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

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Abstract

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

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

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

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

KEYWORDS
competition, determinants of community structure and diversity, drylands, ecological networks, facilitation, plant diversity, signed networks, spatial patterns

1 | INTRODUCTION

Network analyses are being increasingly used in ecology to unveil the complexity of species interactions and to study their effects on the functioning and stability of ecosystems (Heleno et al., 2014). Theoretical studies have linked network topologies with the stability of ecological communities (Allesina et al., 2015; Rohr, Saavedra, & Bascompte, 2014), and it has been hypothesized that ecological

networks share common topologies promoting the efficiency of eco-system processes (e.g. nutrient uptake, Arditi, Michalski, & Hirzel, 2005) and the robustness of communities against perturbations (Estrada, 2006). However, most studies in ecological networks have been conducted in a few specific systems (e.g. food webs, plant–pollinator, host–parasite) and at particular study sites, making the establishing of generalizations difficult (Heleno et al., 2014). Thus, comparative studies at regional and global scales are necessary to evaluate whether ecological networks present common topologies across multiple environmental conditions and to explore how they af-fect key ecosystem attributes, such as species diversity and ecosystem functioning (Pellissier et al., 2017; Traveset et al., 2016).

Plant communities are the bottom of the trophic web, play a major role in ecosystem nutrient cycling and are responsible of community physiognomy (Barbour, 1987). Despite their critical ecological role, plant–plant interactions have been largely unnoticed by network studies until very recently (Saiz et al., 2017; Verdú & Valiente-Banuet, 2008). The efforts required for obtaining data on plant–plant interac-tions at the community level over a large number of sites (Soliveres & Maestre, 2014), and the different type of interactions that can be established between plants (Brooker et al., 2008), have tradition-ally hampered the use of network analyses to study the structure of plant communities. However, these limitations are starting to be overcome with the increase in the number of global coordinated ex-periments and surveys (Fraser et al., 2013; Maestre et al., 2012) and with methodological developments in the analysis of social networks involving positive and negative links (e.g. like and dislikes; Doreian & Mrvar, 2009; Szell, Lambiotte, & Thurner, 2010). To our knowledge, no study so far has evaluated the topological structure of plant net-works and how it relates to the diversity of plant communities at the global scale. Such analyses would help to unveil global patterns for plant communities, providing insights about the relative importance of positive and negative interactions and the role of particular spe-cies as determinants of community structure (Saiz, Alados, & Pueyo, 2014). Furthermore, the connection between network structure and resilience against extinctions will provide a valuable information about the vulnerability of plant communities to possible future extinctions due to global environmental change.

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

conditions, local spatial organization could be a suitable proxy of the structure of interactions between plants.

We explored the structure of plant spatial networks and evaluated its effect on the diversity of plant communities, in 185 drylands from all continents except Antarctica. Despite covering over 45% of global terrestrial area (Prăvălie, 2016) and presenting a marked local spatial organization (Rietkerk, Dekker, de Ruiter, & van de Koppel, 2004; Sala & Aguiar, 1996), few studies so far have evaluated the spatial network structure of dryland plant communities (Saiz & Alados, 2014; Saiz et al., 2014). Understanding such structure is particularly relevant for multi-ple reasons. Dryland vegetation is organized as discrete plant patches embedded in a matrix of bare soil, which become sinks for resources (e.g. rainfall, Aguiar & Sala, 1999; Wang, Li, Xiao, Berndtsson, & Pan, 2007). Species responsible of patch formation (nurses) create a micro-environment where other species, less tolerant to dry environmental conditions, are able to establish (Maestre, Bautista, Cortina, & Bellot, 2001). Thus, positive interactions largely structure plant communities in drylands and allow the persistence of communities with higher bio-diversity (Soliveres & Maestre, 2014; Verdú & Valiente-Banuet, 2008), although negative interactions are also important drivers in structur-ing dryland plant communities (e.g. competition for water between species, Fowler, 1986; Soliveres, Smit, & Maestre, 2015). Moreover, several studies have linked vegetation patchiness with ecosystem pro-cesses and degradation status (Berdugo, Kéfi, Soliveres, & Maestre, 2017; Kéfi et al., 2007), so we could expect the structure of plant spa-tial networks to directly influence ecosystem functioning in drylands.

Specifically, we hypothesize that in drylands world-wide plant spatial networks present a common structure due to the organization of vegetation in patches, and that, after accounting for the scaling of network structure with network size, this network structure has a di-rect effect on the diversity of the plant community. We expect plant spatial association networks to have a high number and variety of links between species (i.e. high link density and link weight heterogeneity) due to the importance of biotic interactions, particularly of facilitation (i.e. positive link weight mean), as creators of vegetation patches in drylands. Furthermore, we expect these networks to be organized in blocks (i.e. high global structural balance), representatives of the par-ticular types of vegetation patches present in these ecosystems. After controlling the effect of abiotic factors and network size, we anticipate that this network structure (i.e. high link density, link weight hetero-geneity and global structural balance; and positive link weight mean) will have a significant and positive effect on the diversity of dryland plant communities.

2 | MATERIALS AND METHODS

2.1 | Global drylands vegetation survey

Field data were collected from 185 dryland sites located in 18 coun-tries (Argentina, Australia, Botswana, Brazil, Burkina Faso, Chile, China, Ecuador, Ghana, Iran, Kenya, Mexico, Morocco, Peru, Spain, Tunisia, United States and Venezuela). These sites are a subset of the global survey of 224 sites from Maestre et al. (2012) carried out between

2006 and 2011, plus 12 additional sites from Botswana, Ghana and Burkina Faso surveyed in 2013. As network indices depend on network size and must be tested against null models (Dormann, Fründ, Blüthgen, & Gruber, 2009), we selected all sites where networks had at least five connected species to allow statistical testing (185 sites out of 236 sites available). This subset included the major vegetation types found in drylands, a wide range in plant species richness (from five to 52 species per site) and environmental conditions (mean annual temperature and precipitation ranged from −1.8°C to 28.2°C and from 66 to 1,219 mm, respectively). The sites surveyed encompass a wide range of human uses, ranging from those with very low human impacts over recent time-scales (e.g. National Parks and other protected areas) to those where human activities such as grazing, grass fibre/wood collection and game hunting are currently, or have been recently, carried out. However, we excluded areas that have been heavily impacted by human activities (e.g. agricultural, urban and infrastructure/mining areas) or that have been recently engineered (e.g. planted or recently restored areas).

At each site, vegetation was surveyed using four 30-m long transects located parallel and separated 10 m among them within a 30 m × 30 m plot representative of the vegetation found there (see Maestre et al., 2012 for details). At each transect, 20 quadrats of 1.5 m × 1.5 m were established, and the cover of each perennial species within each quadrat was visually estimated without distinguishing between plant ontogenetic stages.

2.2 | Network construction

For each of the sites studied, we built a plant–plant spatial association network (Saiz et al., 2014, 2017) using the cover data of all the perennial species (S) surveyed. These networks are characterized by the adjacency graph $\mathbf{A}_{S \times S}$ (hereafter **A**), where the nodes (i,j) are the plant species and the links (l_{ij}) are the spatial association between each pair of species. To determine this association, we calculated the correlation between the cover of each pair of species in the 80 quadrats for each plot using Spearman rank tests. Following the recommendations of Weiss et al. (2016), we used Spearman correlations because our data were not normal due to the large number of quadrats having species with a cover of 0. When a correlation between species i and j was significant ($p < .05$), a link $l_{ij} = \rho$ was established (where ρ represents the Spearman correlation coefficient), with $l_{ij} = 0$ otherwise. Thus, our networks are symmetric ($l_{ij} = l_{ji}$), signed and weighted ($-1 < l_{ij} < 1$). As each species only had a single cover value at each quadrat, we could not evaluate the intraspecific spatial association; thus, we set the diagonal of **A** to zero.

We are aware that the use of spatial associations to infer real biotic interactions presents several limitations. Plant spatial patterns are the result of different processes apart from biotic interactions, such as dispersal strategies and environmental heterogeneity (Escudero, Romão, Cruz, & Maestre, 2005). Thus, it is convenient to control these processes to isolate the effect of biotic interactions. In our case, we tried to limit the effect of environmental heterogeneity by measuring spatial patterns at a scale (1.5 × 1.5 m) similar to that used in other studies about biotic interactions at the community level (Cavieres et al., 2006; Verdú & Valiente-Banuet, 2011). This scale has been also suggested as the scale where biotic interactions are the dominant driver of spatial patterns (Morales-Castilla, Matias, Gravel, & Araújo, 2015). Furthermore, biotic interactions are not constant throughout species ontogeny, but can change from seedlings to adults (Tielbörger & Kadmon, 2000; Valiente-Banuet & Verdú, 2008). In our case, as we did not distinguish between ontogenetic stages of the species, spatial association mostly represents the spatial pattern between adult plants, which accounted for most of the cover of the species in each site. Finally, both facilitation and parasitism produce a positive spatial association between species. However, we did not find evidence for parasitic species in our sites (obligate or facultative parasites), so we can assume that in our study area positive spatial association only represents facilitative interactions. Although we cannot ignore the possible effect of other processes such as environmental heterogeneity or dispersal, we believe that in our study, spatial association is a reasonable proxy for biotic interactions.

2.3 | Network indices

We selected four network indices to characterize the structure of the communities studied: link density, link weight mean, link weight heterogeneity, and global network balance. Link density (D) is the average number of links per node in the network ($D = L/S$, where L represented the total number of links and S the total number of nodes in the network) and represents the importance of spatial patterns in the plant community; high D values describe a community where vegetation is spatially structured (i.e. significant positive and negative spatial associations between pairs of species are common). Link weight mean ($\bar{W}$) is the mean 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 dominant type of spatial pattern in the network; $\bar{W} > 0$ and $\bar{W} < 0$ describe a community dominated by spatial aggregation and segregation, respectively. Link weight heterogeneity (H) is the kurtosis of the link weight distribution and represents the variety of spatial patterns found in the community; lower H values indicate a community where spatial associations are more diverse in strength and sign (i.e. more heterogeneous). Finally, global network balance (K) is a specific index for signed networks that accounts for the proportion of closed cycles in the network fulfilling the structural balance criterion (Zaslavsky, 2013). Following this criterion, a network can be divided in blocks; nodes within the same block are positively connected among them while they are negatively connected to nodes in other blocks (Doreian & Mrvar, 2009). We calculated K using the definition of (Estrada & Benzi, 2014), $K = \frac{tr(e^{\mathbf{A}})}{tr(e^{|\mathbf{A}|})}$, where $|\mathbf{A}|$ is the underlying unsigned graph of **A**. High values of K indicate that the network presents a "balanced" structure (with $K = 1$ indicating a perfect balance), while low values indicate that several links do not fulfil this criterion and network is "unbalanced" ("frustrated," sensu Doreian & Mrvar, 2009). In our case, high K indicates the presence of different types of vegetation patches in the community, where species from the same block conform a particular type of patch and present the same spatial pattern respect to the species present in another patch (Saiz et al., 2017). In summary, these indices allow us to cover

different components of the spatial structure of the plant community: the importance (D) and variety (H) of spatial patterns, the dominant type of association (i.e. aggregation or segregation, $\bar{W}$), and the existence of specific types of vegetation patches (K).

2.4 | Null model analyses

To test the significance of the network indices used, we employed two different null models for each network, one that allowed changing the connectivity of the network for D, $\bar{W}$ and H, indices that vary with the number and weight of links, and another that changed the links between nodes while keeping the network linkage distribution constant for K, an index that varies with the position of links within the network. In the first model, we randomized the cover of each species along the quadrats. Specifically, we kept the cover distribution for each species constant, but randomly change their positions in the quadrats. By doing so, we changed the cover values of species co-occurring in the same quadrat while maintaining the original cover distribution for each species at each site (similarly to the SIM2 model of Gotelli, 2000). Then, we built a network using this simulated data and calculated its D, $\bar{W}$ and H. For each site, we simulated 2,000 networks and compared the real values of the indices against a 95% confidence interval created from the simulated networks. In the second null model, we simulated networks at each site using an algorithm based on the configurational model adapted for signed networks (Saiz et al., 2017). This method iteratively changes links in the original network, modifying its structure but keeping constant its linkage distribution. In our case, we made 1,000 iterations per network and simulated 5,000 networks, and then compared the real values of the index K against the simulated values creating a 95% confidence interval. We also calculated the maximal and minimal K (K_{max} and K_{min}) that each network could have considering its degree distribution to evaluate the real K value against all the possible values that it could present at each site. To do so, we iteratively simulated networks with the same null model and selected the network that maximized (or minimized) K at each step. To avoid possible local maxima (or minima), selection was based on a Fermi–Dirac probability function ($f = \frac{1}{1+e^{-\beta\Delta}}$), which selected a network over others based on the difference between the K values of the networks (Δ) and a parameter β that modulates the probability of accepting a change with the number of iterations (with higher β selecting higher Δ, Tsallis & Stariolo, 1996). By doing so, we could explore the behaviour of the index by precisely locating real networks in all the space of parameters of K.

2.5 | Evaluating the effects of network structure on plant diversity

We built structural equation models (SEM, Grace, 2006) including different abiotic variables (latitude, longitude, elevation, slope, aridity, precipitation seasonality, soil organic C, soil pH and soil total P) and network variables as explanatory variables for the richness (SR) and evenness (E = Shannon index/ln SR) of perennial plant species. Specifically, we included geographical variables to control the effect of spatial autocorrelation between sites and selected abiotic variables

that have been shown to be important drivers of the structure and functioning of drylands (Maestre et al., 2012). Abiotic variables were divided in four groups: geographical, topographical, climatic, and soil variables, and a composite variable was built for each group. To build each composite variable, we first fitted a linear model using its corresponding group of abiotic variables as explanatory variables and species richness and evenness as response variables, and then we used this model to calculate the values of the composite variable. For network indices, we included the difference between real network values and the percentile 50 values for the networks simulated with the null models (e.g. $\Delta D = D - D_{null}$, where D_{null} is the percentile 50 for the D simulated with the null model) to remove random effects due to species abundance distribution (Gotelli, 2000) and network size (Dormann et al., 2009). We then created a SEM for each combination of network and diversity variables (eight SEMs in total). In these SEMs, network variables depended on all the composite variables, and diversity indices depended on all the composite variables and the network indices (see Appendices S1 and S2 for a complete description of the variables and the structure of the SEMs used). To evaluate the importance of network indices on community diversity, we compared the explained variance of diversity indices between SEMs built with and without network indices. Specific dependencies between composite variables were included following previous studies using the same dataset (Delgado-Baquerizo et al., 2016). All variables were centred and standardized before calculating the models. All analyses were performed with R 3.2.4 (R Development Core Team, 2014). We used the *lavaan* package for the SEM analyses (Rosseel, 2012).

3 | RESULTS

The analysis of plant spatial association networks revealed that dryland plant communities were variable, as indicated by the variability of observed network indices (Table 1, Figure 1). Particularly, $\bar{W}$ presented both positive and negative values, suggesting that plant communities in drylands are dominated by either spatial aggregation or segregation. However, K presented a very low variability, with values close to 1 (Table 1). These results suggested that, in general, plant spatial networks in drylands presented different types of vegetation patches.

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

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

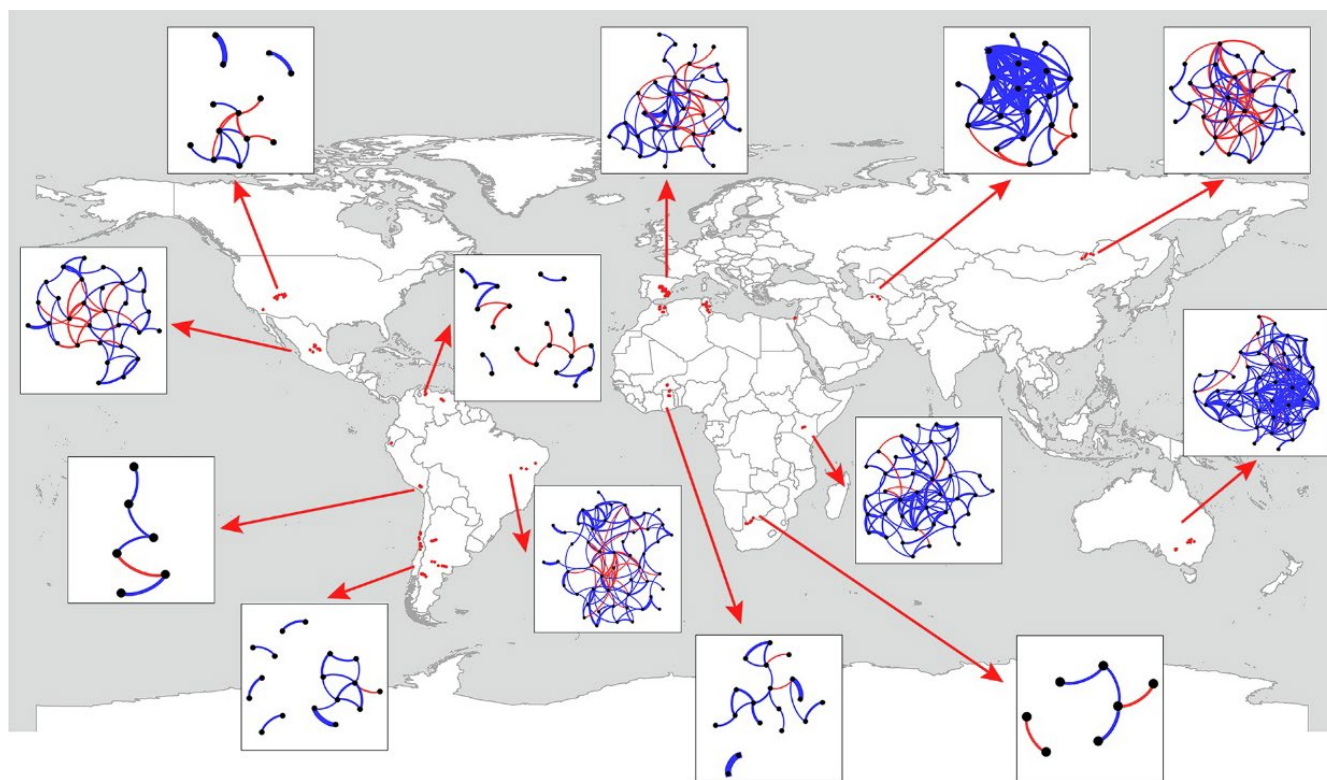|	*S*	*D*	$\bar{W}$	*H*	*K*
Real	16.98 (7, 39.8)	1.874 (0.667, 4.716)	0.113 (−0.164, 0.357)	2.47 (1.114, 7.206)	0.984 (0.83, 1)
CV	0.493	0.602	1.263	0.622	0.041
Δ*I*	—	**1.11 (0.162, 3.192)**	−0.111 (−0.352, 0.099)	0.115 (−3.155, 3.106)	0.067 (−0.001, 0.468)
+	—	133 (0.72)	1 (0.01)	6 (0.03)	130 (0.7)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

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 and negative interactions, respectively, and link width is proportional to link weight. For simplicity, we removed from each network all the species that did not present any link to other species [Colour figure can be viewed at wileyonlinelibrary.com]

Our SEMs revealed that the structure of plant spatial association networks significantly affected the richness and evenness of dryland plant communities (Table 2). All network indices had a significant direct effect on species richness (*SR*), but only *H* and *K* significantly affected community evenness (*E*). Furthermore, although network variables presented lower effect sizes than abiotic variables, their inclusion in the SEM substantially increased the explained variance of *SR* (Figure 2). Finally, some network indices with significant effects on *SR* (*D* and *K*) were also independent from abiotic variables (Figure 3 and Appendix S2).

4 | DISCUSSION

Global studies offer unparalleled insights to build generalities in ecology based on the discovery of common patterns and processes operating across a large number of locations 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

TABLE 2 Summary of structural equation models showing the effects of network indices on species richness (*SR*) and evenness (*E*). *D*, link density; $\bar{W}$, link weight mean; *H*, link weight heterogeneity; *K*, balance; *SR*, community species richness; *E*, community evenness. Bold values indicate a significant direct effect of network index on diversity index. **$p < .01$; ***$p < .001$
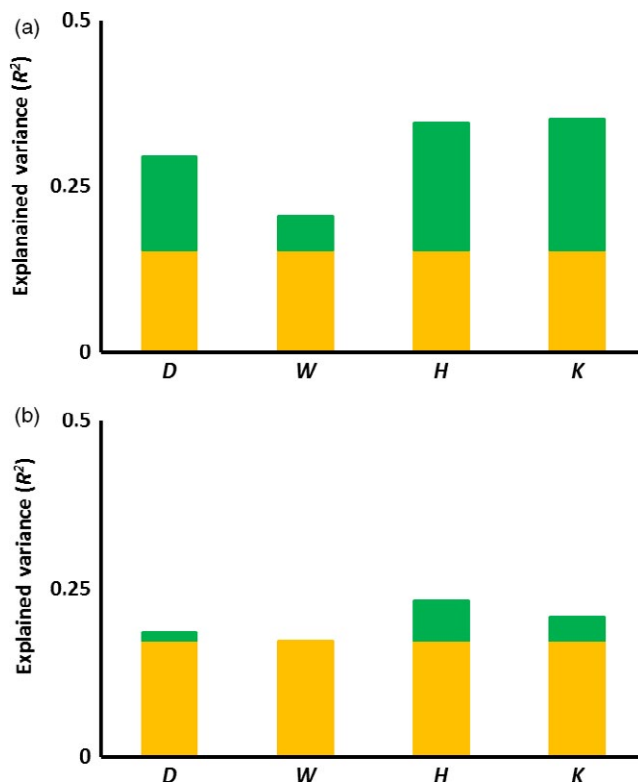
Network index	Biodiversity index	Path estimate	*SE*	*z*-value	*p*-value
D	*SR*	0.368	0.062	5.917	**<.001***
	E	0.099	0.067	1.478	.139
$\bar{W}$	*SR*	0.226	0.07	3.249	**.001**
	E	0.012	0.069	0.18	.857
H	*SR*	−0.466	0.061	−7.619	**<.001***
	E	−0.256	0.068	−3.739	**<.001***
K	*SR*	0.445	0.06	7.463	**<.001***
	E	0.186	0.066	2.82	**.005**

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 contribution of including each network variable in the structural equation models. *D*, link density; $\bar{W}$, link weight mean; *H*, link weight heterogeneity; *K*, global balance [Colour figure can be viewed at wileyonlinelibrary.com]

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 world-wide 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).

4.1 | 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, 2000) and responding differently to the same environmental factor (Pueyo, Moret-Fernández, Saiz, Bueno, & Alados, 2013; Saiz & Alados, 2011).

We found that most plant species presented many spatial associations among them, and that dryland communities could be dominated by spatial aggregation or segregation, as found in many local studies (Fowler, 1986; Soliveres & Maestre, 2014). However, and regardless of the dominant spatial pattern found at each site, vegetation patches seem to be organized according to the structural balance criteria in drylands. Thus, within a given plant community, there are different types of patches, and plant species that conform the same type of patch do not appear in patches formed by other species (Saiz et al., 2017). In drylands, usually species responsible of patch formation are well adapted to local conditions and facilitate the establishment of seedlings of less adapted species under their canopies (Valiente-Banuet, Rumebe, Verdú, & Callaway, 2006). Meanwhile, well-adapted species compete among them for the
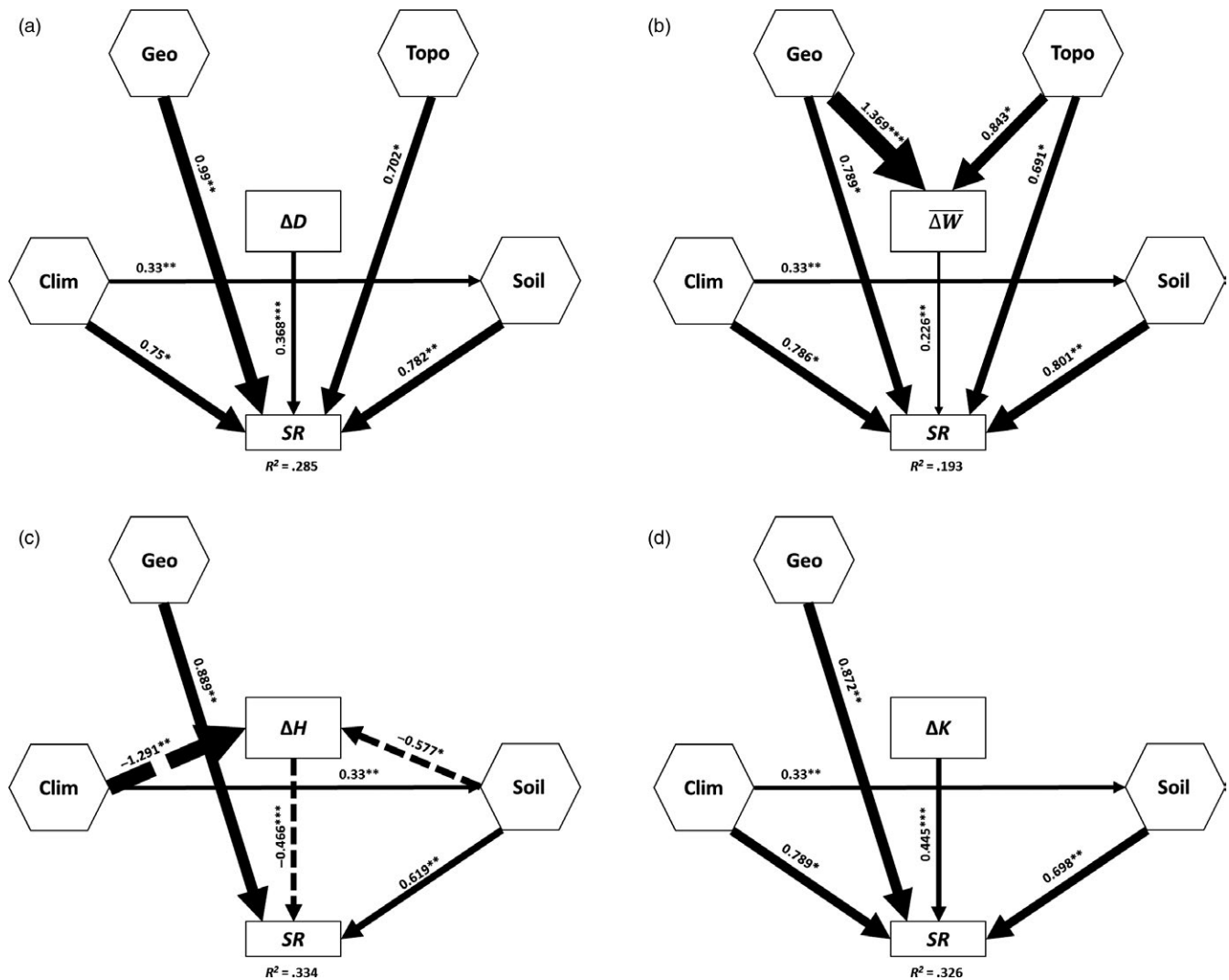
FIGURE 3 Structural equation models (SEM) describing the effects of abiotic drivers and spatial network indices on plant species richness. *Geo*, geographical factors; *Topo*, Topographical factors; *Clim*, climatic factors; *Soil*, Soil factors; *SR*, community species richness. Different SEMs represent different network indices: (a) ΔD, link density; (b) $\Delta \bar{W}$, link weight mean; (c) ΔH, link weight heterogeneity; and (d) ΔK, balance. All network indices are the difference 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 $p > .05$ for the χ^2. For graphical simplicity, only significant arrows and variables with at least one significant relationship are presented

scarce resources present in the environment, and facilitated species compete among them for the space and resources below the canopy of the nurses (Soliveres et al., 2011). It has been found that these interactions can be explained considering the phylogenetic distance between species as a proxy of shared niche requirements, resulting in communities where plant species tend to interact negatively with close relative species (that occupy similar niches) and positively with a subset of the distant relatives (Verdú, Jordano, & Valiente-Banuet, 2010; Verdú & Valiente-Banuet, 2011). Therefore, these differences between plant niches could determine the interactions between plants, ultimately leading to the creation of different types of vegetation patches that result in a balanced spatial structure of vegetation.

The existence of different types of vegetation patches could also help to unveil how biotic interactions shape vegetation spatial patterns and suggest that plant interactions in drylands are species-specific. This is important because there is no clear evidence that facilitative interactions are species-specific, as this depends on how facilitated species benefit from nurses (Callaway, 1998). Thus, while the creation of more benign microenvironments and the capture of wind dispersed propagules by nurses result in the aggregation of multiple species under their canopies (Bullock & Moy, 2004; Soliveres et al., 2011), other facilitative mechanisms can also lead to species-specific aggregations (e.g. protection against herbivory, Saiz & Alados, 2012; attraction of pollinators, Laverty, 1992; modification of soil micro-flora, (Van Der Heijden & Horton, 2009). The

same applies to negative interactions. In drylands, species that do not coexist in the same patches (i.e. present spatial segregation) are likely to compete for the same resources (Ogle & Reynolds, 2004) or produce allopathic compounds (Arroyo, Pueyo, Saiz, & Alados, 2015), resulting in species-specific interactions that drive the spatial structure of plant communities. Hence, the application of network indices to the spatial structure of vegetation allows identifying different types of vegetation patches and exploring the importance of species-specific relationships on facilitative and competitive interactions.

4.2 | The structure of plant spatial networks promotes species diversity

We found a significant effect of network indices on plant species richness and evenness. This result agrees with studies observing that particular vegetation spatial patterns: (1) are related to higher ecosystem resilience (Kéfi et al., 2007) and (2) increase the diversity of plant communities (Pueyo et al., 2013) in drylands, effects associated to facilitative interactions. Contrary to our expectations, the dominance of positive spatial associations presented the weakest effect on plant diversity between all network indices evaluated. A possible explanation is that the coexistence of diverse species in a community depends not only in the presence of positive and negative interactions (sensu Brooker et al., 2005) but also in how these interactions are structured (e.g. identity of the species involved or presence of indirect interactions, Soliveres, Maestre, et al., 2015). Therefore, our results encourage the use of network approaches in plant ecology as they not only account for the importance of biotic interactions but also for their structure in the community, and are able to consider simultaneously facilitation and competition.

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

4.3 | Future directions and concluding remarks

The use of networks in ecology is in continuous development, and recently has started to consider systems other than the traditional food webs and mutualistic networks (Kéfi et al., 2012). However, the use of spatial networks requires further development before being considered a general tool to study biotic

interactions (see Section 2). Studies in communities where biotic interactions are strongly linked to spatial patterns (i.e. drylands) are a good starting point to evaluate this type of networks, but more effort is required. Specifically, conducting experiments to measure true interactions between species (e.g. measuring pair-wise interactions in controlled conditions, Godoy, Stouffer, Kraft, & Levine, 2017) and compare them with field spatial associations would be a good starting point to better understand the link between interactions and spatial patterns in plant communities. Furthermore, controlling other effects such as herbivory or plants ontogenetic stages, which have a significant effect on plant interactions (Smit, Rietkerk, & Wassen, 2009; Tielbörger & Kadmon, 2000), will help to clarify the mechanisms behind spatial pattern. In general, working at local scales and controlling for environmental heterogeneity during field surveys are a proper way to improve the reliability of spatial patterns as proxies of biotic interactions.

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

AUTHORS' CONTRIBUTIONS

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

DATA ACCESSIBILITY

Data used in this study are available from Figshare: https://doi.org/10.6084/m9.figshare.4763302.v1 (Saiz & Maestre, 2018).

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