

RESEARCH ARTICLE

Intransitivity increases plant functional diversity by limiting dominance in drylands worldwide

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Abstract

1. Biotic interactions are key determinants of plant community structure. Indirect interactions such as intransitivity (i.e., the absence of competitive hierarchies among species) have been hypothesized to benefit diversity within plant communities. However, their effect on functional diversity remains scarcely explored in real communities. Here, we develop a novel approach to infer intransitivity from plant spatial patterns and functional traits (height and specific leaf area) and quantify its effect on different components of plant diversity along environmental gradients in 100 drylands from all continents except Antarctica.
2. We first calculated the spatial association pattern for all perennials to infer competition between species. Trait values were used as a proxy of competitive hierarchies to infer the direction of these interactions. We used multiple regression models to evaluate how intransitivity responds to environmental variables (mean annual temperature and precipitation, precipitation seasonality, soil pH, sand content and woody cover). We also used confirmatory path analysis to evaluate the effects of intransitivity on species richness and evenness, trait dispersion and functional diversity.
3. Intransitivity mostly responded to climatic variables and significantly increased with precipitation scarcity and seasonality. We found that intransitivity had significant effects on functional diversity, mostly by promoting plant community evenness. However, the dominance of woody vegetation (steppes versus shrublands) modulated this effect.
4. *Synthesis*. Intransitivity increased the functional diversity of drylands, particularly under high rainfall seasonality, by limiting functionally dominant species. Our findings specify how intransitivity structures the functional diversity of dryland vegetation worldwide. Intransitivity may be particularly important in ecosystems where the availability of abiotic resources changes over time, thereby breaking down inherent competitive hierarchies between plant species. Neglecting intransitivity will bias our estimation of the impacts of biotic interactions on plant communities, a fundamental issue to fully understand how plant communities will respond to ongoing environmental changes.

KEYWORDS

climate, community assembly, determinants of plant community diversity and structure, functional diversity, intransitive interactions, plant height, spatial association patterns, specific leaf area

1 | INTRODUCTION

Disentangling the effects of biotic interactions from those of the abiotic environment as determinants of the structure of plant communities remains a central question of ecology (Grime, 1973; Keddy, 1992; Vellend, 2010). However, the actual effects of biotic interactions on plant community structure and diversity are not fully understood yet (Bruno, Stachowicz, & Bertness, 2003; Grime, 1973; Tylianakis, Didham, Bascompte, & Wardle, 2008). Most studies on this topic focused on direct interactions such as facilitation and competition, while very few studies have considered indirect interactions such as intransitive competition (i.e., when species cannot be ranked in a simple linear competitive hierarchy, Levine, 1999; but see Soliveres & Allan, 2018; for a review). Intransitive competition (hereafter, intransitivity) can commonly occur in communities together with direct interactions, and empirical studies suggest that it can have an important effect on community structure and functioning (Maynard, Bradford, et al., 2017; Maynard, Crowther, & Bradford, 2017; Soliveres, Maestre, et al., 2015). However, we still lack a clear understanding of how intransitivity responds to environmental gradients and ultimately influences the functional diversity of real plant communities, a key determinant of ecosystem functioning (Gross et al., 2017; Mouillot, Villéger, Scherer-Lorenzen, & Mason, 2011).

Plant functional traits have been proposed as a useful tool to scale the effect of biotic interactions up to the community level (Götzenberger et al., 2012; Gross et al., 2009; Lavorel & Garnier, 2002). Competition has been primarily hypothesized to favour higher trait diversity within communities (see the “limiting similarity theory,” MacArthur & Levins, 1967). However, superior competitors can also have a disproportionately large effect on other species, and thus may act as a filter that reduces trait diversity (e.g., in the case of competition for light, Chesson, 2000; Grime, 1973; Mayfield & Levine, 2010). On the other hand, facilitation has been shown to allow maladapted species to persist within communities, thus increasing trait diversity by promoting the coexistence of functionally contrasted species (Butterfield & Briggs, 2011; Gross, Liancourt, Butters, Duncan, & Hulme, 2015; Le Bagousse-Pinguet et al., 2017). However, studies about the effect of intransitivity on functional trait diversity are scarce (Maynard, Bradford, et al., 2017), although functional diversity is a major attribute of plant communities with strong effects on ecosystem functioning. Theoretical studies propose that intransitivity could have contrasted effects on trait diversity ranging from negative to positive (Gallien, 2017). Thus, there is a clear need to evaluate how intransitivity contributes to functional diversity to achieve a more complete understanding of the role of biotic interactions in affecting community structure and functioning.

Evaluating the importance of intransitivity for community structure is not an easy task because of the large number of interacting species within communities and the diversity of interactions at play. Experiments are the most fruitful approach to link biotic interactions with community structure (Gross et al., 2009; Le Bagousse-Pinguet, Maalouf, Touzard, & Michalet, 2014; Suding, Goldberg, & Hartman, 2003). However, experimental approaches are typically limited to a

small number of species and provide results that can hardly be generalized across contrasted ecosystems and large spatial scales. In contrast, fine-scale spatial associations between plant species can be used as an alternative approach to quantify biotic interactions (Saiz & Alados, 2012; Tirado & Pugnaire, 2005). Although they have several limitations arising from the multiplicity of factors that affect plant spatial patterns (Chacón-Labela, de la Cruz, & Escudero, 2017; Wiegand et al., 2012), data on fine-scale spatial associations can be easily collected across multiple sites and represent a valuable alternative to experiments when studying biotic interactions at macro-ecological scales (Saiz, Gómez-Gardeñes, Borda, & Maestre, 2018). Specifically, if species aggregate in space more often than expected by chance, it is possible to assume a benefit from this aggregation and, by doing so, to estimate the existence of a positive interaction (Pugnaire, Armas, & Valladares, 2004). On the other hand, if species appear segregated more often than expected by chance, an interference and, consequently, a negative interaction between species can be assumed. However, to infer the direction of the biotic interactions (i.e., whether the effect goes from species A to B or vice versa) using spatial associations is not feasible (Illian, Penttinen, Stoyan, & Stoyan, 2008). As a result, using the spatial association between pairs of species to evaluate indirect interactions, such as intransitivity, has limitations because inferring intransitivity requires knowing the direction of the interactions (Petraitis, 1979). Thus, new approaches able to infer the directionality of biotic interactions are needed to evaluate the effect of indirect interactions on plant communities.

Here, we propose a new approach to infer the directionality of biotic interactions based on functional traits and to evaluate the effect of indirect interactions on plant communities. We quantified the relative contribution of intransitivity as a driver of functional diversity along climatic, soil and vegetation gradients. To do this, we used field data generated from 100 drylands from six continents. Drylands are ideal systems to test our approach for multiple reasons. First, intransitivity is common and influences plant species richness (Soliveres, Maestre, et al., 2015). Second, dryland plant communities are functionally diverse (Freschet et al., 2011; Gross et al., 2017; Le Bagousse-Pinguet et al., 2017). And third, vegetation typically shows marked spatial patterns driven by biotic interactions (Kéfi et al., 2007), which can be inferred from species traits (Gross et al., 2013). We first evaluated how intransitivity changed along global climatic and edaphic gradients. Specifically, we expect that intransitivity will increase with higher scarcity and lower predictability of resources in the more arid areas (Soliveres, Maestre, et al., 2015). For instance, higher seasonality in water pulses may break competitive hierarchy between species, and therefore, promote higher intransitivity. Second, we quantified the contribution of intransitivity to plant functional diversity in the drylands studies. There are no clear theoretical predictions on how intransitivity would impact functional trait diversity (Gallien, 2017). However, we expect that intransitivity will have a positive effect on functional diversity by either promoting rare species with contrasted functional traits or by increasing the evenness between dominant and subordinate species within communities (Maynard, Bradford, et al., 2017).

2 | MATERIALS AND METHODS

2.1 | Vegetation survey

Field data were collected from 100 dryland sites located in 14 countries (Argentina, Australia, Brazil, Chile, China, Ecuador, Iran, Kenya, Mexico, Morocco, Spain, Tunisia, United States and Venezuela), which are a subset of the global survey of 236 sites (Ochoa-Hueso et al., 2018). This subset included the most representative vegetation types found in drylands (i.e., shrublands, grasslands, open woodlands and savannahs) and a wide range in plant species richness (from 5 to 44 species per site) and environmental conditions (mean annual temperature and precipitation ranged from -1.3 to 27.2°C and from 141 to 1,177 mm, respectively).

At each site, vegetation was surveyed within a 30 m x 30 m plot including the representative vegetation of the area. In each plot, four parallel 30-m long transects, separated by 10 m were established, and within each transect 20 quadrats of 1.5 m x 1.5 m were surveyed. For each quadrat, we identified all perennial plant species present and estimated their cover (i.e., proportion of the quadrat covered by the species) visually without distinguishing between ontogenetic stages (see Maestre et al., 2012 for full details on the field survey).

2.2 | Spatial analysis

For each of the study sites, we recorded the total number of species (S) and calculated the spatial association between each pair of species i and j . Specifically, we calculated the correlation between the cover of each pair of species in the quadrats within each site using the Spearman rank correlation test. This test is appropriate to calculate spatial correlation for co-occurrence data when, as in our case, data are not normal and contain a large number of zeroes (Weiss et al., 2016). In our case, we used the Spearman correlation coefficient as a spatial association measure (w_{ij} , ranging from total segregation, $w_{ij} = -1$; to total aggregation, $w_{ij} = +1$) and considered $w_{ij} > 0$ and $w_{ij} < 0$ as indicators of facilitative and competitive interactions, respectively. As each species only had a single cover value at each quadrat, we could not evaluate the intraspecific spatial association; thus we set all $w_{ii} = 0$.

We calculated two indices to evaluate the contribution of positive ($I+$) and negative ($I-$) spatial associations to community structure. These indices were calculated as follows:

$$I+ = \sum_{i=1}^S \sum_{j=1}^S w_{ij} (c_i + c_j) / K^+, \forall w_{ij} > 0 \quad (1)$$

$$I- = \sum_{i=1}^S \sum_{j=1}^S |w_{ij}| (c_i + c_j) / K^-, \forall w_{ij} < 0 \quad (2)$$

where c_i represents the relative cover of species i in the community ($c_i = \sum_{q=1}^{80} c_{iq} / \sum_{i=1}^S \sum_{q=1}^{80} c_{iq}$; where q represents each quadrat of the

site), and K^+ and K^- represent the total number of positive ($K^+ =$ number of $w_{ij} > 0$) and negative ($K^- =$ number of $w_{ij} < 0$) spatial associations per site, respectively. Previous studies on biotic interactions have found that weak interactions can contribute importantly to the structure and functioning of ecological communities (McCann, Hastings, & Huxel, 1998). Thus, we decided to include the spatial associations between all pairs of species in our indices. Nevertheless, as the contribution of each spatial association is weighted by w_{ij} , the contribution of strong spatial associations to the indices will be proportionally higher than the contribution of weak ones.

Although spatial pattern analyses have been commonly used to study biotic interactions in plant communities (Cavieres & Badano, 2009; Raventós, Wiegand, & Luis, 2010; Saiz & Alados, 2012), they have potential limitations. Spatial patterns may result from processes other than biotic interactions, such as dispersal strategies and small-scale environmental heterogeneity (Escudero, Romão, Cruz, & Maestre, 2005). In our case, we tried to limit this shortcoming in two ways. First, we conducted our study in drylands, which are known to show marked spatial patterns that are strongly driven by biotic interactions (Aguar & Sala, 1999). Second, we surveyed vegetation at the local scale, where biotic interactions are the main drivers of spatial pattern (Morales-Castilla, Matias, Gravel, & Araújo, 2015). The sampling scale used (1.5×1.5 m quadrats) is also similar to that used in other studies about biotic interactions at the community level in drylands (Valiente-Banuet & Verdú, 2008). Finally, the use of spatial patterns as a proxy for interactions can also be confounded by the fact that both facilitation and parasitism produce the same spatial pattern (positive spatial association). We did not find any parasitic plant species in the drylands studied, so we assume that in the studied sites positive spatial associations are mostly due to facilitative interactions.

2.3 | Assessing intransitivity from trait information and hierarchies

Estimating intransitivity requires the identification of the direction in competitive interactions (i.e., which species is better competitor than the other sensu Petraitis, 1979). We propose to infer the direction of competitive interactions between species from an a priori knowledge of the relationships between multiple traits and species competitive ability. We obtained functional trait information for maximum plant height and specific leaf area (SLA) from the TRY database (Kattge et al., 2011). We used a subset of 100 sites where trait information was available for the most dominant species, which accounted for $> 80\%$ of the relative plant cover at each site (data for both traits were available for 274 species out of 461 species). These two traits capture the global spectrum of plant form and function in terrestrial ecosystems (Díaz et al., 2016) and are key determinants of functional diversity and ecosystem functioning in drylands (Gross et al., 2013, 2017; Le Bagousse-Pinguet et al., 2017; Valencia et al., 2015). In addition, previous studies in Mediterranean environments have related higher height and lower SLA with higher competitive capacity (Kraft, Godoy, & Levine,

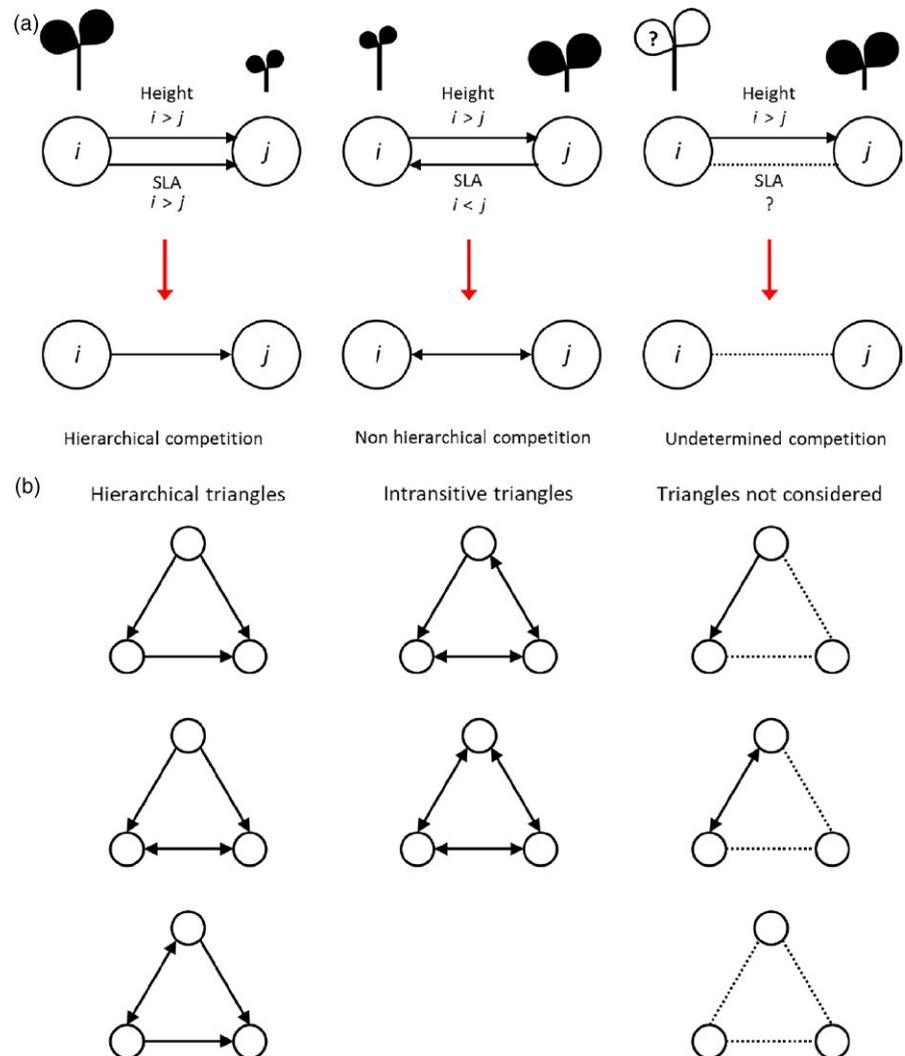
2015). Maximum plant height has been commonly used as a proxy of the capacity of plants to obtain resources (e.g., light), so taller plants will theoretically be more competitive than shorter species (Grime, 1973; Gross et al., 2013; Schamp, Chau, & Aarssen, 2008). Specific leaf area relates directly to the evapotranspiration capacity of plants and to their growth rates (Wright et al., 2004). Plants with low SLA are the dominant strategy in drylands (Le Bagousse-Pinguet et al., 2017), as they are more photosynthetically efficient in water-limited systems (Maire et al., 2015). We, thus, define low SLA species as more competitive in drylands than species with higher SLA (Ackerly, 2004; Gross et al., 2013).

We selected all negative spatial associations ($w_{ij} < 0$) at each site and compared the height and SLA values between each pair of species to infer directionality (Figure 1a). If species i was a better competitor than species j for both traits (e.g., i had higher height and lower SLA than j), then we assumed a competitive hierarchy and the direction of the competition was set to $i \rightarrow j$. On the other hand, if species i was a better competitor than species j for only one trait (e.g., i had higher height and SLA than j), we could not assume a competitive hierarchy and the direction of the

competition was set to $i \leftrightarrow j$. We then quantified the importance of intransitivity at each site focusing on the intransitive triangles in the community (Figure 1b). Intransitive triangles are subgroups of three species that compete between each other without a competitive hierarchy (Godoy, Stouffer, Kraft, & Levine, 2017; Laird & Schamp, 2006). We selected all negative triangles at each site (i.e., groups of three species that only had negative spatial associations between them) and, by combining the directions of the negative spatial associations based on both height and SLA, we separated intransitive triangles from hierarchical ones (see Figure 1b for the definition of transitive and intransitive triangles). Note that our index does not consider strong intransitive triangles ($A > B > C > A$) with competitive links reversals, unlike other indices such as Soliveres, Maestre, et al. (2015). Furthermore, we weighted the contribution of each triangle to the community (T_{ijk}) by including the cover and the spatial association of the three species forming it as follows:

$$T_{ijk} = \left(|w_{ij}| (c_i + c_j) + |w_{jk}| (c_j + c_k) + |w_{ik}| (c_i + c_k) \right) / 2 \quad (3)$$

FIGURE 1 Inference of the direction of the interactions and definition of the types of competitive triangles considered. (a) For each pair of species, we used the competitive hierarchies established for both traits together to infer the direction of the competitive interactions. Specifically, when species i was more competitive than species j in both hierarchies (e.g., i was taller and had lower SLA than j), $i \rightarrow j$. However, when each species was more competitive only in one hierarchy (e.g., i was taller but had higher SLA than j), $i \leftrightarrow j$. Finally, when there were no data for a given trait, the link between i and j was undetermined. (b) We identified all the possible competitive triangles that can exist and divided them in hierarchical and intransitive triangles depending on the existence of an unequivocal best (worst) competitor in the triangle. If a triangle included an undetermined link, that triangle was not considered in the intransitivity analysis. Note that our method cannot detect strong intransitive triangles ($A > B > C > A$) and does not consider competitive links reversals [Colour figure can be viewed at wileyonlinelibrary.com]



where i , j and k represent the species within the triangle. We measured the observed intransitivity for the community (Int_{obs}) as the weighted proportion of intransitive triangles in the community:

$$Int_{obs} = T_{int} / (T_{hie} + T_{int}) \quad (4)$$

where T_{int} is the sum of T_{ijk} value for all the intransitive triangles and T_{hie} is the sum of T_{ijk} value for all the hierarchical triangles. As we did not have trait information for all species, we ran a sensitivity analysis to evaluate the effect of trait data completeness on Int_{obs} (Appendix S1). Sensitivity analysis showed that, independent of the amount of trait data available, our dataset always included Int_{obs} values representative of the complete data set, although for high levels of trait data availability (>80%) Int_{obs} increased. This result suggests that our index could be underestimating community intransitivity in our dataset by not including intransitive relationships involving rare species.

Importantly, as we used spatial and functional trait information to evaluate intransitivity, we needed to evaluate potential effects that may bias our index. We, thus, conducted a null model analysis that controlled for the effect of space and functional traits. Specifically, we randomized the cover within the quadrats for each species at each site to remove spurious spatial associations. This randomization keeps the cover distribution within each site for each species constant while removing the correlations between the cover of each species. Furthermore, we also randomized species identity considering all the species from the 100 sites surveyed. By doing so, we removed any potential effects that may bias the observed relationship between our intransitivity index and functional trait diversity. We ran 1,000 randomizations for each site and calculated intransitivity as $Int = Int_{obs} - Int_{null}$, where Int_{null} was the mean intransitivity index calculated by the randomizations for each site. We also applied the sensitivity analysis to Int , with similar results as for Int_{obs} (Appendix S1).

In a previous study, Soliveres, Maestre, et al. (2015) evaluated intransitivity in the same dataset using an index based on the relative cover of the species. We found a weak but positive correlation between both indices ($r = 0.095$) for the 100 sites. One possible explanation for this difference is based on how both indices were built. Soliveres, Maestre, et al. (2015) calculated intransitivity based on pure intransitive triangles ($A < B < C < A$) considering the abundance of the five most abundant species per site, while we considered potential intransitivity triangles based on the abundance distribution in the quadrats for all the species per site (Figure 1b). Commonly, rare species are less adapted to environmental conditions, and it has been suggested that their persistence depends on biotic interactions (Choler, Michalet, & Callaway, 2001). However, they also contribute less to abundance-weighted community indices. Thus, it is possible that the importance of intransitivity differs between abundant and rare species, and this could influence the outcome of intransitivity indices depending on the component of the community they are focused on.

Finally, it is important to note that our intransitivity index should vary if strong correlation between traits occurs because we used species trait information to infer directionality in competitive

interactions. However, maximum plant height and SLA are poorly correlated across sites in our dataset ($r = -0.16$). Using two independent traits across sites allows us to avoid any a priori bias due to trait covariation. Nonetheless, trait covariation may occur within sites due to environmental filtering effect (Dwyer & Laughlin, 2017). We, therefore, evaluated how trait covariations within sites correlate with intransitivity and assessed the response of trait covariation to environmental predictors (Appendix S2).

2.4 | Macro-scale gradients and functional diversity of plant communities

We evaluated how intransitivity responded to climatic, soil and vegetation variables. Regarding climatic attributes, we considered mean annual temperature (MAT), mean annual precipitation (MAP) and precipitation seasonality (PS: coefficient of variation of 12 monthly rainfall totals). We selected these climatic variables because they: (i) are important drivers of trait variation at both regional and global scales (Le Bagousse-Pinguet et al., 2017; Wright et al., 2004); (ii) explain an important fraction of the variation found in dryland ecosystem functioning worldwide (Maestre et al., 2012); and (iii) describe largely independent climatic features of the studied sites (bivariate correlations, $r < 0.3$ in all cases). For soil, and to assess the true abiotic effect of soil variables on intransitivity, we selected soil variables (sand content and pH) that are not directly influenced by the activity of organisms. These two physico-chemical properties play key roles in the availability of water and nutrients in drylands and are major drivers of the composition and diversity of dryland microbial communities (Dong & Ochsner, 2018; Maestre et al., 2015). Finally, we used relative woody cover (RWC, cover of woody plants/total plant cover) measured at the site level to investigate if and how intransitivity changed depending on the dominance of woody vegetation, which distinguishes major vegetation types in drylands (e.g., grasslands versus shrublands).

Finally, we calculated functional trait diversity (FDIS) using the *dbFD* function in the R package *FD* (Laliberté, Legendre, Shipley, & Laliberté, 2010). Both plant height and SLA were log-transformed before analysis to amplify the probability of detecting functional community patterns (Májeková et al., 2016). FDIS is a commonly used functional diversity metric and denotes the averaged abundance-weighted distance between plant species to the community abundance-weighted functional mean value. This index integrates information on both individual species traits and species relative abundance (Villéger, Mason, & Mouillot, 2008), thus being sensitive to species richness, species abundance distribution and variations on the local trait values (i.e., the unweighted dispersion of trait values observed within the community, de Bello, Carmona, Lepš, Szava-Kovats, & Pärtel, 2016). To understand intransitivity impacts on other diversity features, we also calculated species richness (S) and evenness (Ev , calculated as $Ev = -\sum_{i=1}^S c_i \ln c_i / \ln S$), and local trait variation as the nonweighted FDIS ($TVar$) for each site. We then evaluated how intransitivity influenced all these plant diversity components.

2.5 | Statistical analyses

We used multiple linear regressions to assess the effect of environmental (climatic, soil and relative woody cover) variables on intransitivity and on trait covariation (Appendix S2). We then used the same approach to test the effects of environmental variables together with biotic indices (importance of positive and negative spatial associations) and intransitivity as predictors of species richness (S), species evenness (Ev) and trait variation ($TVar$). We also considered quadratic terms for all abiotic predictors since functional structure and trait diversity do not necessarily change linearly along abiotic gradients (Le Bagousse-Pinguet et al., 2017). Finally, we included the interaction between environmental variables and biotic indices in all models because environmental variables can modulate the effects of biotic processes on dryland plant community structure (Gross et al., 2013). We also considered the latitude and longitude of our study sites in our analyses because these geographical variables can have potential confounding effects in our dataset (Gross et al., 2017; Le Bagousse-Pinguet et al., 2017). We used the sinus and cosinus of the longitude to avoid any bias due to intrinsic circularity of longitude in the statistical models (i.e., Longitude (sin) and Longitude (cos) hereafter, respectively).

We used a model selection procedure, based on minimizing the corrected Akaike information criterion (AICc), to select the best predictors in our models. In a first step, we simplified our models by using a backward regression procedure. We subsequently removed nonsignificant terms that did not affect model predictive ability (adjusted R^2). Then, a model selection procedure based on AICc selection ($\Delta AICc < 2$) was applied on the resulting full models to select the predictors most supported by the data. This procedure was performed using the function *dredge* in the R package *MuMIn* (Barton, 2009). Model averaging was performed based on AICc thresholds ($\Delta AICc < 2$; Burnham & Anderson, 2003) when multiple models were selected. Model residuals were inspected for constant variance and normality. All predictors were standardized before analyses using the Z-score to facilitate the interpretation of parameter estimates. Response variables were log-transformed when necessary before analysis to meet the assumptions of the tests used. Furthermore, we evaluated the relative effect of each predictor on the biotic indices and on plant community attributes with an analogue of the variance decomposition analysis based on

Z-scores. Since predictors were all Z-scored prior to analyses, the relative effect of each predictor can be simply calculated as the ratio between its parameter estimate and the sum of all parameter estimates.

Finally, a confirmatory path analysis (CPA, Shipley, 2009) was conducted to test the relationships between intransitivity, species richness and evenness, trait variation, and functional diversity. Note that we also controlled for all significant variables from the multiple regression model in the CPA (see details in Appendix S3). All statistical analyses were performed using the R statistical software 2.15.1 (R Development Core Team, 2014).

3 | RESULTS

At our study sites, the average proportion of intransitive triangles represented 39% of the total number of negative triangles ($T_{\%}$) and the average Intransitivity (Int) was slightly lower than expected by the null model ($Int = -0.045$, Table 1). However, intransitivity was highly variable across sites, ranging from “fully transitive” communities to “fully intransitive” communities where all negative triangles considered were intransitive (Table 1).

Macro-scale gradients explained 55% of the variance observed in Int (Figure 2). Climate explained 27% of the variation in Int , a fraction higher than that explained by soil variables (4%). Precipitation seasonality (PS) was the main climatic driver (19%) and had a significant positive relation with intransitivity. Mean annual temperature (MAT) and mean annual precipitation (MAP) had significantly negative and positive relationships, respectively, with Int , each explaining 4% of the variation found in this index. Interestingly, all climatic variables had nonlinear relationships with Int (Figure 2). Intransitivity increased for PS values of >60 CV, decreased for MAT values of $>15^{\circ}\text{C}$ and increased for MAP values of >500 mm (Figure 2b–d).

The models explaining plant community structure showed that intransitivity had a contrasted effect on the different diversity components evaluated (Figure 3). Specifically, intransitivity significantly increased species evenness (7%), particularly in communities characterized by low relative woody cover (significant interaction between Int and RWC, Figure 4). In contrast, intransitivity had no effect on species richness and a small effect on trait variation (p -value < 0.1 and selected in $<50\%$ of the models, Appendix S4), which were more

TABLE 1 Values of the biotic components and community structure in the drylands studied. S : species richness; K^+ : total number of positive spatial associations; K^- : total number of negative spatial associations; $T_{\%}$: proportion of intransitive triangles respect the total number of competitive triangles; I_{Int} : intransitivity corrected by the null model; $TVar$: local trait variation; $FDIS$: functional trait diversity. K^+ and K^- are presented as $K/2$ because $w_{ij} = w_{ji}$. Values are presented as the mean for all sites ($n = 100$), the confidence interval (taking the percentile 0.025 and 0.975 from the whole dataset) and the coefficient of variation (CV)

| | S | K^+ | K^- | $T_{\%}$ | I_{Int} | $TVar$ | $FDIS$ |
|-----------|-----------------|------------------|------------------|-----------------|------------------------------|----------------------------|----------------------------|
| Mean (CI) | 16.18 (6; 37.5) | 57.64 (4.5; 258) | 99.51 (7.5; 442) | 0.389 (0.04; 1) | -0.045 (-0.376; 0.661) | 0.286 (0.252; 0.316) | 0.212 (0.061; 0.305) |
| CV | 0.515 | 1.174 | 1.124 | 0.709 | 7.52 | 0.058 | 0.281 |

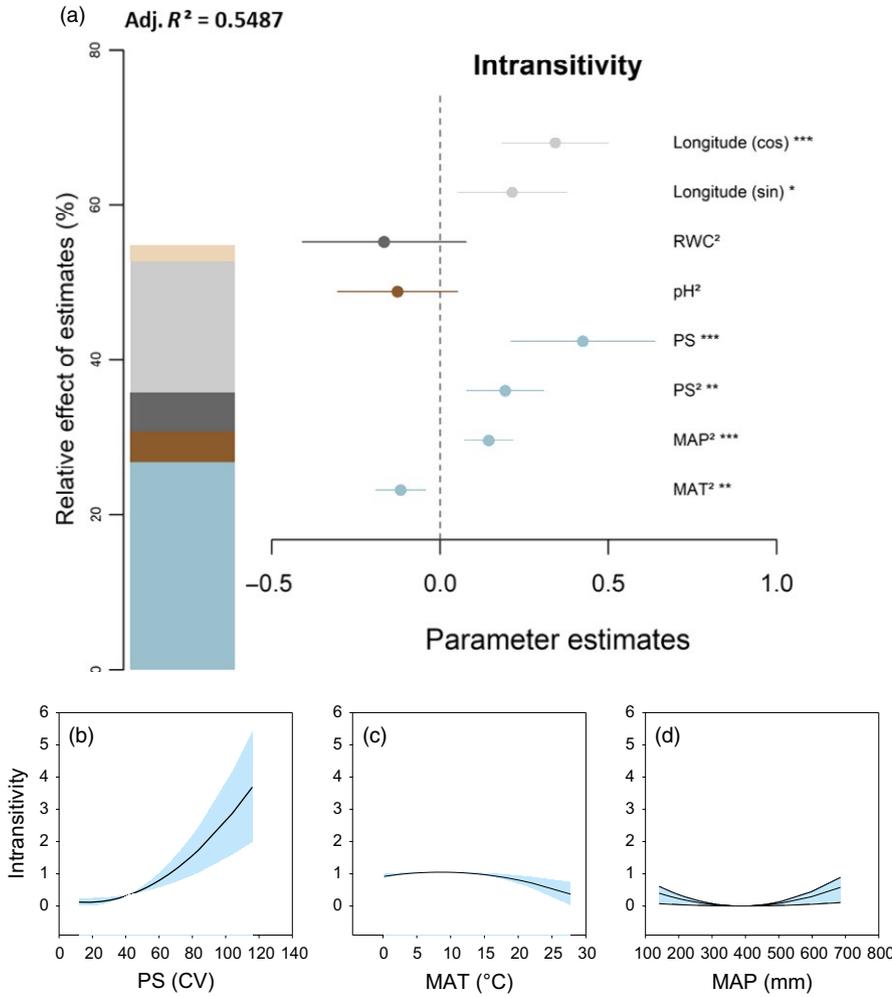


FIGURE 2 Effects of abiotic variables on intransitivity (a) and predicted nonlinear response of intransitivity and climatic variables (b–d). In (a) the averaged parameter estimates (standardized regression coefficients) of model predictors, the associated 95% confidence intervals and the relative importance of each factor, expressed as the percentage of explained variance, are shown. The adjusted R^2 of the averaged models and the p -value of each predictor are given as follows: * $p < 0.05$; ** $p > 0.01$; *** $p < 0.001$. For simplicity, only significant predictors ($p < 0.05$) or predictors that were selected in at least 75% of the models are represented. The fraction at the top of the bar includes the explained variance for all predictors not included in the plot. In (b–d), the 95% confidence intervals for each relationship are shown. RWC: relative woody cover; PS: precipitation seasonality; MAT: mean annual temperature; MAP: mean annual precipitation [Colour figure can be viewed at wileyonlinelibrary.com]

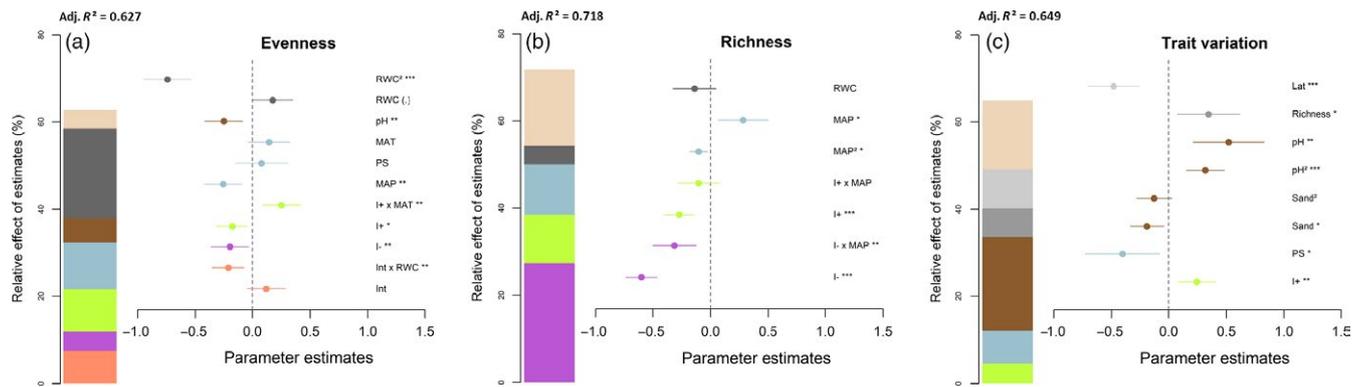


FIGURE 3 Effects of environmental predictors, intransitivity, negative and positive spatial associations on (a) species evenness (Ev), (b) species richness (S), and (c) trait variation (TVar). The averaged parameter estimates (standardized regression coefficients) of model predictors, the associated 95% confidence intervals and the relative importance of each factor, expressed as the percentage of explained variance, are shown. The adjusted R^2 of the averaged models and the p -value of each predictor are given as follows: (.) $p < 0.1$; * $p < 0.05$; ** $p > 0.01$; *** $p < 0.001$. For simplicity, only significant predictors or predictors that were selected in at least 75% of the models are represented. The fraction at the top of the bar includes the explained variance for all predictors not included in the plot. RWC, relative woody cover; MAT: mean annual temperature; MAP: mean annual precipitation; PS: precipitation seasonality; Int: intransitivity, I-: negative spatial associations, I+: positive spatial associations [Colour figure can be viewed at wileyonlinelibrary.com]

influenced by other biotic effects (spatial aggregation and segregation as proxies of facilitation and competition, Figure 4). Confirmatory path analysis showed that positive effects of species evenness and

trait dispersion mainly drove variation in functional diversity (FDIS), and that the effect of intransitivity on diversity was mediated by the positive effect of intransitivity on species evenness (Figure 5).

4 | DISCUSSION

In the present study, we evaluated the response of intransitivity to environmental gradients and its effects on plant functional diversity in global drylands. Intransitivity strongly responded to macro-scale climatic gradients, with a main effect of precipitation seasonality. Intransitivity also affected the functional diversity of the drylands studied through changes in the evenness of their plant communities. By limiting functional dominance, intransitivity, therefore, appears as a central biotic process maintaining high functional diversity on drylands under variable precipitation regimes.

4.1 | Environmental determinants of intransitivity

Our methodological framework detected a high degree of variability in the presence of intransitivity within dryland plant communities, which can be largely attributed to macro-scale environmental gradients. This result agrees with Soliveres, Maestre, et al. (2015), who found that intransitivity varied with aridity using the same database (but with another subset of sites than that used here). In our case, intransitivity also varied strongly with climate, but with a primary response to precipitation seasonality and, to a lesser extent, to the amount of precipitation and temperature (Figure 2a). Our results reinforce the view that intransitive interactions within communities increase with abiotic stress, and specifically in response to higher temporal heterogeneity in local limiting resources (Gallien, 2017), precipitation in our case. Higher precipitation seasonality can allow

different strategies for water uptake to co-occur in these water-limited ecosystems (Chesson et al., 2004), which can lead to situations where none of the species can outcompete others all the time (Edwards & Schreiber, 2010).

Our intransitivity index (*Int*) was based on an assumed relationship between two key functional traits and species competitive ability to infer the direction of the interactions. Although maximum plant height and SLA were not correlated at a global scale, trait covariation can occur within sites (Dwyer & Laughlin, 2017) if the environment selects for particular trait combinations (Grime & Díaz, 2006; Keddy, 1992). Changes in the covariation of traits observed within communities may partly explain the observed patterns of intransitivity (see Appendix S2). We found a strong and positive correlation between *Int* and the covariation of traits within sites (Figure 1 in Appendix S2). Specifically, using our method it is not possible to find high intransitivity when SLA and height are strongly negatively correlated. Accordingly, within-site trait covariation strongly responded to precipitation seasonality (Table 1 in Appendix S2). Strong and negative correlations between maximum plant height and SLA were observed under low precipitation seasonality (i.e., tall plants had low SLA values); while under high precipitation seasonality, this correlation was positive (i.e., tall plants had high SLA values). Under high precipitation seasonality, no species was able to optimize both traits simultaneously, which could drive high intransitivity within the community. Local trait covariation has been presented as one of the underlying mechanisms generating intransitivity within communities (Kraft et al., 2015). Environmental gradients influencing this covariation could

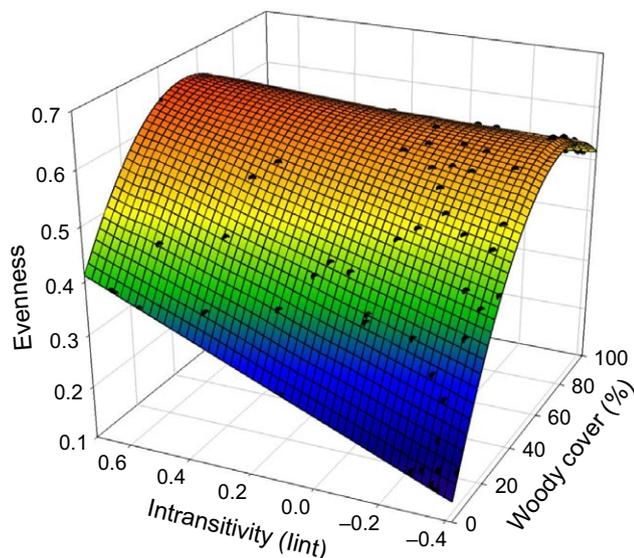


FIGURE 4 Relative woody cover modulates the relationship between intransitivity and species evenness in global drylands. The effect of the interaction is represented using the standardized parameter estimates shown in Figure 3. The predicted value for the two interactive factors (*Int* and woody cover) is shown, with evenness standardized parameter estimate being fixed at its mean value. The colours of the predicted planes change from blue (low evenness) to red (high evenness) [Colour figure can be viewed at wileyonlinelibrary.com]

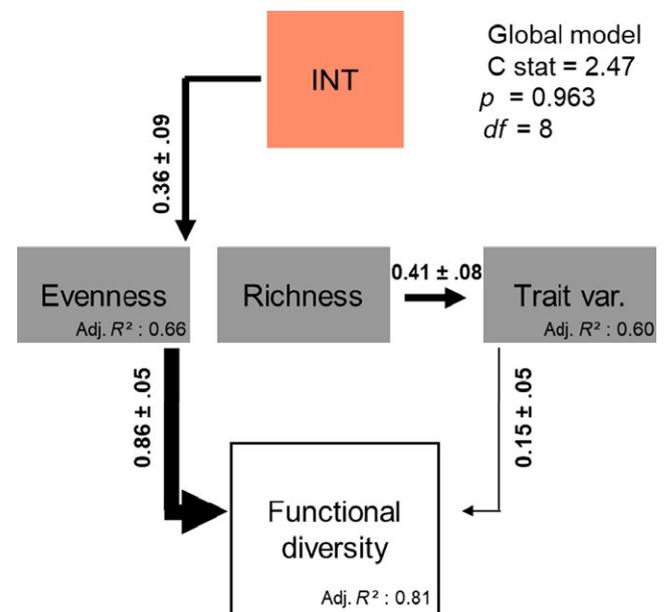


FIGURE 5 Path model for functional diversity (FDIS). Direct and indirect relationships between intransitivity, species richness and evenness, trait variation (Trait var.) and functional diversity are represented. Geographical, climatic, soil, vegetation and biotic variables were maintained in the model when significant. The size of the arrows is proportional to the absolute effect size of the standardized path coefficients. *Int*: intransitivity [Colour figure can be viewed at wileyonlinelibrary.com]

contribute significantly to explaining how intransitivity varies between plant communities. Note that considering a higher number of independent plant traits (e.g., phenological traits, root depth or nutrient preferences) may increase the potential for species to coexist (Kraft et al., 2015; Maire et al., 2012) through higher intransitivity, as none of the species would be able to optimize all traits simultaneously.

Finally, we only found a small effect of soil variables on intransitivity (Figure 2). Recent studies suggest that soil characteristics can change the importance of competition in plant communities, but have limited effects on intransitivity (Ulrich, Kubota, Piernik, Gotelli, & Soliveres, 2018). A possible explanation for this result is that the soil variables that we considered (pH and sand content) are associated with parental rock (Jenny, 1994), and therefore have low temporal and spatial variation within each site. In contrast to precipitation seasonality, predictable edaphic conditions may favour hierarchical competitive interactions (Keddy, 1990) and may limit opportunities for intransitive interactions to occur between competing plant species. Our study, therefore, illustrates that the presence of unpredictable abiotic conditions, such as water pulses in water-limited ecosystems, could be a prerequisite for intransitivity, which increases within plant communities with higher temporal variability of resources.

4.2 | Intransitivity limits dominance and increases plant functional diversity

Intransitivity affected functional diversity through its only positive effect on species evenness (E_v). Therefore, intransitivity appears as an important biotic process favouring functionally diverse plant communities worldwide by limiting functional dominance through promoting species evenness. This result coincides with previous work showing that intransitivity increases community functional diversity (Ulrich et al., 2018), particularly by promoting rare and functionally dissimilar species (Maynard, Bradford, et al., 2017). In arid environments, water is one of the main limiting resources that filters the set of suitable trait values to cope with abiotic constraints (Le Bagousse-Pinguet et al., 2017). The increase in precipitation seasonality (i.e., the increase in the unpredictability of water pulses) could result in the presence of contrasted trait values, linked to different strategies to cope with water scarcity. These changes in local trait covariation could break competitive hierarchies (McCluney et al., 2012), and ultimately result in the positive effect of intransitivity on functional diversity under higher precipitation seasonality levels.

We observed that the positive effect of intransitivity peaked for communities with low woody cover (Figure 4). Our results suggest that intransitivity is maximal for short-statured plant communities, such as those in savannas or steppes. More generally, this result indicates that intransitive interactions are likely to increase species evenness when the different species are similar in height (e.g., within similar vegetation strata). Nonetheless, our approach does not allow us to test properly this hypothesis due to the low number of species

available per strata within our dataset. Thus, testing the importance of intransitivity for different vegetation strata and its effect on functional diversity deserves further attention.

Finally, our study shows that different types of biotic interactions influence functional diversity through contrasted pathways in global drylands. Competition was an important driver of species richness, particularly at sites with low precipitation (significant interaction between I^- and MAP, Figure 3). Hierarchical competition tends to decrease species richness through competitive exclusion, an effect that increased with water scarcity (Tielbörger & Kadmon, 2000). In contrast, we observed a main effect of facilitation on trait variation, suggesting that it mostly benefited to rare and functionally distinct species, as previously suggested (Gross et al., 2013, 2015; Soliveres, Smit, & Maestre, 2015). There is a long-standing debate on the role of biotic interactions in dry environments (e.g., the role of competition versus facilitation in determining plant diversity; Brooker et al., 2008; Soliveres, Smit, et al., 2015). Our study provides new perspectives by showing that plant community functional structure is jointly shaped by multiple direct and indirect interactions that act on contrasted components of plant diversity. In this context, our study highlights the critical role of intransitivity in favouring functionally diverse plant communities by limiting functional dominance through promoting species evenness.

4.3 | Limitations of our approach and future directions

Here, we used spatial association as a proxy for biotic interactions between species. Although this approach is commonly used as a tool to infer biotic interactions at community level (Cavieres & Badano, 2009; Raventós et al., 2010; Saiz & Alados, 2012), it does not measure biotic interactions *sensu stricto*. It is, thus, necessary to establish rigorous survey methodologies to make the link between spatial association and interactions as precise as possible. Combining observational studies with experiments to establish clear links between spatial association and biotic interactions (Schöb, Prieto, Armas, & Pugnaire, 2014), and with highly accurate spatial data that allow the separation of different environmental processes (Chacón-Labela et al., 2017) would help to improve our understanding of the links between spatial patterns and biotic interactions. In our case, we tried to reduce the limitations associated with the use of spatial patterns by selecting the appropriate survey scale and by controlling environmental heterogeneity (Morales-Castilla et al., 2015), among other considerations (e.g., lack of parasitic species). Thus, this study is a first step towards understanding how intransitivity influences the functional diversity of plant communities at the global scale.

We estimated intransitivity using two key functional traits that describe plant functional strategies across terrestrial ecosystems worldwide (Díaz et al., 2016). Maximum plant height and SLA have been successfully related to biotic interactions in the drylands studied (Gross et al., 2013, 2009; Le Bagousse-Pinguet et al., 2015). However, the growing availability of trait data is promising, as it will increase our ability to detect and characterize intransitivity within

communities. In fact, our sensitivity analysis revealed that including trait information for rare species results in an increase of I_{int} . Thus, to have a more realistic evaluation of intransitivity in real communities, it is necessary to consider as many species as possible.

Finally, we measured the importance of intransitivity as the proportion of competitive triangles that are intransitive. Therefore, our approach does not cover all aspects of intransitivity such as more complex intransitive cycles, which are known to affect community structure (Godoy et al., 2017), or the detection of strong intransitive triangles including competitive reversals ($A < B < C < A$, see Figure 1b). Thus, improving the evaluation of intransitivity may also require considering these cases (i.e., higher intransitive cycles and competitive reversals) to elucidate the effect of intransitivity in a more precise way.

5 | CONCLUSIONS

Our study advances our understanding of the large-scale drivers of intransitivity within plant communities, and quantifies, for the first time, the effects of intransitivity and its relative importance on the functional diversity of drylands worldwide. Our framework highlights the importance of considering indirect biotic interactions, such as intransitivity, to properly describe the complex network of interactions arising between plant species and their effects on community structure. Intransitivity may be particularly important in ecosystems where abiotic resources are unpredictable, thereby breaking down the inherent competitive hierarchy between plant species. In addition, intransitivity enhances community functional diversity by limiting functionally dominant species. The effect of these indirect interactions on the diversity of plant communities has been largely overlooked compared with that of facilitation and competition. Our findings indicate that neglecting this process could bias our estimation of the impact of biotic processes on plant communities, ultimately leading to incomplete predictions of plant community responses in the face of upcoming environmental changes.

DATA ACCESSIBILITY

Data used in this study are archived in Figshare: <https://figshare.com/s/b862d6ba7507637afd9d> (Saiz, 2018).

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AUTHOR'S CONTRIBUTIONS

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

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