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

2 **drylands**

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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 (Prăvălie, 2016) and presenting a marked local

87   spatial organization (Rietkerk, Dekker, de Ruiter, & van de Koppel, 2004; Sala & Aguiar, 1996),

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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 ºC, 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 $\mathbf{A}_{SxS}$ (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 ($\overline{W}$) is the mean

181   of link weight distribution in the network ($\overline{W} = \sum_{i=1}^{S} \sum_{j=1}^{S} l_{ij}/L$, $\forall\, l_{ij} \neq 0$), and represents the

182   dominant type of spatial pattern in the network; $\overline{W} > 0$ and $\overline{W} < 0$ 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), $K = \frac{tr(e^A)}{tr(e^{|A|})}$, where $|A|$

192   is the underlying unsigned graph of **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, $\overline{W}$), 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, $\overline{W}$ 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, $\overline{W}$ 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, $\overline{W}$ presented both positive and negative values, suggesting that plant

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

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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

common network structures within ecological communities, such as nested and modular

patterns (Olesen, Bascompte, Dupont, & Jordano, 2007; Thébault & Fontaine, 2010). Some of

these structures have been confirmed by global studies conducted on mutualistic systems such

as plant-pollinators (Traveset et al., 2016), suggesting that biotic interactions at the community

level may be structured following general rules. Our analyses indicate that perennial plant

communities in drylands worldwide present common structures, such as the presence of

frequent spatial associations between species and (less commonly) different types of

vegetation patches. Furthermore, vegetation spatial structure, as characterized by networks, is

significantly linked to plant diversity. Therefore, it is possible that local environmental

processes operating in drylands lead to a particular vegetation spatial structure that, together

with other abiotic factors, contributes to explain plant diversity. Our results constitute, to the

best of our knowledge, the first empirical evidence showing the existence of a common

network architecture structuring terrestrial plant communities at the global scale, and provide

novel evidence about the importance of the structure of species interactions for the

maintenance of biodiversity (Bascompte & Jordano, 2007).

Plant spatial networks in drylands are highly connected and balanced

Drylands are characterized by particular vegetation patterns composed by discrete plant

patches embedded in a "matrix" of bare ground soil devoid of perennial vegetation

(Klausmeier, 1999). Theoretical and empirical results have found that this arises from

hydrological-plant interactions, with bare soil areas and vegetation patches acting as 'sources'

and 'sinks', respectively, for runoff water after precipitation events (Puigdefábregas, Solé,

Gutiérrez, del Barrio, & Boer, 1999; Rietkerk et al., 2004). Furthermore, empirical and

modelling studies have shown a connection between vegetation patchiness and ecosystem

processes. However, these studies consider vegetation as a single unity while in general plant

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, Laverty 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 allopathic 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

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

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604

605 Table 1. Values of the network indices found in our study sites. *S*, network size; *D*, link density;

606 $\overline{W}$, 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).

	S	D	$\overline{W}$	H	K
Real	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)
CV	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; $\overline{W}$, 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
D	SR	0.368	0.062	5.917	**<0.001*****
	E	0.099	0.067	1.478	0.139
$\overline{W}$	SR	0.226	0.07	3.249	**0.001****
	E	0.012	0.069	0.18	0.857
H	SR	-0.466	0.061	-7.619	**<0.001*****
	E	-0.256	0.068	-3.739	**<0.001*****
K	SR	0.445	0.06	7.463	**<0.001*****
	E	0.186	0.066	2.82	**0.005****

620
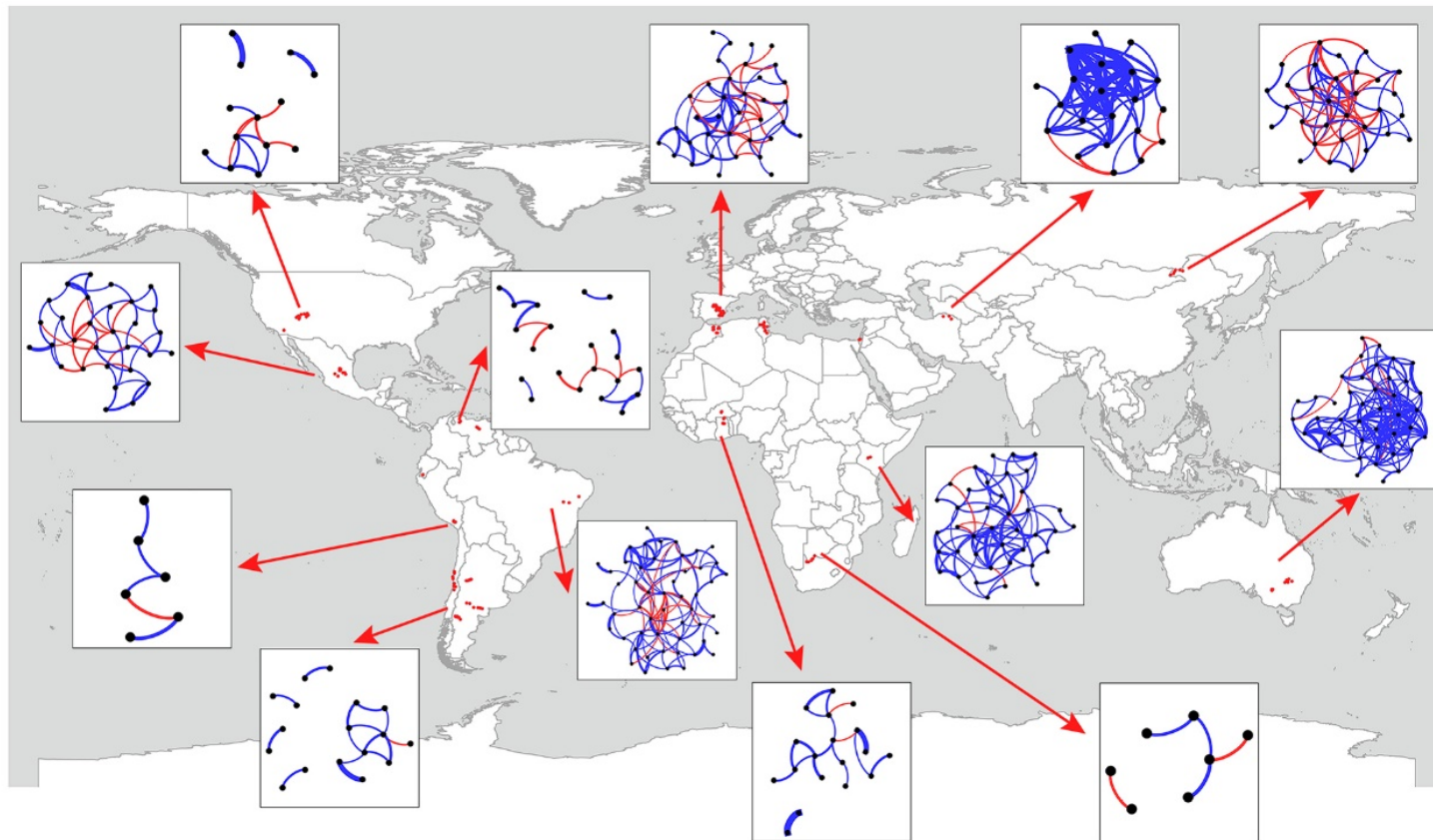
622   Figure 1. World map showing the locations of all study sites and selected examples of the plant spatial networks found. Blue and red links represent positive

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.

625

626
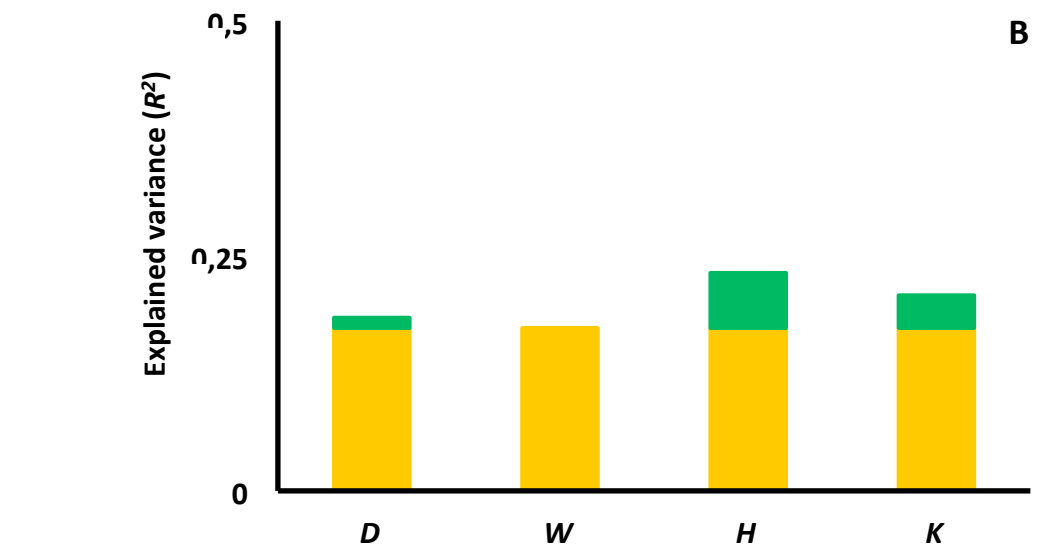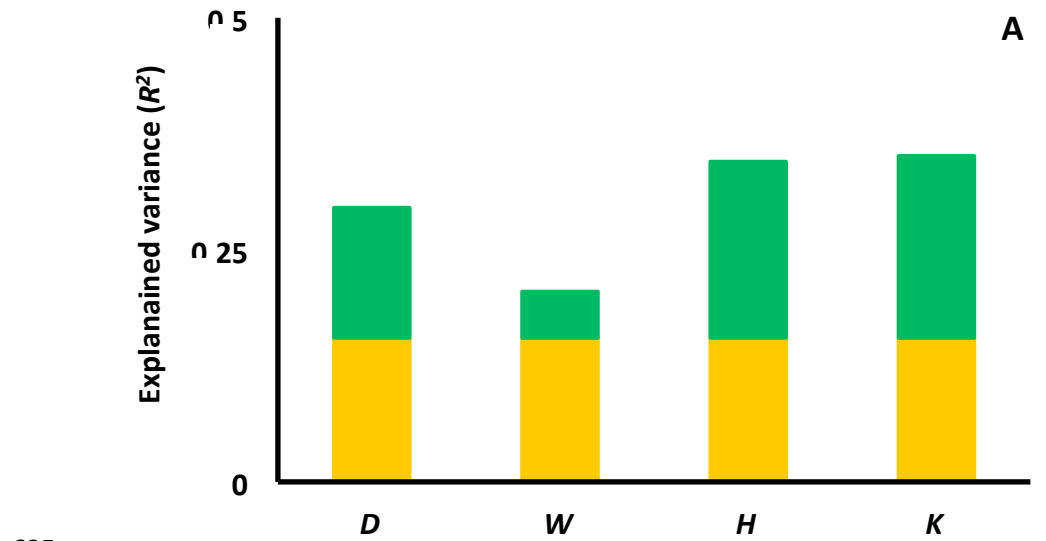
Figure 2. Effects of explanatory variables on species richness (A) and evenness (B). T[...]

part of the bars represents the explanatory power (R^2) of all abiotic factors together [...]

diversity (both direct and indirect effects); the green part of the bars represents the [...]

contribution of including each network variable in the structural equation models. D[...]

density; $\overline{W}$, link weight mean; H, link weight heterogeneity; B, global balance.
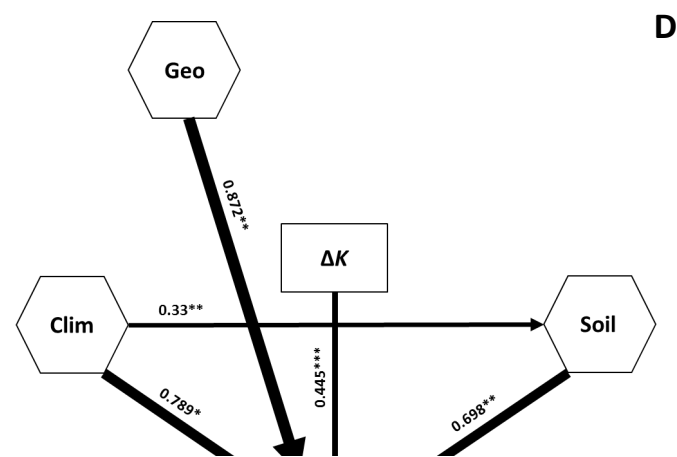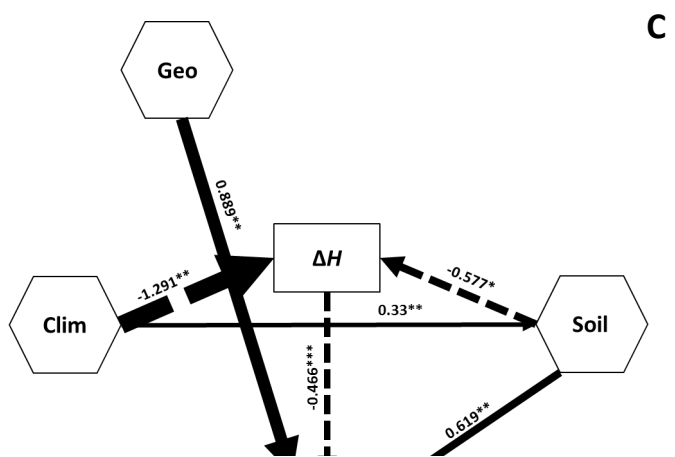
632

633

A

Geo   Topo

0.99**   0.702*

ΔD

Clim   0.33**   Soil

0.75*   0.368***   0.782**

SR

$R^2 = 0.285$

B

Geo   Topo

1.369***   0.843*

0.789*   0.691*

$\overline{\Delta W}$

Clim   0.33**   Soil

0.786*   0.226**   0.801**

SR

$R^2 = 0.193$

C

Geo

0.889**

ΔH   -0.577*

Clim   -1.291**   0.33**   Soil

-0.466***   0.619**

D

Geo

0.872**
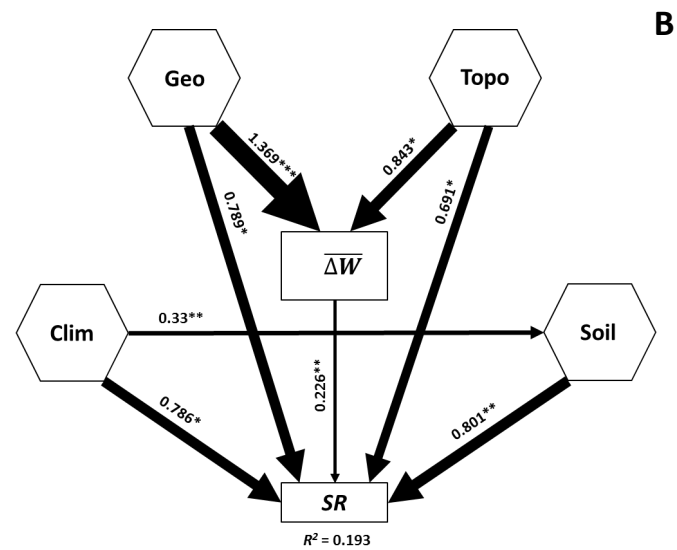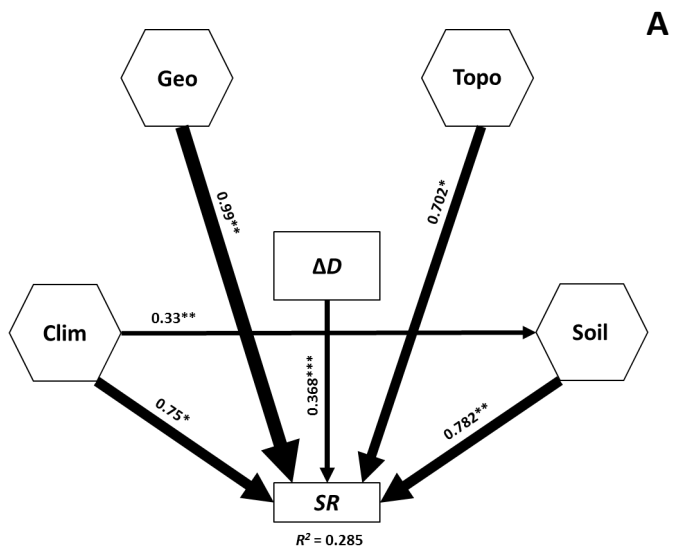
ΔK

Clim   0.33**   Soil

0.789*   0.445***   0.698**

Figure 3. Structural equation models (SEM) describing the effects of abiotic drivers a

network indices on plant species richness. *Geo,* geographical factors; *Topo,* Topogra

factors; *Clim,* climatic factors; *Soil,* Soil factors; *SR,* community species richness. Diffe

represent different network indices: (A) Δ*D*, link density; (B) Δ$\overline{W}$, link weight mean;

weight heterogeneity; and (D) Δ*K*, balance. All network indices are the difference be

value and the percentile 50 of their respective null model. Numbers adjacent to arro

indicative of the effect size of the relationship and its significance. Continuous and d

arrows indicate positive and negative relationships, respectively. R^2 denotes the pro

variance explained for *SR*. Hexagons are composite variables and squares are observ

variables. All models presented a *p*-value > 0.05 for the χ^2. For graphical simplicity, o

significant arrows and variables with at least one significant relationship are present