sites surveyed, the fragmentation of the vegetation cover increases with aridity,
159 driving changes in patch-based metrics that match the expectation from theoretical models (Figs.
160 5 A, B and S7 in SI D). As environmental conditions become more stressful, the loss and
161 fragmentation of vegetation cover led to a change in the shape of the patch size distribution (2, 22,
162 23) and to an increase in the connectivity of bare-soil areas, as shown by increased values of
163 *flowlength* (24). These trends need to be compared to the expected changes caused by the loss of
164 vegetation cover for random spatial structure, hereafter called null model (see Material & Methods),
165 to assess whether the observed changes can be purely explained by a decrease in cover under
166 more arid conditions. We found that the observed breakdown of the patch size distribution in field
167 sites is weaker than expected in the null model (compare the colored and the grey points for patch-
168 based metrics in Figs. 5 A, B and S7). This means that vegetation in drylands is more spatially-
169 structured than expected and is growingly so as aridity increases.

170
171 Separate analyses of healthier and degraded sites revealed that the relative increase in spatial
172 structure with aridity mainly occurs for the healthier sites (Fig. 5 C left). These results indicate that
173 healthier sites thereby keep adapting their spatial structure as environmental conditions worsen.
174 For all patch-based metrics evaluated, the deviation from randomness increases with aridity. This
175 result suggests an increasing role of mechanisms enhancing the spatial aggregation of plants along
176 the aridity gradient (8) (Fig. S8, S9). Indeed, in the absence of such processes, spatial structure
177 emerges in the two theoretical models but is not different from a null expectation (Fig. S8,
178 S9). Possible underlying mechanisms to explain our results include positive plant interactions (7),
179 eco-hydrological feedbacks driving resource (especially water) redistribution in the landscape (24,
180 25), exogenous phenomena (e.g., spatial structure in soil moisture (26)), or a combination of these
181 mechanisms. The nature of our survey and analyses does not allow us to strictly conclude on the
182 presence and importance of such mechanisms. However, the fact that bare-soil connectivity
183 increases with aridity in the healthier group of sites - as shown by a significant increase in *flowlength*
184 - and the fact that it does so more than in the null model (Fig. 5 C left), suggests that at least water
185 distribution within the ecosystem plays a role (25). Indeed, an increase in *flowlength* means that
186 vegetation patches receive resources (e.g., water, nutrients) from a larger bare-soil area than would
187 be expected with a randomized spatial structure.

188
189 In the degraded sites, trends in patch-based and in hydrological connectivity metrics break down
190 along the aridity gradient: all trends are weaker than those in the healthier group of sites – several
191 being not significant -, and they are closer to the null expectation (Fig. 5 C right). These findings
192 indicate that the ability of the sites to undergo spatial reorganization under stress diminishes,
193 associated with a decline in functioning. This is evident from the significant decrease in soil

194 multifunctionality observed for these sites in response to increasing aridity ($p=1.2 \cdot 10^{-5}$, Fig. S13 in
195 SI).

196
197 For the healthier sites, since only spatial variance changes significantly but not spatial
198 autocorrelation, the spatial early warnings suggest no sign of resilience loss as aridity increases
199 (Fig. 5 C left). This is consistent with those sites showing limited signs of 'suffering' from increasing
200 aridity: cover decreases significantly with aridity because of constraints in water availability ($p=3.7$
201 10^{-7} , Fig. S13 in SI), but functioning is maintained through the spatial reorganization of the cover
202 (no significant decrease in soil multifunctionality with aridity; $p=0.8$, Fig. S13 in SI). However, in the
203 degraded group of sites, spatial early warnings do suggest a loss of resilience as aridity increases
204 (Fig. 5 C right), which probably reflects an overall physiological threshold of the vegetation at the
205 end of the aridity gradient (27).

206 207 208 **Discussion**

209
210 Our results, using a thorough evaluation of multiple spatial metrics – which reflect different facets
211 of ecosystem resilience – provide novel insights on how drylands cope with abiotic stress and how
212 their spatial structure contributes to improve their resilience to increased aridity conditions. Despite
213 the large environmental variability found across the different field sites studied, the overall
214 consistency of the observed changes in spatial metrics along an aridity gradient with theoretical
215 predictions is remarkable.

216
217 In this work, we have considered two different minimal models of dryland dynamics that share local
218 facilitation and non-local (long-range) effects as the two necessary drivers that generate self-
219 organized patterns with fat-tailed cluster distributions. Despite their differences, [these two models](#)
220 successfully matched the repertoire of [spatial patterns found in our data](#) (2, 8, 22). This supports
221 the idea of universality as defined in physics: macroscopic patterns in far-from-equilibrium systems
222 can be accounted for from minimal interaction rules (28–30). [In other words, simple mechanistic](#)
223 [models can provide reliable predictions beyond the specific, low-scale details.](#) It is noteworthy that
224 [other types of drylands than the ones studied here](#), such as semiarid savannas, [have been found](#)
225 [to exhibit a different type of behavior: available data](#) (31) and a different class of stochastic models
226 (26) indicate that their spatial patterns [show broadly-similar features as those found in our data but](#)
227 [are](#) caused by exogenous phenomena associated with the formation of soil moisture islands that
228 determine the spatiotemporal dynamics of tree clusters (26). [In these latter systems, we do not](#)
229 [expect the same trends in spatial metrics as those found here along an aridity gradient.](#)

230
231 Disentangling the mechanisms driving the self-organization and stability of drylands may require
232 metrics grounded in empirically-proven mechanisms, such as eco-hydrological feedbacks
233 evaluated in the field by the metric *flowlength*. The fact that bare-soil connectivity increases with
234 aridity in the healthier group of sites, and that it does so more than in the null model (Fig. 5 C left),
235 point towards the fact that such mechanism could include resource distribution within the
236 ecosystem (25). The consequences of this process on ecosystem stability are thought to arise from
237 two main eco-hydrological feedbacks of opposite signs in drylands (25). At a local (patch) scale,
238 an increase in bare-soil connectivity leads to a redistribution of resources from bare areas to
239 vegetation patches; this self-regulating (negative) feedback is overall stabilizing. At the ecosystem
240 scale, bare-soil connectivity increases runoff and therefore the potential losses of resources from
241 the ecosystem; this reinforcing (positive) feedback has been shown to be destabilizing (25). The
242 balance between these two feedback loops determines the hydrological response of the ecosystem
243 in terms of whether connectivity is overall stabilizing or destabilizing (25) and thus the ecosystem
244 ability to maintain itself in a productive state, or degrade into a more barren, less productive state.
245 In the healthier group of sites, the trends in spatial metrics found are consistent with the dominance
246 of a stabilizing feedback: an increase in bare-soil connectivity leads to more resource redistribution
247 from bare to vegetation areas, which leads to more vegetation patchiness (i.e., deviation from
248 random structure) and a further increase in connectivity, which contributes to the overall higher
249 functioning (i.e., higher soil multifunctionality) and cover of these sites compared to the degraded

250 sites. Conversely, the stabilizing feedback appears weaker in the degraded group of sites. Our
251 findings thereby empirically support one key prediction of theoretical models, namely that resource
252 redistribution from bare to vegetated patches, driven by bare soil connectivity, is a fundamental
253 mechanism that determines the emergent spatial structure of arid ecosystems (14, 24, 25).

254
255 Here, our analyses identified two alternative ways in which global drylands respond to increasing
256 abiotic stress through self-organization: one in which the vegetation patterns are building resilience
257 but also another in which this ability of the ecosystem is lost. In the first case, i.e., in self-organized
258 ecosystems, spatial structure reinforces itself with increasing aridity (i.e., the deviation from a
259 random structure increases). These changes in spatial structure, which are associated with
260 maintaining soil multifunctionality, help to mitigate the increased stress despite a decrease in cover
261 by allowing the ecosystem to retain enough water and maintain its overall functioning, which is
262 consistent with the idea that spatial self-organization is a mechanism of resilience at the ecosystem
263 scale (4). Importantly, we also found that failure to perform such changes in spatial structure, and
264 thereby retain resources, in degraded sites leads to a loss in functioning and resilience. Our results
265 empirically highlight the essential role of spatial patterns, and more specifically of the self-
266 organization process, for dryland functioning and resilience.

267 It is noteworthy that if vegetation patchiness allows the maintenance of cover and functioning for a
268 large range of aridity values, it only does so below an aridity threshold of 0.8 (Fig. 2). Indeed, there
269 are no high cover, high soil multifunctionality sites above an aridity level of 0.8. Therefore, if aridity
270 increases beyond that threshold in some of the sites of the healthier group, we expect them to
271 eventually shift to the degraded group of sites, thereby losing their cover and soil multifunctionality.
272 We expect sites to shift because there are only two (or maybe 3; see Fig. S11 in SI) groups of sites
273 globally, meaning that there is a limited number of states for dryland ecosystems to be in. This
274 aridity threshold of 0.8 corresponds to a known documented point at which drylands exhibit a
275 dramatic loss of vegetation cover accompanied by a decrease in species richness as well as a
276 change in plant leaf strategy from stress tolerance to stress avoidance (27).

277
278 Recent studies have suggested that spatial self-organization does not only contribute to increase
279 ecosystem resilience but can also allow them to evade tipping points (4). Interestingly, our results
280 imply that we do not have evidence that the ecosystems studied here are evading a tipping point
281 to desertification thanks to pattern formation (as suggested for regular vegetation patterns (4)).
282 Indeed, the self-organization process seems to only be effective in healthier sites and up to a
283 threshold level in aridity. It is however noteworthy that we are here comparing different ecosystems
284 in space and not following the temporal dynamics of a given ecosystem in time, which could draw
285 a different picture of an ecosystem response to increasing stress. Learning about whether the sites
286 studied are approaching a tipping point or not would require temporal data, a matter for future
287 research.

288
289 The fact that the observed changes in spatial metrics along the aridity gradient in healthier sites
290 are consistent with theoretical predictions is a crucial step in the development of reliable indicators
291 of desertification in drylands. Theoretical studies have suggested for a long time that the spatial
292 structure of vegetation patterns in drylands could be used to inform about the stress level
293 experienced by dryland ecosystems (2, 3, 11). Patch-based and hydrological metrics inform about
294 the ability of the ecosystem to adapt to increasing stress through self-organization (i.e., they inform
295 about 'ecological resilience' *sensu* C.S. Holling (32)), while spatial early warnings inform about the
296 recovery of the system after a perturbation (i.e., 'engineering resilience'). Both types of metrics
297 provide different but complementary information about the ecosystem's ability to respond to
298 increasing stress (Fig. S4). Finding consistent trends in spatial metrics in data and models is a
299 significant progress, but a knowledge gap still remains before we can build reliable spatial indicators
300 of ecosystem degradation, in particular indicators which can allow us to determine which
301 ecosystems are more fragile than others. In particular, one of the issues is that we need to get a
302 better understanding of how different mechanisms, e.g., due to the external pressures applied on
303 ecosystems, can affect the spatial patterns and possibly blur the signals observed here (23, 33–
304 36). Explicit data on land use intensity is needed to be able to address that concern.

305 By combining remote sensing, field data, and model simulations, our study contributes to
306 building a more robust framework to assess dryland degradation status. Our findings are relevant
307 to help identifying which drylands are more fragile, and, therefore, where efforts to preserve them
308 and prevent their degradation should be focused on. They also highlight the need for a system-
309 level, spatial picture of dryland vegetation, since spatial structure is both a driver of increasing
310 resilience and an early warning indicator of future ecosystem changes. Such efforts are
311 instrumental to avoid declines in ecosystem functioning that will reduce the delivery of essential
312 ecosystem services, forcing dryland inhabitants (which are already vulnerable) to either migrate or
313 change their livelihood drastically in the near future.
314

315 **Materials and Methods**

316 Data

317 The field data set contains vegetation and soil data from for 115 dryland ecosystems located in 13
318 countries (the data is described in details in (21)). The sites used (Fig. 1) differ widely in their abiotic
319 (elevation, temperature and precipitation) and biotic (vegetation type, cover and number of species)
320 characteristics (see database in figshare: <https://figshare.com/s/3db3640a61ebc975bcda>).
321

322 At each site, a 30 m x 30 m plot representative of the vegetation present in that area was
323 established in the field and plant cover was estimated using the line intercept method (see more
324 details in (21)). Five soil cores (0-7 cm depth) were taken in areas devoid of perennial vegetation
325 (to avoid implicit effects of vegetation cover within multifunctionality measurements) and 16
326 variables were measured related to the carbon (C; organic C, β -glucosidase activity, pentoses,
327 hexoses, aromatic compounds, and phenols), nitrogen (N; nitrate, ammonium, total N, potential N
328 transformation rate, aminoacids and proteins) and phosphorus (P; Available P, phosphatase
329 activity, inorganic P and total P) cycles. Variables are considered to be critical determinants of
330 ecosystem functioning in drylands. They were used to calculate a soil multifunctionality index,
331 multifunctionality, obtained as the average Z-score across these variables (21). High values of soil
332 multifunctionality have been associated with more functional ecosystems (20).
333

334 Values of the aridity index (AI, precipitation/potential evapotranspiration) were obtained from Zomer
335 *et al.* (37), who used the data interpolations provided by Worldclim (38). To facilitate the
336 interpretation of the results, we calculated the aridity level of each site as $1 - AI$ (39). Indeed, as
337 formulated, AI decreases when aridity increases, which is not intuitive; Using $1-AI$ instead of AI
338 solves this issue as our proxy of aridity increases as aridity does (so higher values of this aridity
339 level indicate drier conditions), which makes our results easier to understand.

340 For each study site, remote sensing data was obtained from ref. (20). The data consists in Google
341 EarthTM (<https://earth.google.com/>) or VirtualEarthTM (<http://www.bing.com/maps>) images of
342 sufficient quality to visually identify vegetation patches. For each field site, three 50 m x 50 m
343 images were collected, one of them was centered on the 30 m x 30 m plot surveyed in the field,
344 and the other two were located nearby, avoiding strong slopes and man-made structures like roads
345 or buildings. Each image was transformed to identify vegetation vs bare soil pixels: A k-mean
346 classification approach implemented in Matlab (The MathWorks Inc., MATLAB v. 7.5.0.342,
347 R2007b) was used to partition the pixels in clusters of luminance intensity (using a monochromatic
348 version of the image) (see ref. (20) for details). The transformed images contain information about
349 the presence or absence of vegetation in each pixel.

350 As a surrogate of plant productivity, we used the Normalized Difference Vegetation Index (NDVI),
351 which provides a global measure of the “greenness” of vegetation across the Earth’s landscapes
352 and is positively linked with vegetation productivity (40). This data was retrieved from previous
353 papers (20, 21) in which NDVI data for each plot was acquired using Landsat 5 TM and Landsat 7
354 ETM+, at a 30 m x 30 m resolution (<https://landsat.gsfc.nasa.gov/>), i.e., at the resolution of the
355 sampled plots. For each site, the mean annual NDVI for each year between 2000 and 2015 was
356 calculated and then averaged for the entire period.
357

358 Characterization of the spatial structure of the vegetation

359 We computed the spatial metrics on the matrices of presence-absence of vegetation inferred from
360 the satellite images using the R package spatialwarnings (v3.0.3) (41, 42). Self-organized systems

361 exhibit common changes in spatial structure as they approach a transition (5, 41). We calculated
362 the generic spatial early warnings that are known to capture such changes (5, 41): spatial variance,
363 near-neighbor correlation (*Moran's I*), and spectral density ratio (*sdr*). Spatial variance, spatial
364 correlation, and *sdr* are expected to increase as a dynamical system approaches a transition (a
365 "bifurcation" point) (see Fig. S6 and S7 for expected trends along a stress gradient based on model
366 simulations) (5, 17, 43, 44). Indeed, as an ecosystem is approaching a transition, neighboring cells
367 are expected to become more similar (5). In the results, we did not display *Moran's I* as it was highly
368 correlated with *sdr* (correlation=0.897).

369 For spatial variance, the matrices of presence-absence of vegetation were coarse-grained using 4
370 x 4 submatrices as explained in refs. (5, 18, 45). Note that this was not the case for spatial
371 correlation which does not require coarse-graining. The principle of coarse-graining is that each
372 matrix of dimension $n \times n$ is transformed into nonoverlapping submatrices of size $s \times s$ (with here
373 $s=4$). Each submatrix is then replaced by its average to obtain a smaller 'coarse-grained matrix' of
374 size $c_g \times c_g$ where $c_g=n/s$ (5).

375 For each matrix, two pixels are assumed to be part of the same vegetation patch if they are
376 neighbors (one of the four nearest neighbors, i.e., von Neumann neighborhood). We thereby
377 calculated the size of all the patches in a given matrix and extracted a number of 'patch-based
378 metrics'. We fitted a truncated power law to the patch size distribution of each matrix and recorded
379 the exponent and the cutoff of the fit. We also recorded the fraction of the image covered by the
380 largest patch using $\log_{10}(\text{largest patch}/\text{image size})$, where 'image size' is the number of pixels (2,
381 5, 20, 22).

382 We calculated *flowlength*, a metric that measures the potential hydrological connectivity of runoff-
383 source areas (e.g., bare soil) according to the vegetation cover, its spatial structure and the
384 topography (14). *Flowlength* is defined as the average length of all the potential runoff pathways in
385 the plot. Thus, a higher value of *flowlength* indicates a higher hydrological connectivity of runoff
386 source areas. *Flowlength* has been suggested to be an indicator of dryland functional status by
387 assessing potential water and soil losses in patchy landscapes (14, 24). See SI B and Fig. S3 for
388 additional information about *flowlength* calculations.

389 To estimate whether the spatial metrics for each plot differ from what would be expected based on
390 the amount of cover, null expectations for the values of each of the spatial metric were obtained by
391 reshuffling the pixels of the transformed matrices 199 times (5, 18, 41). The number 199 is
392 estimated to be sufficient in this case because subsequent analyses only depended on the means
393 of the null distributions created. The reshuffling process removes any spatial structure from the
394 original data while keeping the vegetation cover fixed. The same spatial metrics were then
395 calculated on the reshuffled matrices. Note that this works well in the model, where each pixel is
396 assumed to be a plant, but in the images, depending on the plant species, a pixel can contain many
397 individuals or a plant (tree) can be composed of many pixels.

398 Each of these metrics is quantified on the three matrices obtained for each field site (i.e., 345
399 values), except for *flowlength* which could only be measured on the plot among the three that was
400 centered on the field plot (i.e., 115 values) since the slope of the field site is required to calculate
401 *flowlength* and that information was only available for the plots sampled in the field.

402

403 Clustering analysis: splitting sites in groups

404 Clustering analyses were performed to see whether the data set could be split in different groups
405 of sites and, if so, in how many groups. We combined multiple clustering methods to build a
406 consensus on the number of groups in the dataset as clustering results are sensible to the chosen
407 method and the underlying assumptions. We started by clustering the distributions of vegetation
408 cover and multifunctionality values in our dataset (i.e., two-dimensional clustering) using
409 hierarchical clustering (*hclust*) based on a Euclidean distance matrix and a Ward distance, which
410 is appropriate for globular clusters (using the stats package included in R v.4.2.0 (42)). Inspecting
411 the resulting tree (see Fig. S11) suggested that the dataset could be well-described by either two
412 or three groups, which was confirmed by the result of a permutation-based analysis carried out
413 using the function *simprof* in the *clustsig* R package v1.1 (42, 46), suggesting three significant
414 groups. We further investigated this pattern based on a Gaussian mixture approach, using the best
415 number of clusters based on the Bayesian Information Criterion (BIC). This was done using the
416 *mclust* R package v6.0.0 in R (42, 47). This latter approach suggested the split of the dataset into

417 two groups for all but one type of cluster shape, and in this specific case, only a small increase (<2)
418 in BIC was found by going from two to three groups (see Fig. S11). We thus considered the
419 consensus classification into two groups as the most relevant to characterize the distribution of
420 cover and multifunctionality in our dataset but provide all analyses for three groups in Fig. S16-
421 S19. We used the two groups predicted by the original hierarchical clustering (Fig. S11 in SI), but
422 those were in very close agreement (14 sites out of 345 are classified differently, 4%) with the
423 clustering based on the Gaussian mixture approach. We refer to these two groups of sites as
424 'healthier' (high cover – high soil multifunctionality) and 'degraded' (low cover – low soil
425 multifunctionality).

426 Identification of potential stable states

427 We used a density-based approach to detect dominant modes, which potentially reflect alternative
428 states of the ecosystem, along the aridity gradient evaluated (48–50). This approach is based on
429 the relationship between the empirical distribution of a set observations of a dynamical system and
430 its potential. Assuming the following dynamical system with a single state variable z , and dynamics
431 defined by a potential U (i.e., $dU/dz = - dz/dt$) along with a Wiener process dW

$$432 dz = -U'(z)dt + \sigma dW$$

433 where dW is a Wiener process and σ is the noise level, it can be shown (48–50) that there is a link
434 between the empirical distribution of observations p_d and U as

$$435 U = \frac{-\sigma^2}{2} \log(p_d)$$

436
437
438
439 p_d can be directly estimated from data using kernel density estimation. The above relationship
440 formalizes the intuition that a dynamical system will tend to spend more time fluctuating around its
441 stable equilibria, and away from its unstable equilibria. It gives a direct way to estimate what are
442 assumed to be stable and unstable equilibria: the local minima of the potential or stable equilibria
443 correspond to the local maxima of the density, and the local maxima of the potential or unstable
444 equilibria correspond the local minima of the density.

445
446 To estimate p_d along a gradient of aridity, we used a rolling-window approach in which for each
447 value of aridity, all observations of cover or multifunctionality are taken within a range of $x - \text{wdw}/2$
448 and $x + \text{wdw}/2$, where x is the aridity value and wdw is the window size (here $\text{wdw} = 0.15$). These
449 are used to compute the distribution p_d , and thus the hypothesized stable and unstable equilibria.
450 Doing so for all values of aridity x provides a visualization of possible stable and unstable equilibria
451 along the gradient and an estimation of the assumed potential. The distribution of states p_d was
452 estimated using a gaussian kernel density estimator of width 0.3 (function density() in base R). This
453 analysis was used for Fig. 2 A, B.

454 Slope of patterns along aridity & other statistical analyses

455 For the variables for which there was no replicate per site, i.e., 115 values (meaning all the variables
456 measured in the field and *flowlength*), comparisons among two groups were done with t-tests and
457 comparisons among the three groups with one-way ANOVA with Bonferroni adjustments of P-
458 values.

459 For all the spatial metrics for which there are three replicates per site (because of the three images),
460 we used linear regressions to test the trends of the spatial metrics along the aridity gradient
461 evaluated. To do so, we used a mixed-effect linear model with the site as random effect on the
462 intercept and with either aridity or group ('healthier' or 'degraded') as the sole fixed effect. These
463 models were fitted using the R package lme4 v1.1-29 (42). More specifically, for the analysis of the
464 effect of aridity on spatial metrics, for example, the linear mixed model: $l \sim \text{Aridity} + (1 | \text{site})$ was
465 fitted to the data for each spatial metric, l . Note that the theoretical predictions provide the expected
466 directions of change in the spatial metrics along a stress gradient (i.e., increase or decrease). The
467 significance of the fixed effect (either aridity or group) was tested by likelihood ratio test between
468 the full model (with the fixed and the random effect) and a model without the fixed effect (i.e., with
469 only the random effect).

471 The slope coefficient estimated for the fixed effect in this linear model indicates how the spatial
472 metrics (observed or null) change along the aridity gradient (a positive slope means that the metric
473 increases with aridity). To make the slopes easier to compare across indicators and to be
474 represented in figures, we standardized the observed and null indicator values. We computed the
475 mean and standard deviation of all observed and null values taken together, then subtracted this
476 mean to both the observed and null values, and divided by the standard deviation, obtaining a
477 standardized effect size. This yielded slopes that are within the same order of magnitude for all
478 indicators, while still allowing the comparison of observed and null slopes for a given indicator.
479 To obtain confidence intervals on the slope estimates (and thus test significant departure from
480 zero), we used ordinary bootstrap in which the slope was reestimated based on 2999 resampling
481 with replacement of the data used to carry out the fit. To determine confidence intervals using
482 bootstrapping, we need a high number of resamples so that the tails of the resulting distribution of
483 slopes are well-sampled; we used BOOTN=2999 based on recommendations in the literature (51).
484 The *flowlength* metric had only one value per site, thus it did not require the use of mixed-effect
485 modelling – for this spatial metric, we used a simple linear model but did use bootstrap to get
486 confidence intervals on the slope.

487

488 Spatial models of dryland vegetation dynamics

489 We ran simulations from two mathematical models of the spatio-temporal dynamics of vegetation
490 in dryland ecosystems. Only the results of Model 1 are displayed in the main text, while the results
491 of Model 2 are in SI E.

492 **Model 1** (Kéfi et al. 2007). We simulated the spatio-temporal dynamics of a dryland ecosystem
493 using a stochastic cellular automaton model that produces spatial structure of the vegetation like
494 the one observed in empirical data (2, 5, 13, 22–24). In this model, an ecosystem is represented
495 by a grid of cells, each of which can be in one of three states: vegetated, empty, or degraded (2).
496 Empty cells represent fertile soil, whereas degraded cells represented eroded soil locations that
497 are unsuitable for recolonization by vegetation. A key ecological mechanism is local facilitation, i.e.,
498 the positive effect of vegetation on its local neighborhood through increased regeneration of
499 degraded cells. Because of this local facilitation, vegetated cells tend to form patches, i.e., sets of
500 vegetated cells connected by a shared edge (von Neumann neighbors, i.e., the four nearest
501 neighbors). When aridity increases, there is a point at which the vegetation dies out and the system
502 becomes a desert through a saddle-node (or fold) bifurcation. The model exhibits bistability for a
503 range of aridity values (parameter $1-b$ in the model, see SI A for a detailed model description), with
504 the coexistence of a vegetated and a desert state (13). To evaluate the effect of the facilitation
505 mechanism on the trends in spatial metrics observed, we also ran simulations without the facilitation
506 mechanism. A more detailed description of the model as well as the parameter values used are
507 available in SI A.

508 **Model 2** (Scanlon et al. 2007). We checked whether the results we obtained were similar in a
509 second model (8), which is also a cellular automaton but considers only two possible states for the
510 cells, namely trees and empty. The probability of establishment of new trees is assumed to increase
511 with the neighborhood tree density, where the effect of the neighborhood tree density is a weighted
512 as a function of the distance to the focal cell. Conversely, the probability of tree mortality increases
513 with more empty cells in the neighborhood of a given tree. The model description, parameter values
514 are in SI A and the results in SI E, Fig. S8 and S9.

515 **Simulations of the two models.** We ran simulations on lattices of 100x100 cells. For each aridity
516 level, we recorded the final landscape after 10000 timesteps (for which steady state in overall cover
517 was typically reached). All spatial metrics and their corresponding null values were computed on
518 these landscapes (transformed into matrices of presence/absence of vegetation, i.e., removing
519 information about whether empty sites are fertile or degraded for Model 1) in exactly the same way
520 as previously explained for the data.

521

522

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524

Data sharing:

525 The code to reproduce the analyses of the paper is available on GitHub:

526 https://github.com/skefi/spatialews_biocom
527 The data is in this folder and will be put on the GitHub repository once the paper is accepted:
528 <https://www.dropbox.com/sh/8j4y4zm9an32rlw/AACB2O3T9vZJNYtOaBShsEQa?dl=0>
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530

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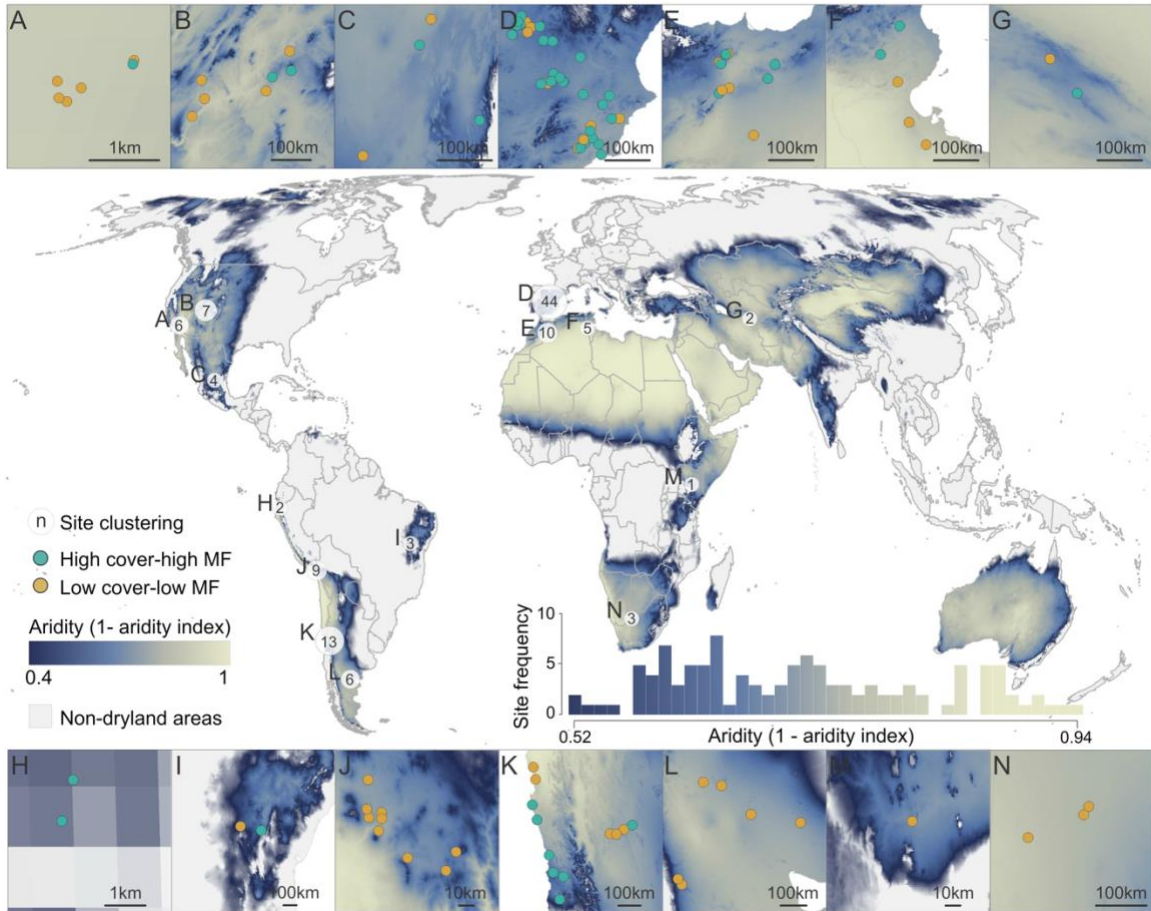
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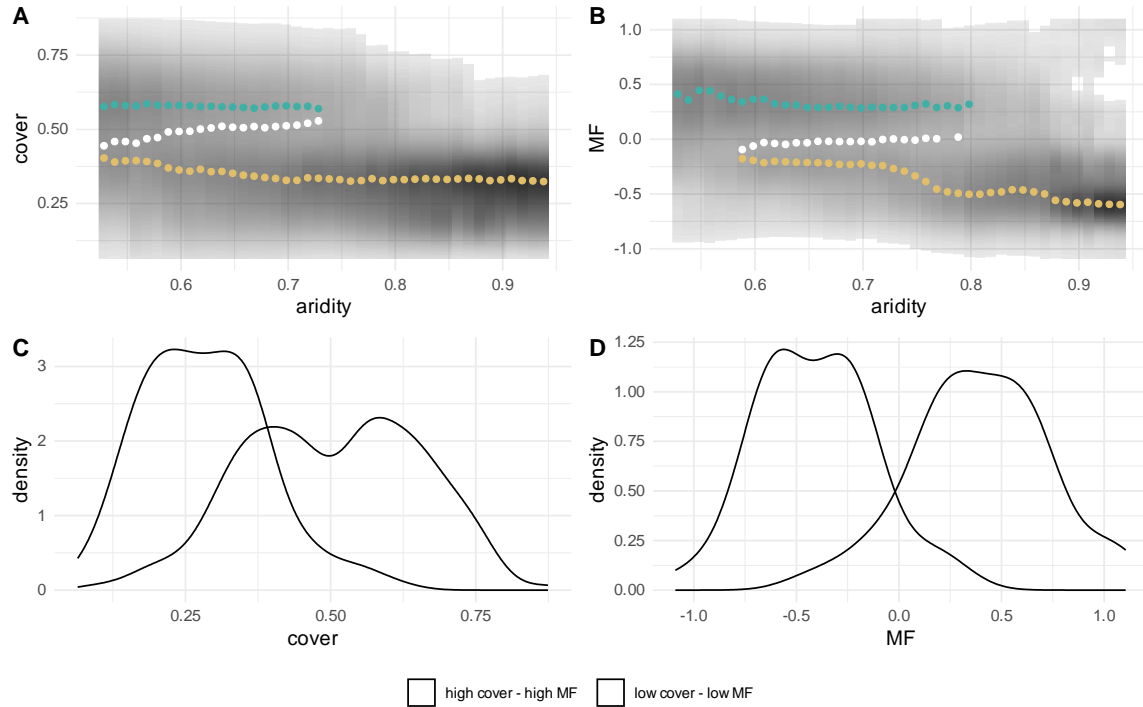
Figure legends

Figure 1. Location of the 115 plots in the global drylands data set used. Surveyed sites are colored in green for the healthier sites (high vegetation cover - high soil multifunctionality, MF) and yellow for the degraded sites (low vegetation cover - low multifunctionality, MF). Numbers reflect the number of sites in a given geographical area (characterized by the letters A-N), for which a corresponding zoom can be found in the panels above and below the map.



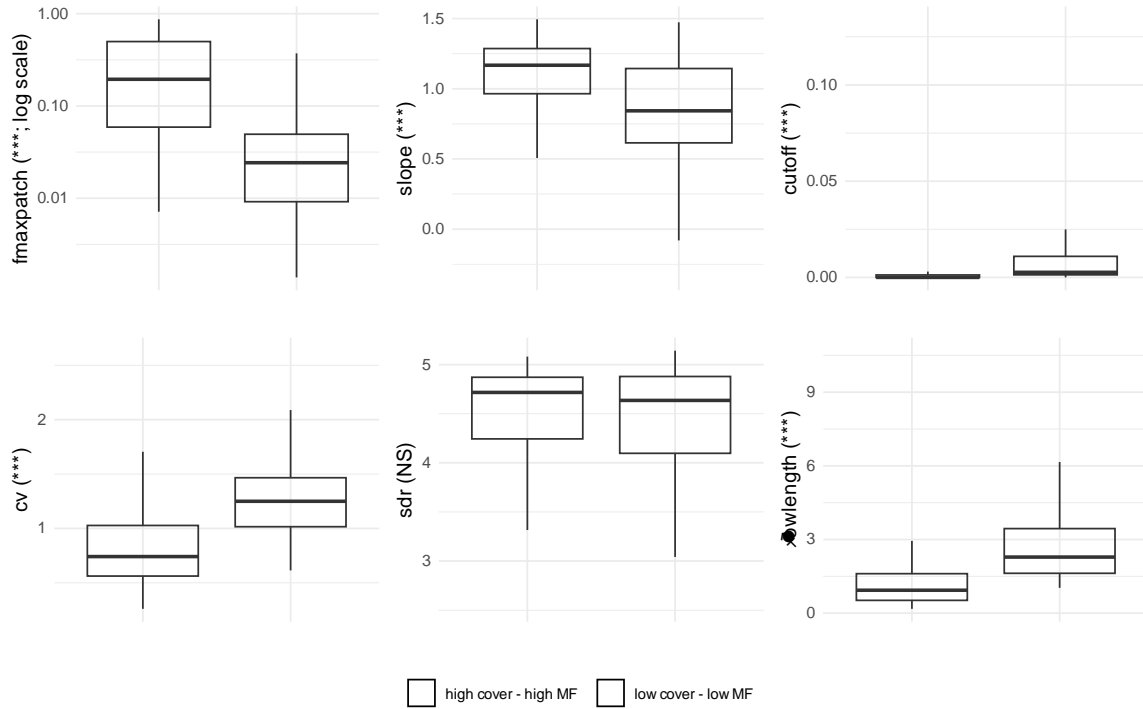
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689 **Figure 2. Dryland ecosystems were categorized into two groups using vegetation cover and**
 690 **soil multifunctionality data. (A)** Cover and **(B)** soil multifunctionality (MF) along aridity for all 115
 691 sites colored by the two groups: healthier (high cover-high soil multifunctionality values; in green)
 692 and degraded (low cover-low soil multifunctionality values; in yellow). Aridity was calculated as: $1 -$
 693 $\text{Aridity Index (AI} = \text{precipitation/potential evapotranspiration)}$, so that higher values indicate drier
 694 conditions. Colored points are the maxima of reconstructed stability landscapes based on potential
 695 analysis (i.e., possible attractors), while the white ones are the minima (see Materials and
 696 Methods). Small panels below **A** display examples of stability landscapes for aridity values 0.55,
 697 0.7 and 0.85, where valleys in the landscape are the colored points of panel A and the hills the
 698 white points (see Materials and Methods). **(C and D)** Densities of sites for each of the two groups
 699 for cover **(C)** and soil multifunctionality data **(D)**.
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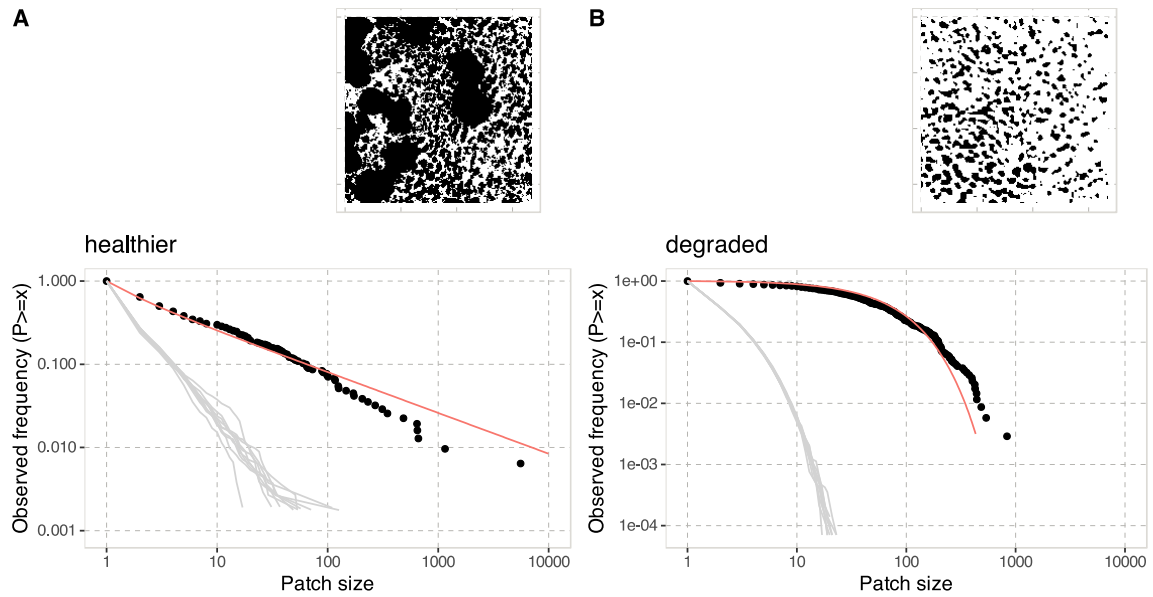
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704 **Figure 3. Differences in the spatial structure of the vegetation cover between healthier (high**
 705 **cover - high soil multifunctionality) and degraded (low cover - low soil multifunctionality)**
 706 **drylands.** The spatial metrics are the proportion of the image covered by the largest vegetation
 707 patch (*fmaxpatch*, (largest patch/image size), with the y axis on a log scale), the slope of the patch
 708 size distribution, the cutoff of the patch size distribution, spatial variance, the Spatial Density Ratio
 709 (*sdr*), and the bare soil connectivity (*flowlength*). For all metrics but *sdr*, the differences between
 710 the two groups are significant (Table S3 in SI).
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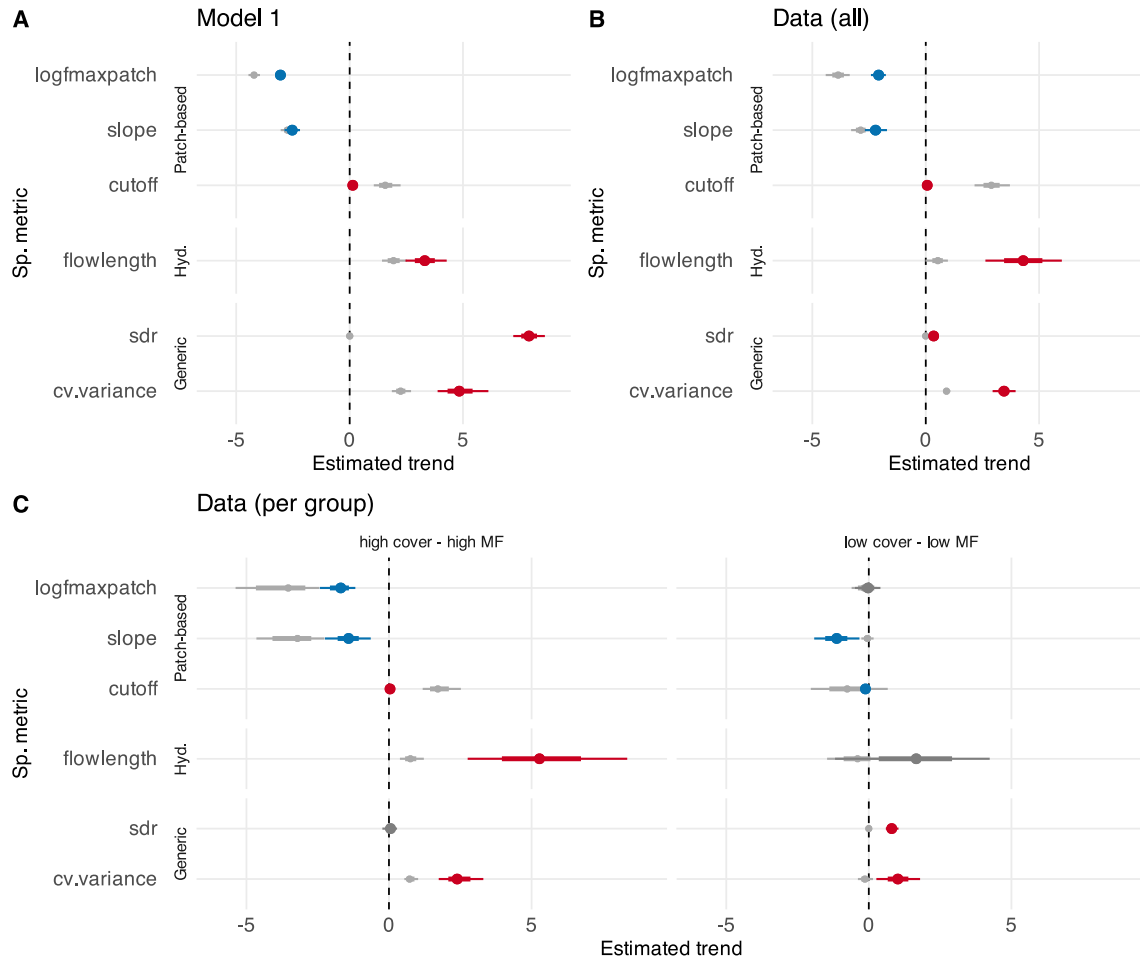
715 **Figure 4: Examples of patch size distributions of a healthier site (A) and a degraded one**
 716 **(B).** Sites are two grasslands (images 148-b and 192-c of the data set). Graphs display the
 717 fraction of patches larger than a certain size. Black points are observations from the image and
 718 grey curves are random expectations (based on 10 randomizations of the image). The red curve
 719 is the best fit. Snapshots on the top right are the images (black reflects vegetation).
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Figure 5. Estimated slope of the trends in spatial metrics along the aridity gradient evaluated in the model (A), in all the field sites of the data set (B) and in the two groups of sites separately (C; healthier sites on the left and degraded sites on the right; MF stands for soil multifunctionality). Points reflect the value of the slope of the spatial metrics with aridity. Significant positive and negative slopes are in red and blue, respectively. Observed slopes are in color, while expected trends of randomized landscapes (keeping cover constant but with reshuffled image pixels) are in grey. See legend of Fig. 3 and Materials and Methods for definitions of the spatial metrics. See SI D for a discussion of the difference in the slopes of SDR in the model and in the data.



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