1 **The structure of plant spatial association networks increases plant diversity in global**

2 **drylands**

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17 Abstract

18 Aim: Despite their widespread use and value to unveil the complex structure of the

19 interactions within ecological communities and their value to assess the resilience of

20 communities, network analyses have seldom been applied in plant communities. We aim to

21 evaluate how plant-plant interaction networks vary in global drylands, and to assess whether

22 network structure is related to plant diversity in these ecosystems.

23 Location: 185 dryland ecosystems from all continents except Antarctica.

24 Methods: We built networks using the local spatial association between all the perennial plant

25 species present in the communities studied, and used structural equation models to evaluate

26 the effect of abiotic factors (including geography, topography, climate and soil conditions) and

27 network structure on plant diversity.

28 Results: The structure of plant networks found at most study sites (72%) was not random and

29 presented properties representative of robust systems, such as high link density and structural

30 balance. Moreover, network indices linked to system robustness had a positive and significant

31 effect on plant diversity, sometimes higher that the effect of abiotic factors.

32 Main conclusions: Our results constitute the first empirical evidence showing the existence of a

33 common network architecture structuring terrestrial plant communities at the global scale,

34 and provide novel evidence of the importance of the network of interactions for the

35 maintenance of biodiversity. Furthermore, they highlight the importance of system-level

36 approaches to explain the diversity and structure of interactions in plant communities, two

37 major drivers of terrestrial ecosystem functioning and resilience against the likely impacts

38 derived from global change.

39   Introduction

40   Network analyses are being increasingly used in ecology to unveil the complexity of species

41   interactions and to study their effects on the functioning and stability of ecosystems (Ings *et*

42   *al.*, 2009; Heleno *et al.*, 2014). Theoretical studies have linked particular network properties

43   with the stability of ecological communities (Rohr *et al.*, 2014; Allesina *et al.*, 2015), and it has

44   been hypothesized that real ecological networks are more prone to have properties promoting

45   the efficiency of ecosystem processes (*e.g.* nutrient uptake, Arditi *et al.*, 2005) and the

46   robustness of communities against perturbations (Estrada, 2006). However, most studies in

47   ecological networks have focused in a few specific systems (*e.g.* food webs, plant-pollinator,

48   host-parasite) and have been conducted at particular study sites, making the establishing of

49   generalizations difficult (Heleno *et al.*, 2014). Thus, comparative studies of networks at

50   regional and global scales are necessary to evaluate whether ecological communities present

51   common properties across multiple environmental conditions, and to explore how they affect

52   key ecosystem attributes such as species diversity and ecosystem functioning (Traveset *et al.*,

53   2016).

54   Plant communities are the bottom of the trophic web, play a major role in ecosystem

55   nutrient cycling and are responsible of community physiognomy (Barbour, 1987). Despite their

56   critical ecological role, and the long tradition of ecological studies with plants, they have been

57   largely unnoticed by network studies until very recently (Verdú *et al.*, 2008; Saiz *et al.*, 2016).

58   The efforts required for obtaining data on plant-plant interactions at community level over a

59   large number of sites (Soliveres & Maestre, 2014), and the different interactions that can be

60   established between plants, such as facilitation or competition (Brooker *et al.*, 2008), have

61   traditionally hampered the use of network analyses to study the structure of plant

62   communities. However, these limitations are starting to be overcome with the increase in the

63   number of coordinated experiments and surveys being conducted globally (Maestre *et al.*,

64   2012b; Fraser *et al.*, 2013), and with methodological developments in the analysis of social

65   networks with positive and negative links (*e.g.* like and dislikes; (Doreian & Mrvar, 2009; Szell

66   *et al.*, 2010). To our knowledge, no study so far has evaluated the structure of plant networks

67   and how it relates to the diversity of plant communities at the global scale. Such analyses

68   would help to unveil global patterns for plant communities, providing simultaneously

69   information about the community (*e.g.* the relative importance of positive and negative

70   interactions) and the species forming it (*e.g.* the role of each species structuring the

71   community, Saiz *et al.*, 2014). Furthermore, the connection between the structure and

72   resilience against extinctions of the network will provide a valuable information about the

73   vulnerability of plant communities facing possible future extinctions due to global change.

74   In this study we explored the structure of plant spatial networks, and evaluated its

75   effects on the diversity of plant communities in global drylands. Despite covering over 45% of

76   global terrestrial area (Prăvălie, 2016), few studies so far have evaluated the network structure

77   of dryland plant communities (Saiz & Alados, 2014; Saiz *et al.*, 2014). Understanding the

78   network structure of dryland plant communities is particularly relevant for multiple reasons.

79   Dryland vegetation is organized as patches embedded in a matrix of bare soil, which become

80   sinks for resources (*e.g.* rainfall, Aguiar & Sala, 1999; Wang *et al.*, 2007). Species responsible of

81   patch formation ('nurses') create a microenvironment where other species, less tolerant to

82   dry environmental conditions, are able to establish (Maestre *et al.*, 2001). Thus, positive

83   interactions play a key role structuring plant communities in drylands, and allow the

84   persistence of communities with higher biodiversity (Verdú *et al.*, 2008; Soliveres & Maestre,

85   2014). However, a network approach can include not only facilitation, but also negative

86   interactions, which also are important drivers in structuring dryland plant communities

87   (Fowler, 1986; Soliveres *et al.*, 2015b). Moreover, several studies have linked vegetation

88   patchiness with ecosystem processes (Berdugo *et al.*, 2017), so we could expect that plant

89   network structure will have a direct effect on the functioning of dryland ecosystems. On the

90   other hand, it has been predicted that drylands will experience the greatest proportional

91   change in biodiversity in the near future (Sala *et al.*, 2000), so a better understanding of the

92   connection between the plant-plant interaction network structure and plant diversity can

93   provide clues about how dryland communities will respond to the upcoming changes that they

94   will face under ongoing global environmental change.

95   Dryland vegetation presents a marked spatial organization resulting from the interplay

96   between climatic conditions, soil properties and plant-plant interactions (Sala & Aguiar, 1996;

97   Rietkerk *et al.*, 2004). Therefore, we expect that, under a given soil conditions and climate, this

98   organization will be a good proxy of the structure of interactions between plants. Hence, we

99   built plant-plant networks with positive and negative links considering the spatial association

100   between all perennial plants present in 185 plant communities from all continents except

101   Antarctica, and used structural equation models (Grace, 2006) for testing the effect of network

102   structure on the plant community diversity. Specifically, we hypothesize that in drylands a)

103   plant spatial networks present a common structure that promotes the resilience of the system

104   against the extinction of species and interactions, and b) this structure has a direct effect on

105   the diversity of the plant community. We expect that plant spatial networks in drylands

106   present a high number and variety of connections between species (*i.e.* high link density and

107   heterogeneity) due to the importance of biotic interactions, and to that of facilitation in

108   particular, as drivers of community assembly. Furthermore, and after controlling the effect of

109   abiotic factors, we anticipate that both a high link density and heterogeneity and the

110   dominance of positive links will have a significant and positive effect on the diversity of dryland

111   plant communities.

112   Methods

113   Global drylands vegetation survey

114   Field data were collected from 185 dryland sites located in 17 countries (Argentina, Australia,

115   Botswana, Brazil, Burkina Faso, Chile, China, Ecuador, Ghana, Iran, Kenya, Mexico, Morocco,

116   Peru, Spain, Tunisia, USA and Venezuela). These sites are a subset of the global network of 236

117   sites from Ulrich *et al.* (2016). As network indices depend on network size and must be tested

118   against null models (Dormann *et al.*, 2009), we selected all sites which networks had at least 5

119   connected species to allow statistical testing (185 sites out of 236 sites available). This subset

120   included the major vegetation types found in drylands, a wide range in plant species richness

121   (from 5 to 52 species per site) and environmental conditions (mean annual temperature and

122   precipitation ranged from -1.8 to 28.2 ºC, and from 66 to 1219 mm, respectively).

123   At each site, vegetation was surveyed using four 30-m-long transects located parallel

124   among them within a 30 m x 30 m plot representative of the vegetation found there (see

125   Maestre *et al.*, 2012b for details). At each transect, 20 quadrats of 1.5 m x 1.5 m were

126   established, and the cover of each perennial species within each quadrat was visually

127   estimated

128   Network construction

129   For each of the study sites, we built a plant-plant spatial association network (Saiz *et al.*, 2014,

130   2016) using the cover data of all the perennial species (*S*) surveyed. These networks are

131   characterized by the adjacency graph $\mathbf{A_{SxS}}$ (hereafter $\mathbf{A}$), where the nodes (*i,j*) are the plant

132   species and the links (l_{ij}) are the spatial association between each pair of species. To determine

133   this association, we calculated the correlation between the cover of each pair of species in the

134   quadrats within each site using Spearman rank tests. When a correlation between species *i*

135   and *j* was significant ($p < 0.05$), a link $l_{ij} = \rho$ was established (where ρ represents the Spearman

136   correlation coefficient), with $l_{ij} = 0$ otherwise. Thus, links in our networks are signed (can have

137   positive and negative values) and weighted (can present values between -1 and +1). For each

138   site, *L* represented the total number of links in the network. As each species only had a single

139   cover value at each quadrat, we could not evaluate the intra-specific spatial association; thus,

140   we set the diagonal of **A** to zero.

141   We are aware that the use of spatial association to infer real biotic interactions

142   presents several limitations. For example, factors different from biotic interactions, such as

143   plant dispersal strategies or environmental heterogeneity, can influence vegetation spatial

144   patterns (Escudero *et al.*, 2005; Getzin *et al.*, 2008). However, it has been suggested that biotic

145   interactions are the main driver of spatial pattern formation at local scales (Pearson & Dawson,

146   2003; Morales-Castilla *et al.*, 2015), and previous studies have found a good agreement

147   between the outcome of spatial association and that of experiments evaluating plant-plant

148   interactions in dryland communities (Tirado & Pugnaire, 2003). Therefore, we considered

149   spatial pattern in a local scale, similar to that used in other studies about biotic interactions in

150   plant communities (Cavieres *et al.*, 2006; Verdú & Valiente-Banuet, 2011). Another possible

151   shortcoming of our approach is that different types of biotic interactions can lead to the same

152   spatial pattern, like facilitation and parasitism (*i.e.* positive spatial association). Thus, it would

153   not be possible to differentiate between both interactions. However, we did not find parasitic

154   species in our sites, so we can approach that positive spatial association only represents

155   facilitative interactions.

156   Network indices

157   We selected four network indices to characterize the structure of the communities studied:

158   link density, link weight mean, link weight heterogeneity, and global network balance. Link

159   density (D) is the average number of links per node in the network ($D = L/S$), and represents

160   the importance of spatial patterns in the plant community, with high D describing a community

161   where vegetation is more spatially structured (*i.e.* significant spatial association between pairs

162   of species are common). Link weight mean ($\overline{W}$) is the mean of all link weights in the network

163   ($\overline{W} = \sum_{i=1}^{S} \sum_{j=1}^{S} l_{ij}/L, \forall\, l_{ij} \neq 0$) and represents the dominant type of links in the network,

164   with $\overline{W} > 0$ and $\overline{W} < 0$ describing a community dominated by spatial aggregation and

165   segregation, respectively. Link weight heterogeneity (*H*) is the kurtosis of the link weight

166   distribution, with high *H* indicating a network where most links present similar weights. Global

167   network balance (*K*) is a specific index for signed networks that accounts for the proportion of

168   closed cycles in the network fulfilling the structural balance criterion (Zaslavsky, 2013).

169   Following this criterion, a network can be divided in blocks; nodes within the same block are

170   positively connected among them while they are negatively connected to nodes in other

171   blocks (Doreian & Mrvar, 2009; Traag & Bruggeman, 2009). We calculated *K* using the

172   definition of Estrada & Benzi (2014), $K = \frac{tr(e^{A})}{tr(e^{|A|})}$, where |**A**| is the underlying unsigned graph

173   of **A**. High values of *K* indicate that the network presents a 'balanced' structure (with *K* = 1

174   indicating a perfect balance), while low values indicate that several links do not fulfill this

175   criterion and network is 'unbalanced' (*sensu*, network is 'frustrated', Doreian & Mrvar, 2009).

176   Null model analyses

177   To test the significance of the network indices used, we employed two different null models

178   for each network: one that allowed changing the connectivity of the network, and another that

179   allowed changing the links between nodes while keeping the network linkage distribution

180   constant. In the first model, we randomized the cover of each species along the quadrats.

181   Specifically, we kept the cover distribution for each species constant, but changed randomly

182   their positions in the quadrats. This way, we changed the cover values of species co-occurring

183   in the same quadrat while maintaining the original cover distribution for each species at each

184   site. Then, we built a network using this simulated data and calculated its D, $\overline{W}$ and H. For each

185   site, we simulated 2000 networks and compared the real values of the indices against a 95%

186   confidence interval created from the simulated networks. In the second null model, we

187   simulated networks at each site using an algorithm based on the configurational model

188   adapted for signed networks (Saiz *et al.*, 2016). This method iteratively changes links in the

189   original network, modifying its structure but keeping constant its linkage distribution. In our

190   case, we made 1000 iterations per network and simulated 1000 networks, and we calculated K

191   for each of the simulated networks. We also calculated the maximal and minimal K (K_{max} and

192   K_{min}) that each network could have considering its degree distribution to evaluate the real K

193   value against all the possible values that it could present at each site. To do so, we iteratively

194   simulated networks with the same null model, and selected the network that maximized (or

195   minimized) K at each step. To avoid possible local maxima (or minima), selection was based on

196   a Fermi-Dirac probability function ($f = \frac{1}{1+e^{-\beta\Delta}}$), which selected a network over others based

197   on the difference between the K values of the networks (Δ) and a parameter β that modulates

198   the probability of accepting a change with the number of iterations (with higher β selecting

199   higher Δ, Tsallis & Stariolo, 1996). By doing so we could precisely locate real networks in all the

200   space of parameters of K.

201   Evaluating the effects of network structure on plant diversity

202   We built structural equation models (SEM, Grace, 2006) including different abiotic variables

203   (Latitude, Longitude, Elevation, Slope, Aridity, Seasonality, Soil organic C, Soil pH and soil total

204   P) and network variables as explanatory variables for the richness (SR) and evenness (E) of

205   perennial plant species. Specifically, we divided abiotic variables in four groups: geographical,

206   topographical, climatic, and soil variables, and created a composite variable for each of them.

207   We included the difference between real network values and the percentile 50 values for the

208   networks simulated with the null models (*e.g.* $\Delta D = D - D_{null}$, where D_{null} is the percentile 50 for

209   the D simulated with the null model) to remove random effects due to species abundance

210   distribution (Gotelli, 2000) and network size (Dormann *et al.*, 2009) from network indices. We

211   then created a SEM for each combination of network and diversity variables (for a total of 4 x 2

212   = 8 SEMs). In these SEMs, network variables depended on all the composite variables, and

213   diversity indices depended on all the composite variables and the network indices (see

214   supplementary figures S1 and S2 for a complete description of the variables and the structure

215   of the SEMs used). Specific dependencies between composite variables were included

216   following previous studies using the same dataset (Delgado-Baquerizo *et al.*, 2016). All

217   variables were centered and standardized before calculating the models. All the SEM analyses

218   were performed with the *lavaan* package (Rosseel, 2012) for R.3.2.4 (R Development Core

219   TeamTeam, 2014).

220

221   Results

222   The analysis of plant spatial association networks revealed that dryland plant communities

223   present a wide variety of linkage structures (*i.e.* network indices were quite variable, Table 1,

224   Figure 1). Particularly, $\overline{W}$ presented both positive and negative values, suggesting that

225   drylands can be dominated by spatial aggregation or segregation. However, K presented a very

226   low variability, with values close to 1 (Table 1). These results suggested that, in general, plant

227   spatial networks in drylands organize their linkages fulfilling the structural balance criteria.

228   The studied plant spatial networks did not organize randomly (Table 1). Specifically,

229   plant communities showed significantly more spatial associations per species (D) than

230   expected. Furthermore, 72% of communities presented significantly higher D values, and no

231   single community had a lower D than expected. These results confirm that plant communities

232   in drylands present a strong spatial structure. Furthermore, 92% of plant communities are

233   closer to the optimal K than to the expected value, indicating the prevalence of balanced

234   spatial structures in drylands.

235   Our structural equation models revealed that the structure of spatial networks

236   significantly affected the richness and evenness of dryland plant communities (Table 2). All

237   network indices had a significant effect on plant community species richness (SR), but only H

238   and K had a significant effect on community evenness (E). Furthermore, network variables

239   were the single predictors that had a higher explanatory power on *SR*, while abiotic variables

240   had similar or higher effect than network variables on *E* (Figure 2). Interestingly, the effects of

241   network indices were largely independent from those of other variables, albeit geography and

242   topography had a significant relationship with $\overline{W}$ and climate and soil affected *H* (Figures 3 and

243   S2).

244

245   Discussion

246   Studies at global scales offer unparalleled insights to build generalities in ecology based on the

247   discovery of common patterns and processes operating in a large number of locations and/or

248   ecosystems (Fraser *et al.*, 2013). Studies on biotic interactions have often found several

249   network structures that commonly repeat in ecological communities, such as nested and

250   modular patterns (Olesen *et al.*, 2007; Thébault & Fontaine, 2010). Some of these structures

251   have been confirmed by global studies conducted on mutualistic systems such as plant-

252   pollinators (Traveset *et al.*, 2016), suggesting that biotic interactions at the community level

253   may be structured following general rules. Our results indicate that perennial plant

254   communities present a common network structure, and that network attributes such as high

255   connectivity, link heterogeneity, and balanced structure are positively related to plant diversity

256   in drylands worldwide. Therefore, it is possible that general processes operating in drylands

257   lead to a particular community structure and, as suggested by our results, that this particular

258   structure contributes to increment plant diversity regardless other abiotic factors. Our results

259   constitute, to the best of our knowledge, the first empirical evidence showing the existence of

260   a common network architecture structuring terrestrial plant communities at the global scale,

261   and provide novel evidence of the importance of the network of interactions for the

262   maintenance of biodiversity (Bascompte & Jordano, 2007).

263   Plant spatial networks in drylands are highly connected and balanced

264   Drylands are characterized by particular vegetation patterns, composed by bare soil and

265   vegetation patches (Klausmeier, 1999). Theoretical and empirical results have found that this

266   pattern is the result of hydrological-plant interactions, with bare soil areas acting as 'sources'

267   and vegetation patches acting as 'sinks' for runoff water after precipitation events

268   (Puigdefabregas *et al.*, 1999; Rietkerk *et al.*, 2004). Furthermore, empirical and modelling

269   studies have shown a connection between vegetation patchiness and ecosystem processes.

270   For example, Maestre (2006) reported a positive relationship between the spatial pattern of

271   vegetation patches and their water use efficiency, and Berdugo *et al.* (2017) found that this

272   pattern was related to ecosystem multifunctionality (*i.e.* the simultaneous provision of

273   multiple ecosystem functions) in global drylands, being also able to identify the bimodal

274   distribution of multifunctionality observed. However, these studies consider vegetation as a

275   single unity while in general vegetation patches are composed by multiple species that are

276   interacting among them (Tielbörger & Kadmon, 2000), and can respond differently to the same

277   environmental factor (Saiz & Alados, 2011; Pueyo *et al.*, 2013).

278   We found that most plant species presented many spatial associations among them,

279   and that dryland communities could be dominated by spatial aggregation or segregation, as

280   found in many local studies (Fowler, 1986; Soliveres & Maestre, 2014). An interesting pattern

281   observed is that, regardless of the dominant spatial pattern found at each site, vegetation

282   patches in drylands seem to organize following the structural balance criteria worldwide. Thus,

283   within a given plant community, plant species that aggregate within the same patches do not

284   appear in patches formed by other species (Saiz *et al.*, 2016). In drylands, species responsible

285   of patch formation facilitate the establishment of seedlings under their canopies, but when

286   seedlings become adults, these interaction may change to competition (Tielbörger & Kadmon,

287   2000). Particularly, this change is more common between phylogenetically related species

288   which share niche requirements, resulting in communities where plant species tend to interact

289   negatively with close relative species and positive with a subset of the distant relatives (Verdú

290   *et al.*, 2010). In our case, as we only consider mature plant communities, we could expect that

291   the different blocks observed within our networks represent the different types of vegetation

292   patches present in the community (Saiz *et al.*, 2014), and that the balanced organization is the

293   result of niche processes among species (*e.g.* promotion of competition between closely

294   related species and facilitation between distant ones, Verdú & Valiente-Banuet, 2011).

295   Furthermore, although not specifically tested in ecology so far, studies on signed networks

296   suggest that the balance criterion would promote the resilience of the network (*e.g.* reducing

297   the disturbances within the network, Cartwright & Harary, 1956; or increasing the adaptability

298   of the system, Ilany *et al.*, 2013). Hence, our results suggest that the balanced spatial

299   structures observed could increase the resilience of dryland plant communities worldwide.

300   Substantial research efforts have been developed to understand the links between

301   network structure and community robustness. For example, the nested structure of

302   mutualistic networks makes the community robust to the random extinction of species

303   (Memmott *et al.*, 2004), while modularity is linked to higher resilience in trophic networks

304   (Thébault & Fontaine, 2010). A recent study by (Gao *et al.*, 2016) posits that both network

305   resilience against the random extinction of nodes and changes in the number and strength of

306   links increase with higher link density and more heterogeneous link strength distributions. The

307   plant spatial association networks studied here present one of these conditions, high link

308   density, while we did not found a significant difference for link strength heterogeneity

309   between real networks and the null model. This could be explained by the high dominance of

310   links with low weight, which is the typical case for ecological networks and it has been

311   suggested to play an essential role maintaining the persistence in food webs (McCann *et al.*,

312   1998). Thus, our results suggest that plant spatial association networks present a structure

313   which enhances community resilience against perturbations affecting both species and

314   interactions among them.

315   The structure of plant spatial networks promotes species diversity

316   We found a significant effect of network indices on plant species richness and evenness in

317   drylands worldwide. All indices linked to network resilience, such as D and H, had positive

318   effects on the diversity metrics studied (higher link density and link weight heterogeneity

319   values where linked to a higher plant diversity), and the positive effect of K on diversity

320   supports the idea that balanced spatial structures increase the resilience of plant communities.

321   On the other hand, and contrary to our expectations, we did not find any effect of the

322   importance of positive interactions on plant diversity. A possible explanation is that the

323   importance of positive and negative interactions alone (*sensu* Brooker *et al.*, 2005) does not

324   suffice to explain the coexistence of diverse species in a community, and thus is imperative to

325   explore also the structure of these interactions (Soliveres *et al.*, 2015b). For example, it has

326   been proposed that coexistence of more species can be enhanced when competitive

327   interactions are not hierarchical, but are intransitive (Wootton, 2001), something that has

328   been found in a previous analyses of our global database (Soliveres *et al.*, 2015a). Therefore,

329   our results encourage the use of approaches as networks in plant communities, which not only

330   account for the importance of biotic interactions but also for their structure in the community,

331   and are able to consider simultaneously different types of interactions as facilitation and

332   competition.

333   Additionally, we found that the effects of network structure on the diversity of plant

334   communities are largely independent from those of abiotic factors. Previous studies conducted

335   in arid environments have suggested that nested network structures of facilitative interactions

336   help to preserve the diversity of plant communities (Verdú *et al.*, 2008). Furthermore, a

337   positive relationship between the spatial organization of vegetation patches and plant species

338   richness has also been found (with more patchy communities associated to higher number of

339   species; Maestre, 2006; Pueyo *et al.*, 2013). Our results represent a step forward, as the

340   network approach used considers both facilitation and competition, and show that the

341   structure of both facilitative and competitive interactions have a direct effect in plant

342   community diversity. On the other hand, recent studies have found that attributes such as

343   plant species richness are positively related to multifunctionality in drylands (Maestre *et al.*,

344   2012b), which is also affected by other community attributes such as species composition and

345   spatial pattern (Maestre *et al.*, 2012a; Berdugo *et al.*, 2017). Therefore, it is very likely that the

346   structure of plant interaction networks is not only responsible for the resilience of the

347   community against the extinction of species and interactions, but also plays a key role in the

348   maintenance of ecosystem functions against future environmental changes.

349   Concluding remarks

350   The analysis of the plant spatial association networks revealed new insights on the structure of

351   plant communities in drylands worldwide. These communities showed common patterns but,

352   in contrast to previous studies focused on local communities and positive interactions (Verdú

353   *et al.*, 2008), we found that these patterns apply worldwide to plant communities including

354   both positive and negative interactions. The structure of the networks studied showed a high

355   density of connections between species and followed a balanced criterion, properties that are

356   related with the resilience of the communities against disturbances (Gao *et al.*, 2016).

357   Furthermore, networks with dense and heterogeneous connections and balanced structures

358   presented higher plant diversity, which supported the idea of these network structures

359   promoting the coexistence of larger number of species. Finally, the independence of these

360   properties from abiotic factors and from the dominance of positive or negative links revealed

361   the need to take into account not only the importance of biotic interactions but also their

362   structure when studying drivers of dryland vegetation assembly. Although challenging, global

363   field studies provide the framework to find common patterns in natural communities and to

364   advance in our understanding of ecosystem processes. Our results highlight the importance of

365   system level approaches to explain the diversity of plant species, a major driver of ecosystem

366   functioning, and to identify the structure of communities that is likely to provide the highest

367   resilience against disturbances, in drylands worldwide.

368

369   Acknowledgements

379

380   Supplementary material

381   S1. Structural equation model used to evaluate the effect of network indices on plant

382   community diversity and explanation of the variables.

383   S2. Structural equation models (SEM) describing the effects of abiotic drivers and spatial

384   network indices on plant community evenness.

385

386   Data availability statements

387   All the materials, raw data, and protocols used in the article are available upon request and

388   without any restriction, and will be published in an online repository (figshare) upon the

389   acceptance of the article (currently available as a private link

390   https://figshare.com/s/6ae331fa92446433d8a4).

391

392   Biosketch

393   Hugo Saiz is a community ecologists specially interested in disentangling the mechanisms that

394   structure plant communities and allow the coexistence and persistence of high diverse

395   ecosystems. Fernando Maestre is a drylands ecologist and his research uses an integrative

396   approach combining a wide variety of tools, biotic communities and scales to understand the

397   functioning of semiarid ecosystems. Jesús Gómez-Gardeñes and Juan Pablo Borda are

398   physicists working on the dynamic of complex systems including both theoretical approaches

399   and its application to real systems ranging from car displacements to ecological systems.

400

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573

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

575 $\overline{W}$, link weight mean; *H*, link weight heterogeneity; *K*, balance. *Real* represents the mean value

576 of the index observed in real networks; *CV* represents the coefficient of variation of *Real*; and

577 *ΔI* represents the mean difference between the index of real networks and the percentile 50

578 value of their corresponding null model. Values in parentheses represent the 95% confidence

579 interval for the index created using the percentiles 2.5 and 97.5 for study sites; bold values

580 indicate a significant difference between Real and Null values. *+* and *−* indicate the number of

581 networks which presented significantly higher or lower values for their indices respect the null

582 model (values in parentheses represent the proportion).

	S	D	$\overline{W}$	H	K
Real	16.99	1.877	0.298	2.472	0.984
	(7, 39.8)	(0.667, 4.763)	(-0.6, 1)	(1.114, 7.326)	(0.83, 1)
CV	0.494	0.608	1.408	0.622	0.041
ΔI	-	1.112	-0.111	0.116	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)	171 (0.92)
_	-	0 (0)	18 (0.1)	1 (0.1)	3 (0.02)

583

584   Table 2. Summary of structural equation models showing the effects of network indices on

585   species richness (*SR*) and evenness (*E*). *D*, link density; $\overline{W}$, link weight mean; *H*, link weight

586   heterogeneity; *K*, balance; *SR*, community species richness; *E*, community evenness. Bold

587   values indicate a significant direct effect of network index on diversity index. **$p < 0.01$; ***p

588   < 0.001.

Network index	Biodiversity index	Path estimate	Standard error	z-value	p-value
D	*SR*	0.371	0.062	5.961	**<0.001***
	E	0.103	0.067	1.537	0.103
$\overline{W}$	*SR*	0.227	0.07	3.253	**0.001**
	E	0.014	0.069	0.207	0.836
H	*SR*	-0.446	0.061	-7.616	**<0.001***
	E	-0.256	0.068	-3.739	**<0.001***
K	*SR*	0.445	0.06	7.391	**<0.001***
	E	0.186	0.066	2.82	**0.005**

589

590
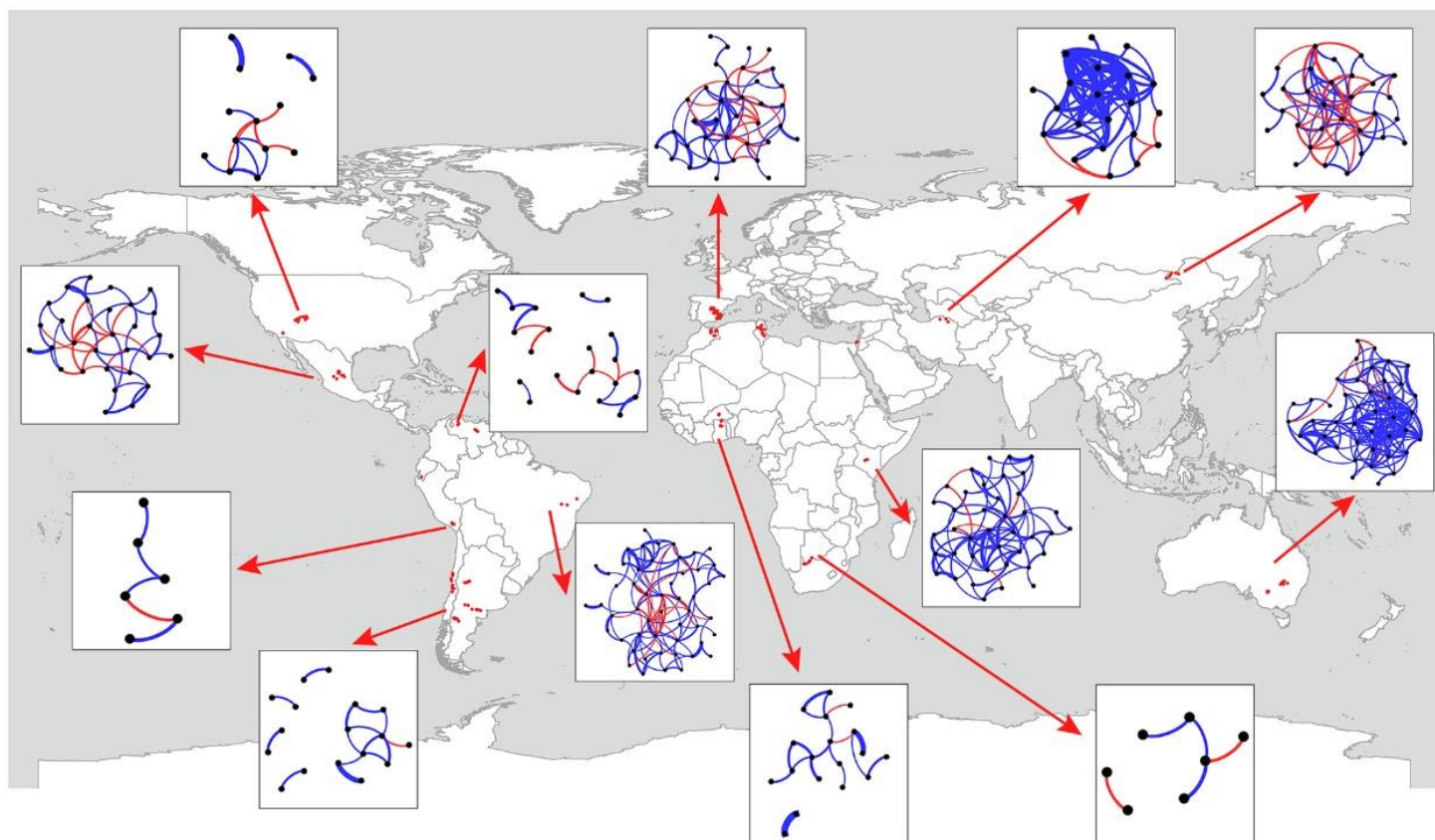
591   Figure 1. World map showing the locations of all study sites and selected examples of the plant spatial networks found. Blue and red links represent positive

592   and negative interactions, respectively, and link width is proportional to link weight. For simplicity we removed from each network all the species that did

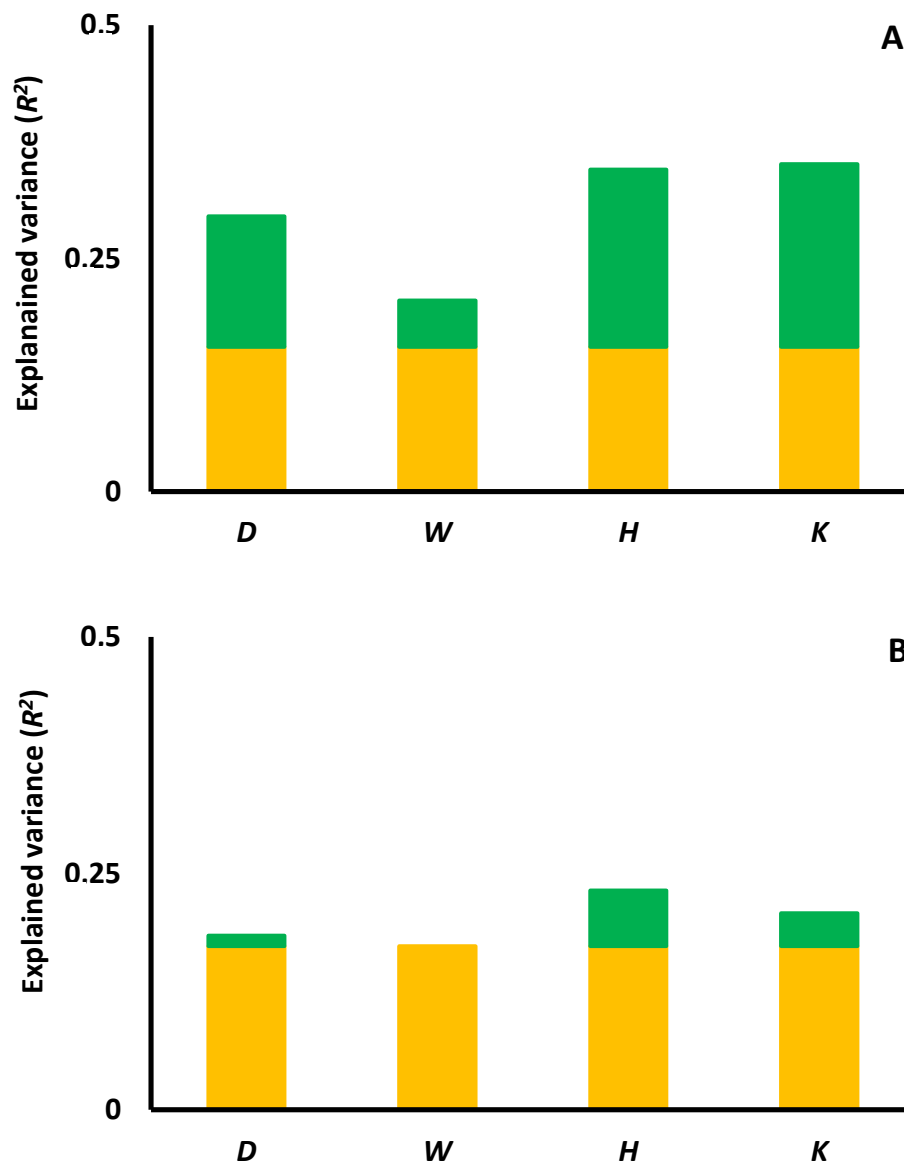593   not present any link to other species.

Figure 2. Effects of explanatory variables on species richness (A) and evenness (B). The orange part of the bars represents the explanatory power (R^2) of all abiotic factors together on diversity (both direct and indirect effects); the green part of the bars represents the direct contribution of including each network variable in the structural equation models. D, link density; $\overline{W}$, link weight mean; H, link weight heterogeneity; B, global balance.
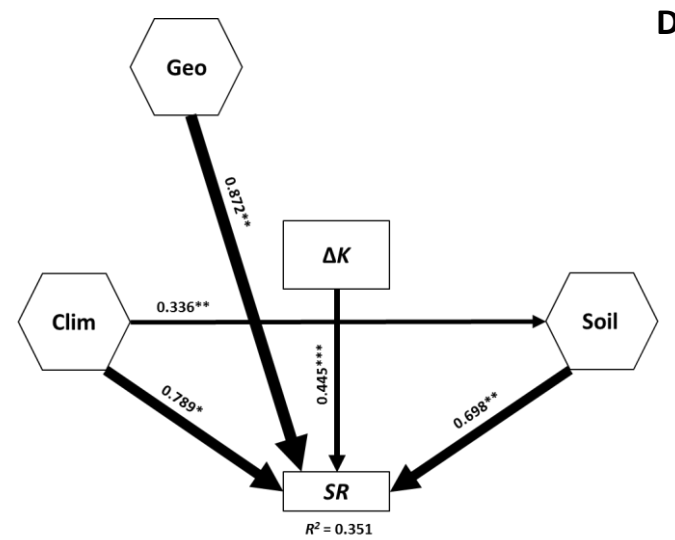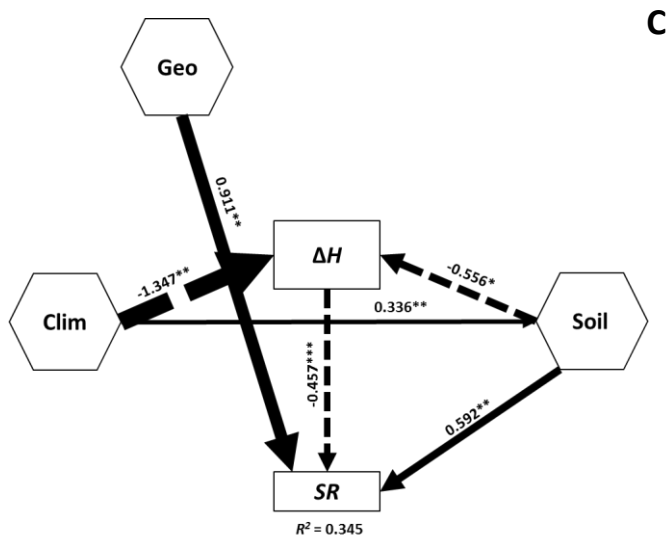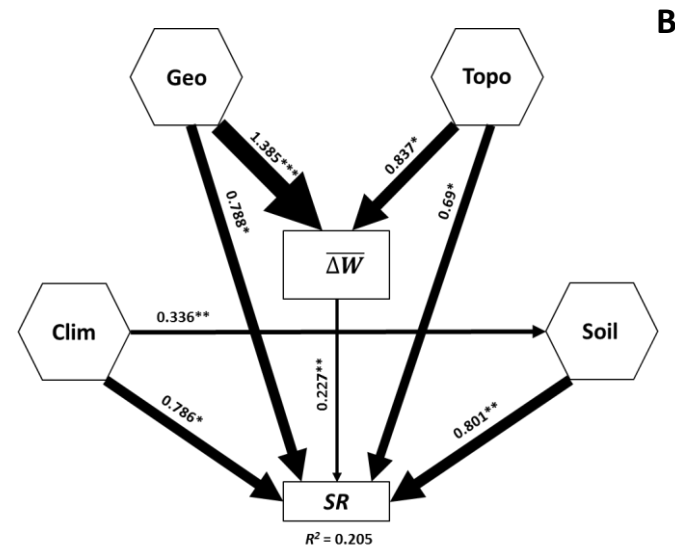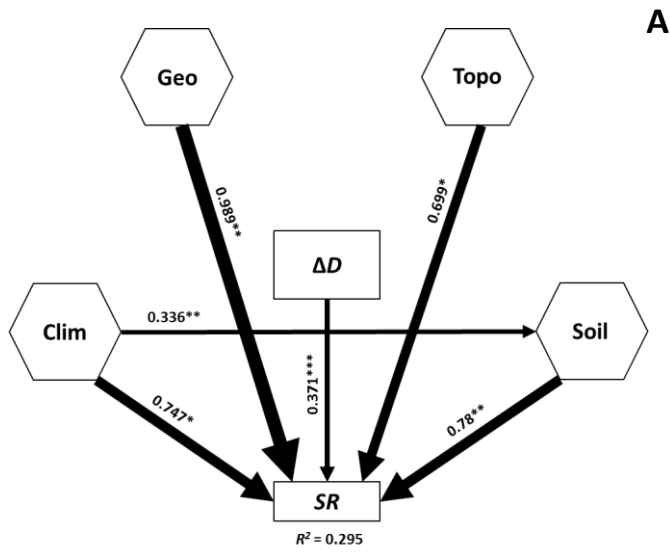
Figure 3. Structural equation models (SEM) describing the effects of abiotic drivers and spatial network indices on plant community diversity. *Geo,* geographical factors; *Topo,* Topographical factors; *Clim,* climatic factors; *Soil,* Soil factors; *SR*, community species richness. Different SEMs represent different network indices: (A) ΔD, link density; (B) $\Delta \overline{W}$, link weight mean; (C) ΔH, link weight heterogeneity; and (D) ΔK, balance. All network indices are the difference the between real 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 observable 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 presented.