

1 **The structure of plant spatial association networks is linked to plant diversity in global**
2 **drylands**

3 Authors: Saiz, Hugo¹., Gómez-Gardeñes, Jesús^{2,3}., Borda, Juan Pablo²., Maestre, Fernando T.¹

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

7 ²Departamento de Física de la Materia Condensada, Universidad de Zaragoza. C/ Pedro
8 Cerbuna 12, 50009 Zaragoza, SPAIN.

9 ³GOTHAM lab, Institute for Biocomputation and Physics of Complex Systems (BIFI), Universidad
10 de Zaragoza. C/ Mariano Esquillor (Edificio I+D), 50018, Zaragoza, SPAIN.

11 Corresponding author: Saiz, H.

12 E-mail: saizhugo@gmail.com

13 Abstract

14 1. Despite commonly used to unveil the complex structure of interactions within ecological
15 communities and their value to assess their resilience against external disturbances, network
16 analyses have seldom been applied in plant communities. We evaluated how plant-plant
17 spatial association networks vary in global drylands, and assessed whether network structure
18 was related to plant diversity in these ecosystems.

19 2. We surveyed 185 dryland ecosystems from all continents except Antarctica and built
20 networks using the local spatial association between all the perennial plants species present in
21 the communities studied. Then, for each network we calculated four descriptors of network
22 structure (link density, link weight mean and heterogeneity, and structural balance), and
23 evaluated their significance with null models. Finally, we used structural equation models to
24 evaluate how abiotic factors (including geography, topography, climate and soil conditions)
25 and network descriptors influenced plant species richness and evenness.

26 3. Plant networks were highly variable worldwide, but at most study sites (72%) presented
27 common structures such as a higher link density than expected. We also find evidence of the
28 presence of high structural balance in the networks studied. Moreover, all network descriptors
29 considered had a positive and significant effect on plant diversity, and on species richness in
30 particular.

31 *Synthesis.* Our results constitute the first empirical evidence showing the existence of common
32 network architectures structuring dryland plant communities at the global scale, and suggest a
33 relationship between the structure of spatial networks and plant diversity. They also highlight
34 the importance of system-level approaches to explain the diversity and structure of
35 interactions in plant communities, two major drivers of terrestrial ecosystem functioning.

36 Keywords: Competition, Determinants of community structure and diversity, Drylands,
37 Ecological networks, Facilitation, Plant diversity, Signed networks, Spatial patterns.

38 Introduction

39 Network analyses are being increasingly used in ecology to unveil the complexity of species
40 interactions and to study their effects on the functioning and stability of ecosystems (Heleno
41 et al., 2014). Theoretical studies have linked network topologies with the stability of ecological
42 communities (Allesina et al., 2015; Rohr, Saavedra, & Bascompte, 2014), and it has been
43 hypothesized that ecological networks share common topologies promoting the efficiency of
44 ecosystem processes (*e.g.* nutrient uptake, Arditi, Michalski, & Hirzel 2005) and the robustness
45 of communities against perturbations (Estrada, 2006). However, most studies in ecological
46 networks have been conducted in a few specific systems (*e.g.* food webs, plant-pollinator,
47 host-parasite) and at particular study sites, making the establishing of generalizations difficult
48 (Heleno et al., 2014). Thus, comparative studies at regional and global scales are necessary to
49 evaluate whether ecological networks present common topologies across multiple
50 environmental conditions, and to explore how they affect key ecosystem attributes such as
51 species diversity and ecosystem functioning (Pellissier et al., 2017; Traveset et al., 2016).

52 Plant communities are the bottom of the trophic web, play a major role in ecosystem
53 nutrient cycling and are responsible of community physiognomy (Barbour, 1987). Despite their
54 critical ecological role, plant-plant interactions have been largely unnoticed by network studies
55 until very recently (Saiz et al., 2017; Verdú & Valiente-Banuet, 2008). The efforts required for
56 obtaining data on plant-plant interactions at the community level over a large number of sites
57 (Soliveres & Maestre, 2014), and the different type of interactions that can be established
58 between plants (Brooker et al., 2008), have traditionally hampered the use of network
59 analyses to study the structure of plant communities. However, these limitations are starting
60 to be overcome with the increase in the number of global coordinated experiments and
61 surveys (Fraser et al., 2013; Maestre et al., 2012), and with methodological developments in
62 the analysis of social networks involving positive and negative links (*e.g.* like and dislikes;

63 Doreian & Mrvar 2009; Szell, Lambiotte, & Thurner 2010). To our knowledge, no study so far
64 has evaluated the topological structure of plant networks and how it relates to the diversity of
65 plant communities at the global scale. Such analyses would help to unveil global patterns for
66 plant communities, providing insights about the relative importance of positive and negative
67 interactions and the role of particular species as determinants of community structure (Saiz,
68 Alados, & Pueyo, 2014). Furthermore, the connection between network structure and
69 resilience against extinctions will provide a valuable information about the vulnerability of
70 plant communities to possible future extinctions due to global environmental change.

71 Measuring all the potential plant-plant interactions present in real communities still
72 remains challenging, and studies evaluating plant interactions at the community level usually
73 use proxies for doing so. One of the most commonly used proxies for assessing interactions
74 among plants is the local spatial association between pairs of species calculated from
75 observational data (Cavieres, Badano, Sierra-Almeida, Gómez-González, & Molina-
76 Montenegro, 2006; Raventós, Wiegand, & Luis, 2010; Saiz & Alados, 2012; Soliveres &
77 Maestre, 2014). Specifically, when two species aggregate in space more often than expected
78 by chance it is possible to assume a benefit from this aggregation and to approximate the
79 existence of a positive interaction (Pugnaire, Armas, Valladares, & Lepš, 2004). On the other
80 hand, if species appear segregated more often than expected by chance, an interference
81 between species can be approximated and, consequently, a negative interaction. Therefore,
82 under particular environmental conditions, local spatial organization could be a suitable proxy
83 of the structure of interactions between plants.

84 We explored the structure of plant spatial networks, and evaluated its effect on the
85 diversity of plant communities, in 185 drylands from all continents except Antarctica. Despite
86 covering over 45% of global terrestrial area (Právělie, 2016) and presenting a marked local
87 spatial organization (Rietkerk, Dekker, de Ruiter, & van de Koppel, 2004; Sala & Aguiar, 1996),

88 few studies so far have evaluated the spatial network structure of dryland plant communities
89 (Saiz et al., 2014; Saiz & Alados, 2014). Understanding such structure is particularly relevant for
90 multiple reasons. Dryland vegetation is organized as discrete plant patches embedded in a
91 matrix of bare soil, which become sinks for resources (*e.g.* rainfall, Aguiar & Sala 1999; Wang
92 *et al.* 2007). Species responsible of patch formation (nurses) create a microenvironment where
93 other species, less tolerant to dry environmental conditions, are able to establish (Maestre,
94 Bautista, Cortina, & Bellot, 2001). Thus, positive interactions largely structure plant
95 communities in drylands, and allow the persistence of communities with higher biodiversity
96 (Soliveres & Maestre, 2014; Verdú & Valiente-Banuet, 2008), although negative interactions
97 are also important drivers in structuring dryland plant communities (*e.g.* competition for water
98 between species, Fowler 1986; Soliveres, Smit & Maestre 2015). Moreover, several studies
99 have linked vegetation patchiness with ecosystem processes and degradation status (Berdugo,
100 Kéfi, Soliveres, & Maestre, 2017; Kéfi et al., 2007), so we could expect the structure of plant
101 spatial networks to directly influence ecosystem functioning in drylands.

102 Specifically, we hypothesize that in drylands worldwide plant spatial networks present
103 a common structure due to the organization of vegetation in patches, and that, after
104 accounting for the scaling of network structure with network size, this network structure has a
105 direct effect on the diversity of the plant community. We expect plant spatial association
106 networks to have a high number and variety of links between species (*i.e.* high link density and
107 link weight heterogeneity) due to the importance of biotic interactions, particularly of
108 facilitation (*i.e.* positive link weight mean), as creators of vegetation patches in drylands.
109 Furthermore, we expect these networks to be organized in blocks (*i.e.* high global structural
110 balance), representatives of the particular types of vegetation patches present in these
111 ecosystems. After controlling the effect of abiotic factors and network size, we anticipate that
112 this network structure (*i.e.* high link density, link weight heterogeneity and global structural

113 balance; and positive link weight mean) will have a significant and positive effect on the
114 diversity of dryland plant communities.

115 Methods

116 Global drylands vegetation survey

117 Field data were collected from 185 dryland sites located in 18 countries (Argentina, Australia,
118 Botswana, Brazil, Burkina Faso, Chile, China, Ecuador, Ghana, Iran, Kenya, Mexico, Morocco,
119 Peru, Spain, Tunisia, USA and Venezuela). These sites are a subset of the global survey of 224
120 sites from Maestre et al. (2012) carried out between 2006 and 2011, plus 12 additional sites
121 from Botswana, Ghana and Burkina Faso surveyed in 2013. As network indices depend on
122 network size and must be tested against null models (Dormann, Fründ, Blüthgen, & Gruber,
123 2009), we selected all sites where networks had at least 5 connected species to allow
124 statistical testing (185 sites out of 236 sites available). This subset included the major
125 vegetation types found in drylands, a wide range in plant species richness (from 5 to 52 species
126 per site) and environmental conditions (mean annual temperature and precipitation ranged
127 from -1.8 to 28.2 °C, and from 66 to 1219 mm, respectively). The sites surveyed encompass a
128 wide range of human uses, ranging from those with very low human impacts over recent time
129 scales (*e.g.* National Parks and other protected areas) to those where human activities such as
130 grazing, grass fiber/wood collection and game hunting are currently, or have been recently,
131 carried out. However, we excluded areas that have been heavily impacted by human activities
132 (*e.g.* agricultural, urban and infrastructure/mining areas) or that have been recently
133 engineered (*e.g.* planted or recently restored areas).

134 At each site, vegetation was surveyed using four 30-m-long transects located parallel
135 and separated 10 m among them within a 30 m x 30 m plot representative of the vegetation
136 found there (see Maestre et al. 2012 for details). At each transect, 20 quadrats of 1.5 m x 1.5

137 m were established, and the cover of each perennial species within each quadrat was visually
138 estimated without distinguishing between plant ontogenetic stages.

139 Network construction

140 For each of the sites studied, we built a plant-plant spatial association network (Saiz et al.,
141 2014; Saiz et al., 2017) using the cover data of all the perennial species (S) surveyed. These
142 networks are characterized by the adjacency graph $\mathbf{A}_{S \times S}$ (hereafter \mathbf{A}), where the nodes (i, j) are
143 the plant species and the links (l_{ij}) are the spatial association between each pair of species. To
144 determine this association, we calculated the correlation between the cover of each pair of
145 species in the 80 quadrats for each plot using Spearman rank tests. Following the
146 recommendations of (Weiss et al., 2016), we used Spearman correlations because our data
147 were not normal due to the large number of quadrats having species with a cover of 0. When a
148 correlation between species i and j was significant ($p < 0.05$), a link $l_{ij} = \rho$ was established
149 (where ρ represents the Spearman correlation coefficient), with $l_{ij} = 0$ otherwise. Thus, our
150 networks are symmetric ($l_{ij} = l_{ji}$), signed and weighted ($-1 < l_{ij} < 1$). As each species only had a
151 single cover value at each quadrat, we could not evaluate the intra-specific spatial association;
152 thus, we set the diagonal of \mathbf{A} to zero.

153 We are aware that the use of spatial associations to infer real biotic interactions presents
154 several limitations. Plant spatial patterns are the result of different processes apart from biotic
155 interactions, such as dispersal strategies and environmental heterogeneity (Escudero, Romão,
156 Cruz, & Maestre, 2005). Thus, it is convenient to control these processes to isolate the effect of
157 biotic interactions. In our case, we tried to limit the effect of environmental heterogeneity by
158 measuring spatial patterns at a scale (1.5 x 1.5 m) similar to that used in other studies about
159 biotic interactions at the community level (Cavieres et al., 2006; Verdú & Valiente-Banuet,
160 2011). This scale has been also suggested as the scale where biotic interactions are the
161 dominant driver of spatial patterns (Morales-Castilla, Matias, Gravel, & Araújo, 2015).

162 Furthermore, biotic interactions are not constant throughout species ontogeny, but can
163 change from seedlings to adults (Tielbörger & Kadmon, 2000; Valiente-Banuet & Verdú, 2008).
164 In our case, as we did not distinguish between ontogenetic stages of the species, spatial
165 association mostly represents the spatial pattern between adult plants, which accounted for
166 most of the cover of the species in each site. Finally, both facilitation and parasitism produce a
167 positive spatial association between species. However, we did not find evidence for parasitic
168 species in our sites (obligate or facultative parasites), so we can assume that in our study area
169 positive spatial association only represents facilitative interactions. Although we cannot ignore
170 the possible effect of other processes such as environmental heterogeneity or dispersal, we
171 believe that in our study spatial association is a reasonable proxy for biotic interactions.

172

173 Network indices

174 We selected four network indices to characterize the structure of the communities studied:
175 link density, link weight mean, link weight heterogeneity, and global network balance. Link
176 density (D) is the average number of links per node in the network ($D = L/S$, where L
177 represented the total number of links and S the total number of nodes in the network) and
178 represents the importance of spatial patterns in the plant community; high D values describe a
179 community where vegetation is spatially structured (*i.e.* significant positive and negative
180 spatial associations between pairs of species are common). Link weight mean (\bar{W}) is the mean
181 of link weight distribution in the network ($\bar{W} = \sum_{i=1}^S \sum_{j=1}^S l_{ij}/L, \forall l_{ij} \neq 0$), and represents the
182 dominant type of spatial pattern in the network; $\bar{W} > 0$ and $\bar{W} < 0$ describe a community
183 dominated by spatial aggregation and segregation, respectively. Link weight heterogeneity (H)
184 is the kurtosis of the link weight distribution, and represents the variety of spatial patterns
185 found in the community; lower H values indicate a community where spatial associations are
186 more diverse in strength and sign (*i.e.* more heterogeneous). Finally, global network balance
187 (K) is a specific index for signed networks that accounts for the proportion of closed cycles in

188 the network fulfilling the structural balance criterion (Zaslavsky, 2013). Following this criterion,
189 a network can be divided in blocks; nodes within the same block are positively connected
190 among them while they are negatively connected to nodes in other blocks (Doreian & Mrvar,
191 2009). We calculated K using the definition of (Estrada & Benzi, 2014), $K = \frac{\text{tr}(e^{\mathbf{A}})}{\text{tr}(e^{|\mathbf{A}|})}$, where $|\mathbf{A}|$
192 is the underlying unsigned graph of \mathbf{A} . High values of K indicate that the network presents a
193 'balanced' structure (with $K = 1$ indicating a perfect balance), while low values indicate that
194 several links do not fulfill this criterion and network is 'unbalanced' ('frustrated', *sensu*
195 (Doreian & Mrvar, 2009). In our case, high K indicates the presence of different types of
196 vegetation patches in the community, where species from the same block conform a particular
197 type of patch and present the same spatial pattern respect to the species present in another
198 patch (Saiz et al., 2017). In summary, these indices allow us to cover different components of
199 the spatial structure of the plant community: the importance (D) and variety (H) of spatial
200 patterns, the dominant type of association (*i.e.* aggregation or segregation, \bar{W}), and the
201 existence of specific types of vegetation patches (K).

202 Null model analyses

203 To test the significance of the network indices used, we employed two different null models
204 for each network, one that allowed changing the connectivity of the network for D , \bar{W} and H ,
205 indices that vary with the number and weight of links, and another that changed the links
206 between nodes while keeping the network linkage distribution constant for K , an index that
207 varies with the position of links within the network. In the first model, we randomized the
208 cover of each species along the quadrats. Specifically, we kept the cover distribution for each
209 species constant, but randomly change their positions in the quadrats. By doing so we changed
210 the cover values of species co-occurring in the same quadrat while maintaining the original
211 cover distribution for each species at each site (similarly to the SIM2 model of (Gotelli, 2000)).
212 Then, we built a network using this simulated data and calculated its D , \bar{W} and H . For each site,

213 we simulated 2000 networks and compared the real values of the indices against a 95%
214 confidence interval created from the simulated networks. In the second null model, we
215 simulated networks at each site using an algorithm based on the configurational model
216 adapted for signed networks (Saiz et al., 2017). This method iteratively changes links in the
217 original network, modifying its structure but keeping constant its linkage distribution. In our
218 case, we made 1000 iterations per network and simulated 5000 networks, and then compared
219 the real values of the index K against the simulated values creating a 95% confidence interval.
220 We also calculated the maximal and minimal K (K_{max} and K_{min}) that each network could have
221 considering its degree distribution to evaluate the real K value against all the possible values
222 that it could present at each site. To do so, we iteratively simulated networks with the same
223 null model, and selected the network that maximized (or minimized) K at each step. To avoid
224 possible local maxima (or minima), selection was based on a Fermi-Dirac probability function
225 ($f = \frac{1}{1+e^{-\beta\Delta}}$), which selected a network over others based on the difference between the K
226 values of the networks (Δ) and a parameter β that modulates the probability of accepting a
227 change with the number of iterations (with higher β selecting higher Δ , (Tsallis & Stariolo,
228 1996). By doing so, we could explore the behavior of the index by precisely locating real
229 networks in all the space of parameters of K .

230 Evaluating the effects of network structure on plant diversity

231 We built structural equation models (SEM, Grace 2006) including different abiotic variables
232 (Latitude, Longitude, Elevation, Slope, Aridity, Precipitation Seasonality, Soil organic C, Soil pH
233 and Soil Total P) and network variables as explanatory variables for the richness (SR) and
234 evenness ($E = Shannon\ index / \ln SR$) of perennial plant species. Specifically, we included
235 geographical variables to control the effect of spatial autocorrelation between sites, and
236 selected abiotic variables that have been shown to be important drivers of the structure and
237 functioning of drylands (Maestre et al., 2012). Abiotic variables were divided in four groups:

238 geographical, topographical, climatic, and soil variables, and a composite variable was built for
239 each group. To build each composite variable we first fitted a linear model using its
240 corresponding group of abiotic variables as explanatory variables and species richness and
241 evenness as response variables, and then we used this model to calculate the values of the
242 composite variable. For network indices, we included the difference between real network
243 values and the percentile 50 values for the networks simulated with the null models (*e.g.* $\Delta D =$
244 $D - D_{null}$, where D_{null} is the percentile 50 for the D simulated with the null model) to remove
245 random effects due to species abundance distribution (Gotelli, 2000) and network size
246 (Dormann et al., 2009). We then created a SEM for each combination of network and diversity
247 variables (eight SEMs in total). In these SEMs, network variables depended on all the
248 composite variables, and diversity indices depended on all the composite variables and the
249 network indices (see Appendices A and B for a complete description of the variables and the
250 structure of the SEMs used). To evaluate the importance of network indices on community
251 diversity, we compared the explained variance of diversity indices between SEMs built with
252 and without network indices. Specific dependencies between composite variables were
253 included following previous studies using the same dataset (Delgado-Baquerizo et al., 2016).
254 All variables were centered and standardized before calculating the models. All analyses were
255 performed with R.3.2.4 (R Development Core Team, 2014). We used the *lavaan* package for
256 the SEM analyses (Rosseel, 2012).

257

258 Results

259 The analysis of plant spatial association networks revealed that dryland plant communities
260 were variable, as indicated by the variability of observed network indices (Table 1, Fig. 1).

261 Particularly, \bar{W} presented both positive and negative values, suggesting that plant

262 communities in drylands are dominated by either spatial aggregation or segregation. However,

263 *K* presented a very low variability, with values close to 1 (Table 1). These results suggested
264 that, in general, plant spatial networks in drylands presented different types of vegetation
265 patches.

266 Null model analyses indicated that the studied plant spatial association networks
267 presented common not random architectures (Table 1). Specifically, plant communities
268 showed significantly more spatial associations per species (*D*) than expected. Furthermore,
269 72% of communities presented significantly higher *D* values than expected by chance, and no
270 single community had a *D* value lower than expected. These results confirm that plant
271 communities in drylands present a strong spatial structure. On the other hand, and although *K*
272 was not significantly different than expected, 70% of plant communities presented higher *K*
273 than expected (with 92% of plant communities being closer to the optimal *K* than to the
274 expected value), suggesting the prevalence of differentiated vegetation patches in drylands
275 plant communities.

276 Our structural equation models revealed that the structure of plant spatial association
277 networks significantly affected the richness and evenness of dryland plant communities (Table
278 2). All network indices had a significant direct effect on species richness (*SR*), but only *H* and *K*
279 significantly affected community evenness (*E*). Furthermore, although network variables
280 presented lower effect sizes than abiotic variables, their inclusion in the SEM substantially
281 increased the explained variance of *SR* (Fig. 2). Finally, some network indices with significant
282 effects on *SR* (*D* and *K*) were also independent from abiotic variables (Fig. 3 and Appendix B).

283

284 Discussion

285 Global studies offer unparalleled insights to build generalities in ecology based on the
286 discovery of common patterns and processes operating across a large number of locations
287 and/or ecosystems (Fraser et al., 2013). Studies on biotic interactions have often found

288 common network structures within ecological communities, such as nested and modular
289 patterns (Olesen, Bascompte, Dupont, & Jordano, 2007; Thébault & Fontaine, 2010). Some of
290 these structures have been confirmed by global studies conducted on mutualistic systems such
291 as plant-pollinators (Traveset et al., 2016), suggesting that biotic interactions at the community
292 level may be structured following general rules. Our analyses indicate that perennial plant
293 communities in drylands worldwide present common structures, such as the presence of
294 frequent spatial associations between species and (less commonly) different types of
295 vegetation patches. Furthermore, vegetation spatial structure, as characterized by networks, is
296 significantly linked to plant diversity. Therefore, it is possible that local environmental
297 processes operating in drylands lead to a particular vegetation spatial structure that, together
298 with other abiotic factors, contributes to explain plant diversity. Our results constitute, to the
299 best of our knowledge, the first empirical evidence showing the existence of a common
300 network architecture structuring terrestrial plant communities at the global scale, and provide
301 novel evidence about the importance of the structure of species interactions for the
302 maintenance of biodiversity (Bascompte & Jordano, 2007).

303 Plant spatial networks in drylands are highly connected and balanced

304 Drylands are characterized by particular vegetation patterns composed by discrete plant
305 patches embedded in a “matrix” of bare ground soil devoid of perennial vegetation
306 (Klausmeier, 1999). Theoretical and empirical results have found that this arises from
307 hydrological-plant interactions, with bare soil areas and vegetation patches acting as ‘sources’
308 and ‘sinks’, respectively, for runoff water after precipitation events (Puigdefábregas, Solé,
309 Gutiérrez, del Barrio, & Boer, 1999; Rietkerk et al., 2004). Furthermore, empirical and
310 modelling studies have shown a connection between vegetation patchiness and ecosystem
311 processes. However, these studies consider vegetation as a single unity while in general plant
312 patches are composed by multiple species interacting between them (Tielbörger & Kadmon,

313 2000) and responding differently to the same environmental factor (Pueyo, Moret-Fernández,
314 Saiz, Bueno, & Alados, 2013; Saiz & Alados, 2011).

315 We found that most plant species presented many spatial associations among them,
316 and that dryland communities could be dominated by spatial aggregation or segregation, as
317 found in many local studies (Fowler, 1986; Soliveres & Maestre, 2014). However, and
318 regardless of the dominant spatial pattern found at each site, vegetation patches seem to be
319 organized according to the structural balance criteria in drylands. Thus, within a given plant
320 community there are different types of patches, and plant species that conform the same type
321 of patch do not appear in patches formed by other species (Saiz et al., 2017). In drylands,
322 usually species responsible of patch formation are well adapted to local conditions and
323 facilitate the establishment of seedlings of less adapted species under their canopies (Valiente-
324 Banuet, Rumebe, Verdú, & Callaway, 2006). Meanwhile, well adapted species compete among
325 them for the scarce resources present in the environment, and facilitated species compete
326 among them for the space and resources below the canopy of the nurses (Soliveres et al.,
327 2011). It has been found that these interactions can be explained considering the phylogenetic
328 distance between species as a proxy of shared niche requirements, resulting in communities
329 where plant species tend to interact negatively with close relative species (that occupy similar
330 niches) and positively with a subset of the distant relatives (Verdú, Jordano, & Valiente-
331 Banuet, 2010; Verdú & Valiente-Banuet, 2011). Therefore, these differences between plant
332 niches could determine the interactions between plants, ultimately leading to the creation of
333 different types of vegetation patches that result in a balanced spatial structure of vegetation.

334 The existence of different types of vegetation patches could also help to unveil how
335 biotic interactions shape vegetation spatial patterns, and suggest that plant interactions in
336 drylands are species-specific. This is important because there is no clear evidence that
337 facilitative interactions are species-specific, as this depends on how facilitated species benefit

338 from nurses (Callaway, 1998). Thus, while the creation of more benign microenvironments and
339 the capture of wind dispersed propagules by nurses result in the aggregation of multiple
340 species under their canopies (Bullock & Moy, 2004; Soliveres et al., 2011), other facilitative
341 mechanisms can also lead to species-specific aggregations (*e.g.* protection against herbivory,
342 Saiz & Alados 2012; attraction of pollinators, Lavery 1992; modification of soil micro-flora,
343 (Van Der Heijden & Horton, 2009). The same applies to negative interactions. In drylands,
344 species that do not coexist in the same patches (*i.e.* present spatial segregation) are likely to
345 compete for the same resources (Ogle & Reynolds, 2004) or produce allelopathic compounds
346 (Arroyo, Pueyo, Saiz, & Alados, 2015), resulting in species-specific interactions that drive the
347 spatial structure of plant communities. Hence, the application of network indices to the spatial
348 structure of vegetation allows identifying different types of vegetation patches and exploring
349 the importance of species-specific relationships on facilitative and competitive interactions.

350 The structure of plant spatial networks promotes species diversity

351 We found a significant effect of network indices on plant species richness and evenness. This
352 result agrees with studies observing that particular vegetation spatial patterns are: i) related to
353 higher ecosystem resilience (Kéfi et al., 2007) and ii) increase the diversity of plant
354 communities (Pueyo et al., 2013) in drylands, effects associated to facilitative interactions. On
355 the other hand, and contrary to our expectations, the dominance of positive spatial
356 associations presented the weakest effect on plant diversity between all network indices
357 evaluated. A possible explanation is that the coexistence of diverse species in a community
358 depends not only in the presence of positive and negative interactions (*sensu* Brooker *et al.*
359 2005), but also in how these interactions are structured (*e.g.* identity of the species involved or
360 presence of indirect interactions, Soliveres *et al.* 2015a). Therefore, our results encourage the
361 use of network approaches in plant ecology, as they not only account for the importance of

362 biotic interactions but also for their structure in the community, and are able to consider
363 simultaneously facilitation and competition.

364 Importantly, abiotic factors had significant effect on plant community diversity, a result
365 previously found in the sites studied (Maestre et al., 2012). However, we found that some
366 significant effects of spatial network structure on diversity were independent from those of
367 abiotic factors. Previous studies conducted with dryland plant communities found that the
368 nested network structures of facilitative interactions promote their diversity (Verdú &
369 Valiente-Banuet, 2008). Furthermore, a positive relationship between the spatial organization
370 of vegetation patches and plant species richness has also been found (Maestre 2006; Pueyo et
371 al. 2013). Our results represent a step forward, as the network approach used here considers
372 both positive and negative spatial associations of plant species, and shows a positive
373 relationship between community organization in differentiated patches and plant diversity.

374 Future directions and concluding remarks

375 The use of networks in ecology is in continuous development, and recently has started to
376 consider systems other than the traditional food webs and mutualistic networks (Kéfi et al.,
377 2012). However, the use of spatial networks requires further development before being
378 considered a general tool to study biotic interactions (see *Methods*). Studies in communities
379 where biotic interactions are strongly linked to spatial patterns (*i.e.* drylands) are a good
380 starting point to evaluate this type of networks, but more effort is required. Specifically,
381 conducting experiments to measure true interactions between species (*e.g.* measuring pair-
382 wise interactions in controlled conditions, Godoy, Stouffer, Kraft, & Levine, 2017) and compare
383 them with field spatial associations would be a good starting point to better understand the
384 link between interactions and spatial patterns in plant communities. Furthermore, controlling
385 other effects such as herbivory or plants ontogenetic stages, which have a significant effect on
386 plant interactions (Smit, Rietkerk, & Wassen, 2009; Tielbörger & Kadmon, 2000), will help to
387 clarify the mechanisms behind spatial pattern. In general, working at local scales and

388 controlling for environmental heterogeneity during field surveys are a proper way to improve
389 the reliability of spatial patterns as proxies of biotic interactions.

390 Our analyses of the plant spatial association networks revealed new insights on the
391 structure of dryland plant communities. They showed some common patterns that, in contrast
392 to previous studies focusing on few communities and positive interactions (Verdú & Valiente-
393 Banuet, 2008), apply to plant communities including both positive and negative relationships.
394 The studied networks showed a high density of connections, which described a community
395 with a strong spatial organization (Sala & Aguiar, 1996), and often presented balanced
396 structures that have been commonly found in signed networks (Szell et al., 2010).
397 Furthermore, networks with dense and heterogeneous connections and balanced structures
398 presented higher plant diversity, supporting the idea that these network structures promote
399 the coexistence of a larger number of species. Finally, the low effect of positive or negative
400 links revealed the need to take into account not only the importance of biotic interactions but
401 also their structure when studying vegetation assembly drivers in drylands. Our results
402 highlight the importance of system level approaches to explain the diversity of plant species, a
403 major driver of ecosystem functioning, in drylands worldwide.

404

405 Acknowledgements

406 We thank all the members of the EPES-BIOCOM network for the collection of field data and all
407 the members of the Maestre lab for their help with data organization and management, and
408 for their comments and suggestions on early stages of the manuscript. We also thank Isabel
409 Sumelzo for her help with the art of the figures and the editor and two anonymous reviewers
410 for their comments on our manuscript. This work was funded by the European Research
411 Council under the European Community's Seventh Framework Programme (FP7/2007-
412 2013)/ERC Grant agreement 242658 (BIOCOM). FTM and HS are supported by the European

413 Research Council (ERC Grant agreement 647038 [BIODESERT]);HS is supported by a Juan de la
414 Cierva-Formación grant from MINECO, and JGG acknowledges financial support from MINECO
415 (through projects FIS2015-71582-C2 and FIS2014-55867-P) and from the Departamento de
416 Industria e Innovación del Gobierno de Aragón y Fondo Social Europeo (FENOL group E-19).

417

418 Author's contribution

419 H.S. and J.G.G. developed the conceptual and methodological foundation of this study. F.T.M
420 designed the field study and coordinated field data acquisition. H.S., J.G.G. and J.P.B.
421 conducted statistical analyses. H.S. wrote the first draft, and all authors substantially
422 contributed to the subsequent drafts.

423

424 Data availability statements

425 All the materials, raw data, and protocols used in the article are available upon request and
426 without any restriction, and are published in figshare (Saiz & Maestre, 2018).

427

428 Bibliography

429 Aguiar, M. R., & Sala, O. E. (1999). Patch structure, dynamics and implications for the
430 functioning of arid ecosystems. *Trends in Ecology & Evolution*, 14(7), 273–277.

431 Allesina, S., Grilli, J., Barabás, G., Tang, S., Aljadeff, J., & Maritan, A. (2015). Predicting the
432 stability of large structured food webs. *Nature Communications*, 6, 7842.

433 Arditi, R., Michalski, J., & Hirzel, A. H. (2005). Rheagogies: Modelling non-trophic effects in food
434 webs. *Ecological Complexity*, 2(3), 249–258.

435 Arroyo, A. I., Pueyo, Y., Saiz, H., & Alados, C. L. (2015). Plant–plant interactions as a mechanism
436 structuring plant diversity in a Mediterranean semi-arid ecosystem. *Ecology and*
437 *Evolution*, 5(22), 5305–5317.

438 Barbour, M. G. (1987). *Terrestrial Plant Ecology*. Benjamin/Cummings Publishing Company.

439 Bascompte, J., & Jordano, P. (2007). Plant-Animal Mutualistic Networks: The Architecture of
440 Biodiversity. *Annual Review of Ecology, Evolution, and Systematics*, 38, 567–593.

441 Berdugo, M., Kéfi, S., Soliveres, S., & Maestre, F. T. (2017). Plant spatial patterns identify
442 alternative ecosystem multifunctionality states in global drylands. *Nature Ecology &*
443 *Evolution*, 1, 0003.

444 Brooker, R., Kikvidze, Z., Pugnaire, F. I., Callaway, R. M., Choler, P., Lortie, C. J., & Michalet, R.
445 (2005). The importance of importance. *Oikos*, 109(1), 63–70.

446 Brooker, R. W., Maestre, F. T., Callaway, R. M., Lortie, C. L., Cavieres, L. A., Kunstler, G., ...
447 Michalet, R. (2008). Facilitation in plant communities: the past, the present, and the
448 future. *Journal of Ecology*, 96(1), 18–34.

449 Bullock, J. M., & Moy, I. L. (2004). Plants as seed traps: inter-specific interference with
450 dispersal. *Acta Oecologica*, 25(1), 35–41. doi:10.1016/j.actao.2003.10.005

451 Callaway, R. M. (1998). Are Positive Interactions Species-Specific? *Oikos*, 82(1), 202–207.

452 Cavieres, L. A., Badano, E. I., Sierra-Almeida, A., Gómez-González, S., & Molina-Montenegro, M.
453 A. (2006). Positive interactions between alpine plant species and the nurse cushion
454 plant *Laretia acaulis* do not increase with elevation in the Andes of central Chile. *New*
455 *Phytologist*, 169(1), 59–69.

456 Delgado-Baquerizo, M., Maestre, F. T., Reich, P. B., Jeffries, T. C., Gaitan, J. J., Encinar, D., ...
457 Singh, B. K. (2016). Microbial diversity drives multifunctionality in terrestrial
458 ecosystems. *Nature Communications*, 7.

459 Doreian, P., & Mrvar, A. (2009). Partitioning signed social networks. *Social Networks*, 31(1), 1–
460 11.

461 Dormann, C. F., Fründ, J., Blüthgen, N., & Gruber, B. (2009). Indices, graphs and null models:
462 analyzing bipartite ecological networks. *The Open Ecology Journal*, 2, 7–24.

463 Escudero, A., Romão, R. L., Cruz, M., & Maestre, F. T. (2005). Spatial pattern and neighbour
464 effects on *Helianthemum squamatum* seedlings in a Mediterranean gypsum
465 community. *Journal of Vegetation Science*, 16(4), 383–390.

466 Estrada, E. (2006). Network robustness to targeted attacks. The interplay of expansibility and
467 degree distribution. *The European Physical Journal B - Condensed Matter and Complex
468 Systems*, 52(4), 563–574.

469 Estrada, E., & Benzi, M. (2014). Walk-based measure of balance in signed networks: Detecting
470 lack of balance in social networks. *Physical Review E*, 90(4), 042802.

471 Fowler, N. (1986). The role of competition in plant communities in arid and semiarid regions.
472 *Annual Review of Ecology and Systematics*, 17(1), 89–110.

473 Fraser, L. H., Henry, H. A., Carlyle, C. N., White, S. R., Beierkuhnlein, C., Cahill, J. F., ...
474 Turkington, R. (2013). Coordinated distributed experiments: an emerging tool for
475 testing global hypotheses in ecology and environmental science. *Frontiers in Ecology
476 and the Environment*, 11(3), 147–155.

477 Godoy, O., Stouffer, D. B., Kraft, N. J., & Levine, J. M. (2017). Intransitivity is infrequent and
478 fails to promote annual plant coexistence without pairwise niche differences. *Ecology*,
479 98(5), 1193.

480 Gotelli, N. J. (2000). Null model analysis of species co-occurrence patterns. *Ecology*, 81(9),
481 2606–2621.

482 Grace, J. B. (2006). *Structural equation modeling and natural systems*. Cambridge University
483 Press.

484 Heleno, R., Garcia, C., Jordano, P., Traveset, A., Gómez, J. M., Blüthgen, N., ... Olesen, J. M.
485 (2014). Ecological networks: delving into the architecture of biodiversity. *Biology
486 Letters*, 10(1), 20131000.

487 Kéfi, S., Berlow, E. L., Wieters, E. A., Navarrete, S. A., Petchey, O. L., Wood, S. A., ... others.
488 (2012). More than a meal... integrating non-feeding interactions into food webs.
489 *Ecology Letters*, 15(4), 291–300.

490 Kéfi, S., Rietkerk, M., Alados, C. L., Pueyo, Y., Papanastasis, V. P., ElAich, A., & De Ruiter, P. C.
491 (2007). Spatial vegetation patterns and imminent desertification in Mediterranean arid
492 ecosystems. *Nature*, 449(7159), 213–217.

493 Klausmeier, C. A. (1999). Regular and irregular patterns in semiarid vegetation. *Science*,
494 284(5421), 1826–1828.

495 Lavery, T. M. (1992). Plant interactions for pollinator visits: a test of the magnet species effect.
496 *Oecologia*, 89(4), 502–508.

497 Maestre, F. T. (2006). Linking the spatial patterns of organisms and abiotic factors to
498 ecosystem function and management: Insights from semi-arid environments. *Web*
499 *Ecology*, 6(1), 75–87.

500 Maestre, F. T., Bautista, S., Cortina, J., & Bellot, J. (2001). Potential for Using Facilitation by
501 Grasses to Establish Shrubs on a Semiarid Degraded Steppe. *Ecological Applications*,
502 11(6), 1641–1655.

503 Maestre, F. T., Quero, J. L., Gotelli, N. J., Escudero, A., Ochoa, V., Delgado-Baquerizo, M., ...
504 Zaady, E. (2012). Plant Species Richness and Ecosystem Multifunctionality in Global
505 Drylands. *Science*, 335(6065), 214–218.

506 Morales-Castilla, I., Matias, M. G., Gravel, D., & Araújo, M. B. (2015). Inferring biotic
507 interactions from proxies. *Trends in Ecology & Evolution*, 30(6), 347–356.

508 Ogle, K., & Reynolds, J. F. (2004). Plant responses to precipitation in desert ecosystems:
509 integrating functional types, pulses, thresholds, and delays. *Oecologia*, 141(2), 282–
510 294.

511 Olesen, J. M., Bascompte, J., Dupont, Y. L., & Jordano, P. (2007). The modularity of pollination
512 networks. *Proceedings of the National Academy of Sciences*, 104(50), 19891–19896.

513 Pellissier, L., Albouy, C., Bascompte, J., Farwig, N., Graham, C., Loreau, M., ... Gravel, D. (2017).
514 Comparing species interaction networks along environmental gradients. *Biological*
515 *Reviews*.

516 Právělie, R. (2016). Drylands extent and environmental issues. A global approach. *Earth-Science*
517 *Reviews*, 161, 259–278.

518 Pueyo, Y., Moret-Fernández, D., Saiz, H., Bueno, C. G., & Alados, C. L. (2013). Relationships
519 Between Plant Spatial Patterns, Water Infiltration Capacity, and Plant Community
520 Composition in Semi-arid Mediterranean Ecosystems Along Stress Gradients.
521 *Ecosystems*, 16(3), 452–466.

522 Pugnaire, F. I., Armas, C., Valladares, F., & Lepš, J. (2004). Soil as a mediator in plant-plant
523 interactions in a semi-arid community. *Journal of Vegetation Science*, 15(1), 85–92.

524 Puigdefábregas, J., Solé, A., Gutiérrez, L., del Barrio, G., & Boer, M. (1999). Scales and
525 processes of water and sediment redistribution in drylands: results from the Rambla
526 Honda field site in Southeast Spain. *Earth-Science Reviews*, 48(1–2), 39–70.

527 R Development Core Team. (2014). *R: A language and environment for statistical computing*. R
528 *Foundation for Statistical Computing, Vienna, Austria, 2012*. ISBN 3-900051-07-0.

529 Raventós, J., Wiegand, T., & Luis, M. D. (2010). Evidence for the spatial segregation hypothesis:
530 a test with nine-year survivorship data in a Mediterranean shrubland. *Ecology*, 91(7),
531 2110–2120.

532 Rietkerk, M., Dekker, S. C., de Ruiter, P. C., & van de Koppel, J. (2004). Self-organized
533 patchiness and catastrophic shifts in ecosystems. *Science*, 305(5692), 1926–1929.

534 Rohr, R. P., Saavedra, S., & Bascompte, J. (2014). On the structural stability of mutualistic
535 systems. *Science*, 345(6195), 1253497.

536 Rosseel, Y. (2012). lavaan: an R package for structural equation modeling. *Journal of Statistical*
537 *Software*, 48(2), 1–36.

538 Saiz, H., & Alados, C. L. (2011). Structure and spatial self-organization of semi-arid communities
539 through plant–plant co-occurrence networks. *Ecological Complexity*, 8(2), 184–191.

540 Saiz, H., & Alados, C. L. (2012). Changes in Semi-Arid Plant Species Associations along a
541 Livestock Grazing Gradient. *PLoS ONE*, 7(7), e40551.

542 Saiz, H., & Alados, C. L. (2014). Effect of livestock grazing in the partitions of a semiarid plant–
543 plant spatial signed network. *Acta Oecologica*, 59, 18–25.

544 Saiz, H., Alados, C. L., & Pueyo, Y. (2014). Plant–plant spatial association networks in
545 gypsophilous communities: the influence of aridity and grazing and the role of
546 gypsophytes in its structure. *Web Ecology*, 14(1), 39–49.

547 Saiz, H., Gómez-Gardeñes, J., Nuche, P., Girón, A., Pueyo, Y., & Alados, C. L. (2017). Evidence of
548 structural balance in spatial ecological networks. *Ecography*, 40(6), 733–741.

549 Saiz, H., & Maestre, F. T. (2018, January 12). DataNetwork.xlsx.
550 doi:10.6084/m9.figshare.4763302.v1

551 Sala, O. E., & Aguiar, M. R. (1996). Origin, maintenance, and ecosystem effect of vegetation
552 patches in arid lands. Presented at the Fifth International Rangeland Congress, Salt
553 Lake City, Utah.

554 Smit, C., Rietkerk, M., & Wassen, M. J. (2009). Inclusion of biotic stress (consumer pressure)
555 alters predictions from the stress gradient hypothesis. *Journal of Ecology*, 97(6), 1215–
556 1219.

557 Soliveres, S., Eldridge, D. J., Maestre, F. T., Bowker, M. A., Tighe, M., & Escudero, A. (2011).
558 Microhabitat amelioration and reduced competition among understory plants as
559 drivers of facilitation across environmental gradients: towards a unifying framework.
560 *Perspectives in Plant Ecology, Evolution and Systematics*, 13(4), 247–258.

561 Soliveres, S., & Maestre, F. T. (2014). Plant–plant interactions, environmental gradients and
562 plant diversity: A global synthesis of community-level studies. *Perspectives in Plant
563 Ecology, Evolution and Systematics*, 16(4), 154–163.

564 Soliveres, S., Maestre, F. T., Ulrich, W., Manning, P., Boch, S., Bowker, M. A., ... others. (2015).
565 Intransitive competition is widespread in plant communities and maintains their
566 species richness. *Ecology Letters*, *18*(8), 790–798.

567 Soliveres, S., Smit, C., & Maestre, F. T. (2015). Moving forward on facilitation research:
568 response to changing environments and effects on the diversity, functioning and
569 evolution of plant communities. *Biological Reviews*, *90*(1), 297–313.

570 Szell, M., Lambiotte, R., & Thurner, S. (2010). Multirelational organization of large-scale social
571 networks in an online world. *Proceedings of the National Academy of Sciences*,
572 *107*(31), 13636–13641.

573 Thébault, E., & Fontaine, C. (2010). Stability of Ecological Communities and the Architecture of
574 Mutualistic and Trophic Networks. *Science*, *329*(5993), 853–856.

575 Tielbörger, K., & Kadmon, R. (2000). Temporal environmental variation tips the balance
576 between facilitation and interference in desert plants. *Ecology*, *81*(6), 1544–1553.

577 Traveset, A., Tur, C., Trøjelsgaard, K., Heleno, R., Castro-Urgal, R., & Olesen, J. M. (2016). Global
578 patterns of mainland and insular pollination networks. *Global Ecology and*
579 *Biogeography*, *25*(7), 880–890.

580 Tsallis, C., & Stariolo, D. A. (1996). Generalized simulated annealing. *Physica A: Statistical*
581 *Mechanics and Its Applications*, *233*(1–2), 395–406.

582 Valiente-Banuet, A., Rumebe, A. V., Verdú, M., & Callaway, R. M. (2006). Modern Quaternary
583 plant lineages promote diversity through facilitation of ancient Tertiary lineages.
584 *Proceedings of the National Academy of Sciences*, *103*(45), 16812–16817.

585 Valiente-Banuet, A., & Verdú, M. (2008). Temporal shifts from facilitation to competition occur
586 between closely related taxa. *Journal of Ecology*, *96*(3), 489–494.

587 Van Der Heijden, M. G. A., & Horton, T. R. (2009). Socialism in soil? The importance of
588 mycorrhizal fungal networks for facilitation in natural ecosystems. *Journal of Ecology*,
589 *97*(6), 1139–1150.

590 Verdú, M., Jordano, P., & Valiente-Banuet, A. (2010). The phylogenetic structure of plant
591 facilitation networks changes with competition. *Journal of Ecology*, *98*(6), 1454–1461.

592 Verdú, M., & Valiente-Banuet, A. (2008). The Nested Assembly of Plant Facilitation Networks
593 Prevents Species Extinctions. *The American Naturalist*, *172*(6), 751–760.

594 Verdú, M., & Valiente-Banuet, A. (2011). The relative contribution of abundance and
595 phylogeny to the structure of plant facilitation networks. *Oikos*, *120*(9), 1351–1356.

596 Wang, X.-P., Li, X.-R., Xiao, H.-L., Berndtsson, R., & Pan, Y.-X. (2007). Effects of surface
597 characteristics on infiltration patterns in an arid shrub desert. *Hydrological Processes*,
598 *21*(1), 72–79.

599 Weiss, S., Van Treuren, W., Lozupone, C., Faust, K., Friedman, J., Deng, Y., ... others. (2016).
600 Correlation detection strategies in microbial data sets vary widely in sensitivity and
601 precision. *The ISME Journal*, *10*(7), 1669.

602 Zaslavsky, T. (2013). Matrices in the theory of signed simple graphs. *ArXiv Preprint*
603 *ArXiv:1303.3083*.

604

605 Table 1. Values of the network indices found in our study sites. *S*, network size; *D*, link density;
606 \bar{W} , link weight mean; *H*, link weight heterogeneity; *K*, balance. *Real* represents the mean value
607 of the index observed in real networks; *CV* represents the coefficient of variation of *Real*; and
608 ΔI represents the mean difference between the index of real networks and the percentile 50
609 value of their corresponding null model. Values in parentheses represent the 95% confidence
610 interval for the index created using the percentiles 2.5 and 97.5 for study sites; bold values
611 indicate a significant difference between Real and Null values. + and – indicate the number of
612 networks which presented significantly higher or lower values for their indices in respect to the
613 null model (values in parentheses represent the proportion).

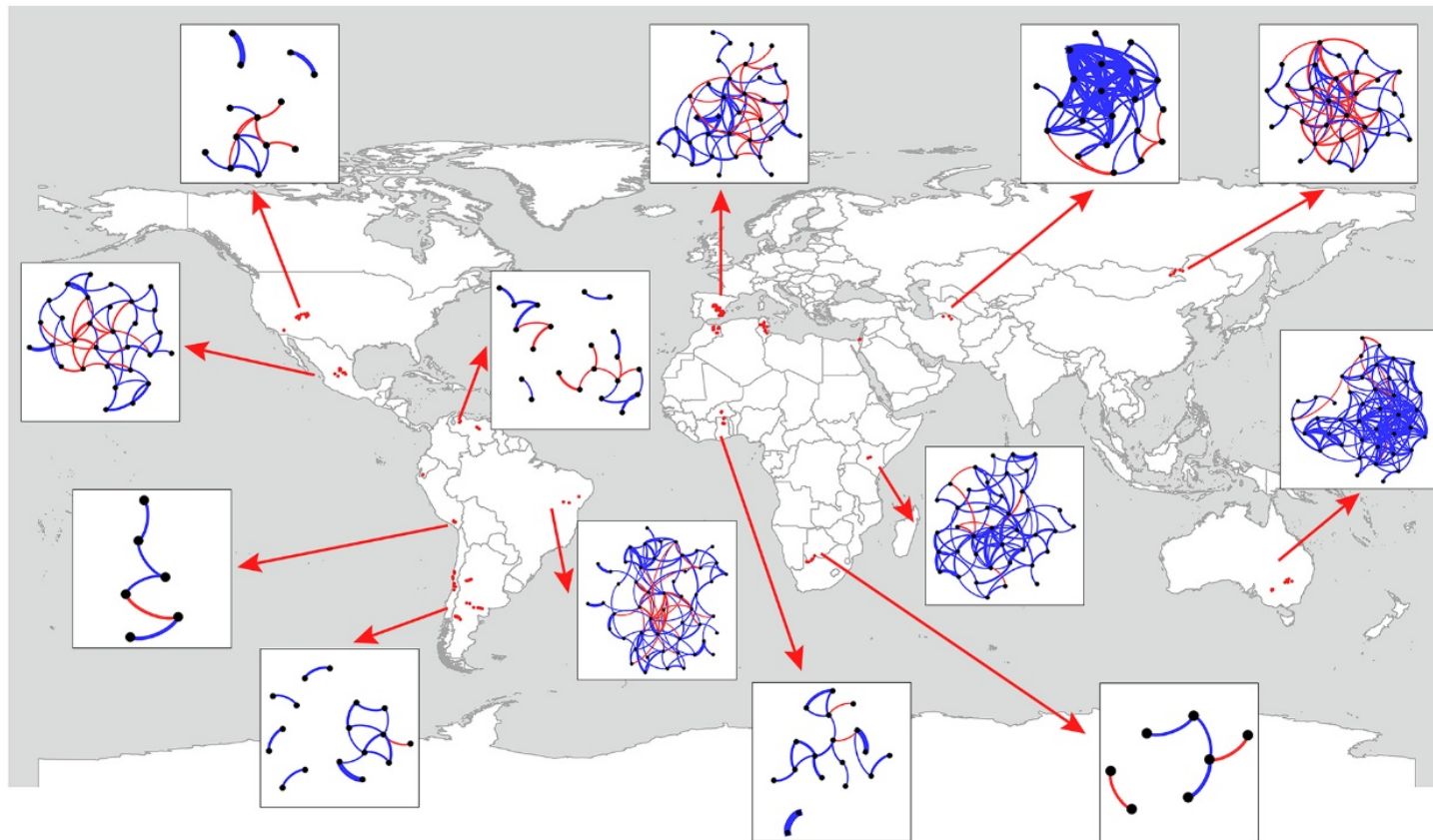
	<i>S</i>	<i>D</i>	\bar{W}	<i>H</i>	<i>K</i>
<i>Real</i>	16.98	1.874	0.113	2.47	0.984
	(7, 39.8)	(0.667, 4.716)	(-0.164, 0.357)	(1.114, 7.206)	(0.83, 1)
<i>CV</i>	0.493	0.602	1.263	0.622	0.041
ΔI	-	1.11	-0.111	0.115	0.067
		(0.162, 3.192)	(-0.352, 0.099)	(-3.155, 3.106)	(-0.001, 0.468)
+	-	133 (0.72)	1 (0.01)	6 (0.03)	130 (0.7)
-	-	0 (0)	18 (0.1)	1 (0.01)	1 (0.01)

614

615 Table 2. Summary of structural equation models showing the effects of network indices on
 616 species richness (*SR*) and evenness (*E*). *D*, link density; \bar{W} , link weight mean; *H*, link weight
 617 heterogeneity; *K*, balance; *SR*, community species richness; *E*, community evenness. Bold
 618 values indicate a significant direct effect of network index on diversity index. ***p* < 0.01; ****p*
 619 < 0.001.

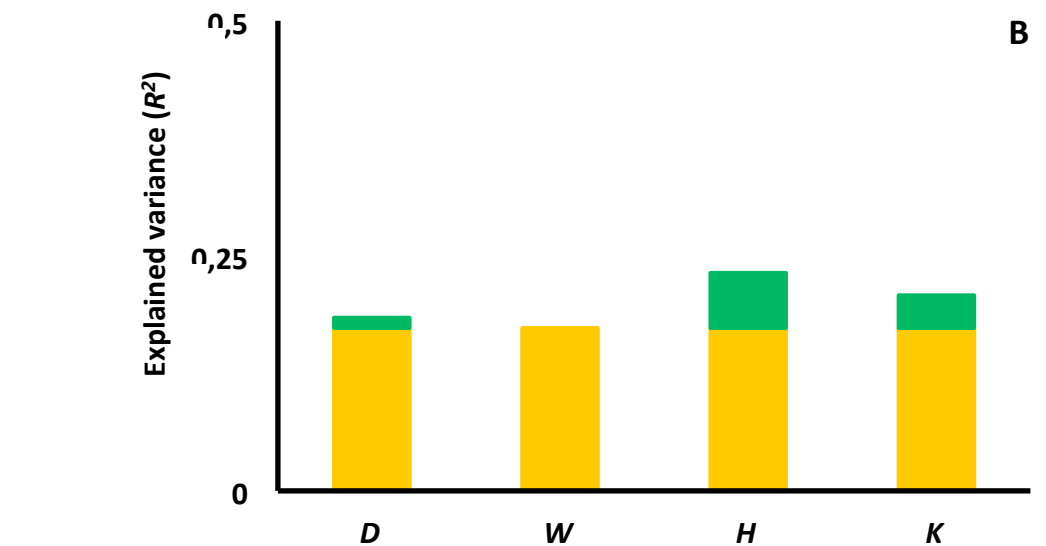
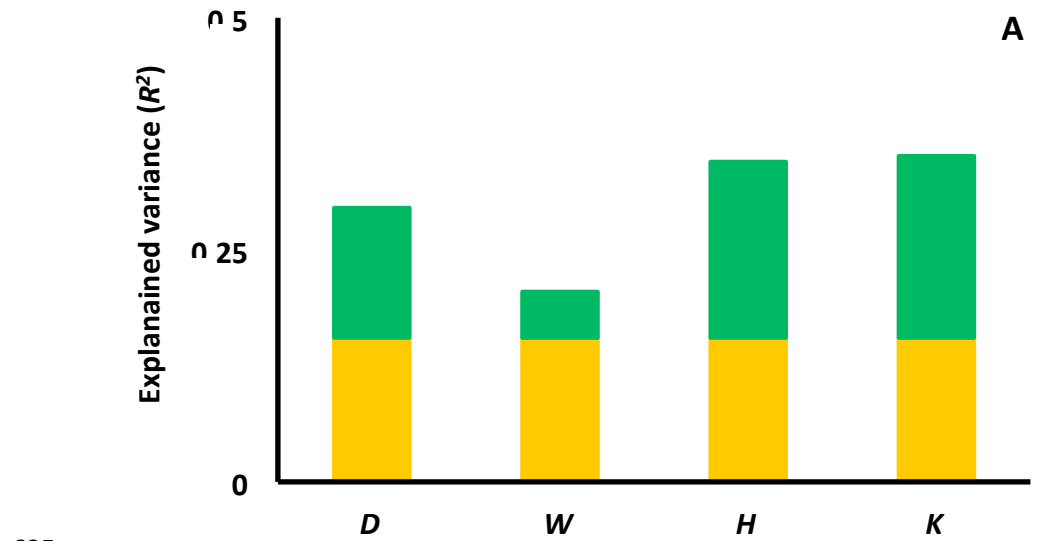
Network index	Biodiversity index	Path estimate	Standard error	z-value	p-value
<i>D</i>	<i>SR</i>	0.368	0.062	5.917	<0.001***
	<i>E</i>	0.099	0.067	1.478	0.139
\bar{W}	<i>SR</i>	0.226	0.07	3.249	0.001**
	<i>E</i>	0.012	0.069	0.18	0.857
<i>H</i>	<i>SR</i>	-0.466	0.061	-7.619	<0.001***
	<i>E</i>	-0.256	0.068	-3.739	<0.001***
<i>K</i>	<i>SR</i>	0.445	0.06	7.463	<0.001***
	<i>E</i>	0.186	0.066	2.82	0.005**

620



621

622 Figure 1. World map showing the locations of all study sites and selected examples of the plant spatial networks found. Blue and red links represent positive
623 and negative interactions, respectively, and link width is proportional to link weight. For simplicity we removed from each network all the species that did
624 not present any link to other species.



627 Figure 2. Effects of explanatory variables on species richness (A) and evenness (B). The
 628 part of the bars represents the explanatory power (R^2) of all abiotic factors together
 629 diversity (both direct and indirect effects); the green part of the bars represents the
 630 contribution of including each network variable in the structural equation models. *D*
 631 density; \bar{W} , link weight mean; *H*, link weight heterogeneity; *B*, global balance.

632

633

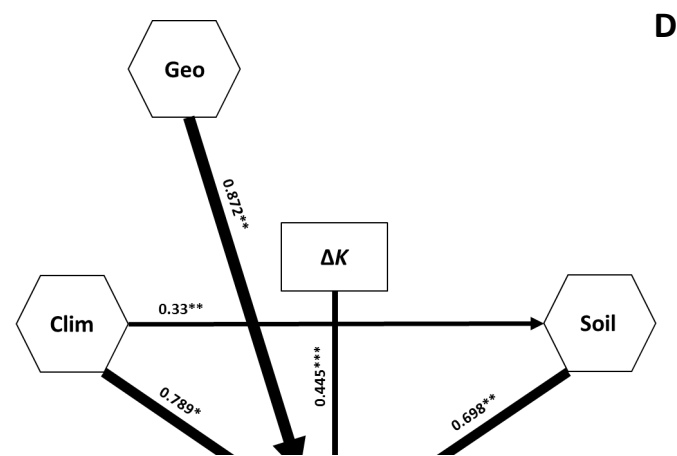
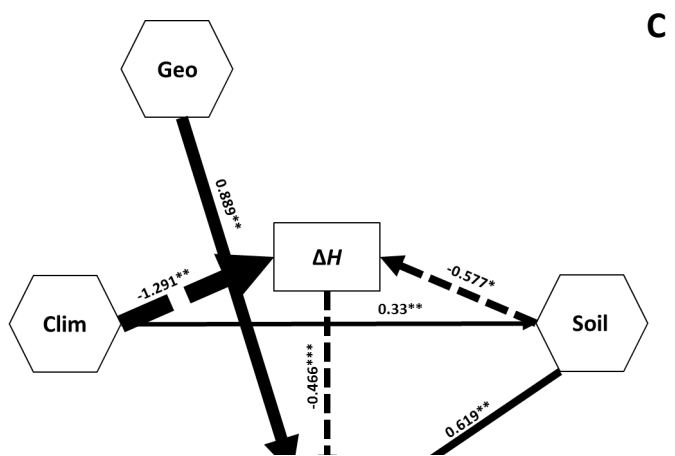
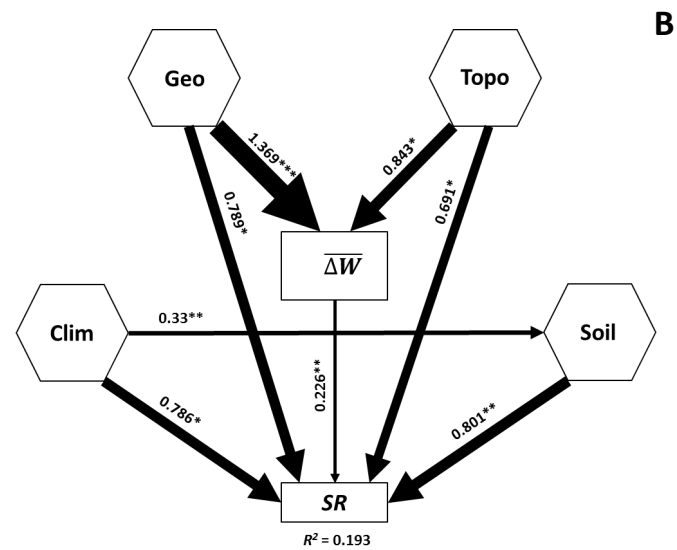
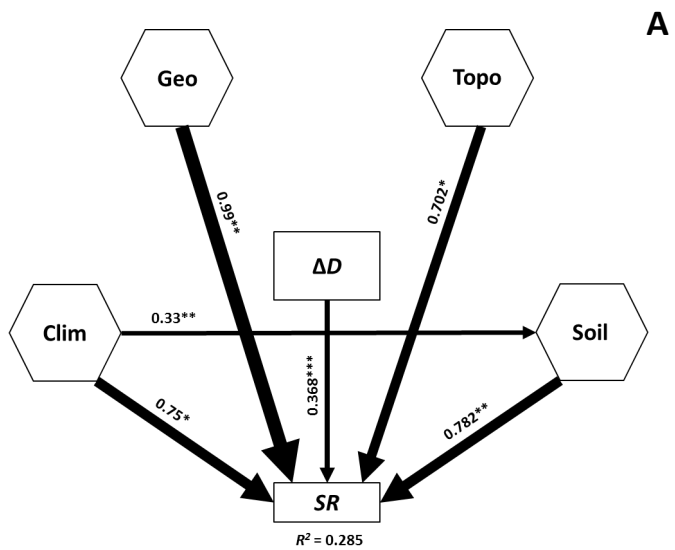


Figure 3. Structural equation models (SEM) describing the effects of abiotic drivers and network indices on plant species richness. *Geo*, geographical factors; *Topo*, Topographical factors; *Clim*, climatic factors; *Soil*, Soil factors; *SR*, community species richness. Different letters represent different network indices: (A) ΔD , link density; (B) $\Delta \bar{W}$, link weight mean; (C) ΔH , link weight heterogeneity; and (D) ΔK , balance. All network indices are the difference between the observed value and the percentile 50 of their respective null model. Numbers adjacent to arrows are indicative of the effect size of the relationship and its significance. Continuous and dashed arrows indicate positive and negative relationships, respectively. R^2 denotes the proportion of variance explained for *SR*. Hexagons are composite variables and squares are observed variables. All models presented a p -value > 0.05 for the χ^2 . For graphical simplicity, only significant arrows and variables with at least one significant relationship are present.