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Phylogenetic and functional constraints of plant facilitation rewiring

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Abstract

Facilitative interactions bind community species in intricate ecological networks, preserving species that would otherwise be lost. The traditional understanding of ecological networks as static components of biological communities overlooks the fact that species interactions in a network can fluctuate. Analyzing the patterns that cause those shifts can reveal the principles that govern the identity of pairwise interactions and whether they are predictable based on the traits of the interacting species and the local environmental contexts in which they occur. Here we explore how abiotic stress and phylogenetic and functional affinities constrain those shifts. Specifically, we hypothesize that rewiring the facilitative interactions is more limited in stressful than in mild environments. We present evidence of a distinct pattern in the rewiring of facilitation-driven communities at different stress levels. In highly stressful environments with a firm reliance on facilitation, rewiring is limited to growing beneath nurse species with traits to overcome harsh stressful conditions. However, when environments are milder, rewiring is more flexible, although it is still constrained to nurses that are close relatives. Understanding the ability of species to rewire their interactions is crucial for predicting how communities may respond to the unprecedented rate of perturbations on Earth.

KEYWORDS
facilitation, functional constraints, gypsum affinity, networks, phylogenetic constraints, rewiring, species turnover, traits

INTRODUCTION

The traditional view of ecological networks as static elements of biological communities neglects the fact that interactions between species in a network may shift in time and space (CaraDonna et al., 2021; Poisot et al., 2015; Trøjelsgaard & Olesen, 2016; Tylianakis & Morris, 2017). The realization of interactions is determined by the community's composition and a complex combination of environmental conditions and interacting species traits (Poisot et al., 2015). Shifts in species interactions may avoid coextinction cascades due to the loss of particular species, potentially increasing a community's robustness to face perturbation (Sheykhali et al., 2020;

Vizentin-Bugoni et al., 2020). However, partner switches (i.e., hereafter interactions turnover) are not unlimited (Montesinos-Navarro et al., 2019; Raimundo et al., 2018) as certain species combinations may be unlikely. Therefore, it is essential to assess whether there are general patterns in the topological shifts of network interactions in order to predict how different communities may respond to perturbations.

These shifts in interactions can be assessed through β-diversity changes between networks (i.e., interactions turnover; Poisot et al., 2012). Interactions turnover between two networks can come from variations in species composition and thus their associated interactions (shifts due to species turnover) or changes in the interactivity patterns among the pool of species shared in the two networks (changes due to rewiring; Poisot et al., 2012). Assessing interactions turnover and whether it follows predictable patterns can be especially important in fragmented landscapes, where the inhospitable matrix may limit the recolonization of a locally extinct species (Corlett & Tomlinson, 2020). This scenario would be critical for those species that depend on disappeared species unless they can rewire with other community species to compensate for the interaction loss, thus alleviating extinction cascades caused by the extinction of key species.

A framework to approach the β-diversity of interactions has been assessed across ecological networks in different spatial and temporal contexts, unveiling patterns in structuring natural communities that cannot be inferred directly from changes in species composition (CaraDonna et al., 2021; Carstensen et al., 2014; Poisot et al., 2012). For instance, Carstensen et al. (2014) demonstrated that species involved in frequent pairwise interactions tended to rewire less often than species involved in rare interactions. Montesinos-Navarro et al. (2019) showed that rewiring between mycorrhizal fungi and plants is not random but phylogenetically constrained. Analyzing the patterns driving rewiring interactions can shed light on the environmental factors and the species evolutionary history behind the establishment of pairwise interactions. Understanding these community dynamics is essential for correctly predicting shifts in the structure of communities facing an unprecedented rate of environmental changes.

The role of rewiring can be critical for the survival of many species in communities governed by facilitation. Facilitation is defined as a biological interaction in which one (nurse) species alters the environment in a way that enhances the performance of a second (facilitated) species (Bronstein, 2009; Mcintire & Fajardo, 2014). These interactions can prevent the loss of species that require facilitation to survive (Bulleri et al., 2018). Mutualistic networks have traditionally been considered sensitive to the extinction of generalist species (i.e., species supporting multiple species), while they seem robust to the extinction of highly specialized species (i.e., species supporting few other species; Bascompte & Jordano, 2007), a pattern also observed for facilitation networks (Verdú & Valiente-Banuet, 2008). However, this static vision of facilitative interactions does not consider the possibility of facilitated plants established beneath a new nurse when the positive association effect compensates for interspecific competition, a balance dependent on the environmental context and the interacting species traits (Qi et al., 2018). For example, it has been shown that some competitive interactions can turn facilitative under an increase in the severity of the stressful conditions (Bertness & Callaway, 1994; Qi et al., 2018), allowing the establishment of new facilitative interactions. However, this rewiring of partners is not unlimited since rewiring with highly competitive species could be very unlikely at any stress level. In contrast, facilitation rewiring would be easier with new species showing facilitative traits similar to those harbored by the original nurses.

Traits driving facilitative interactions depend on the environmental context (Butterfield & Callaway, 2013; Navarro-Cano et al., 2021). If particular traits are essential for the assembly of positive interactions, these traits could coerce the availability of nurses, so the more strict the requirements under specific stressful conditions, the more constrained the rewiring would be. There are several examples in restorations of stressful ecosystems where stress-tolerant nurses harbor more facilitated species than stress-sensitive nurses, suggesting a better amelioration derived from harboring specific traits to overcome harsh stressful conditions (Foronda et al., 2019, 2020; Saiz et al., 2014). In contrast, in milder environments, facilitation could occur with a broader range of nurse species because the traits that limit facilitation in stressful contexts may be meaningless in milder conditions where other less specific traits can shape facilitative interactions (Catorci et al., 2016; Chen et al., 2015), allowing for more alternative facilitative interaction configurations. Phylogeny can provide clues about the relevant traits for the establishment of interactions when they are phylogenetically conserved, and therefore closely related species are expected to show similar patterns of responses to environmental pressures (Ackerly, 2003; Gómez et al., 2010; Webb et al., 2002). However, some selection pressures can lead to adaptive convergence in distantly related species that respond similarly to the selection pressure (Freeman et al., 2014; Webb et al., 2002). Convergent evolution has been revealed, for instance, in harsh edaphic environments where specialized traits appear in distantly related taxa across phylogeny (Moore et al., 2014).

Understanding how abiotic stress and phylogenetic constraints modulate rewiring will help us to predict ecological community responses to different disturbance scenarios. Here, we hypothesize that the rewiring of facilitative interactions is more limited in stressful than in mild environments. Specifically, we propose that facilitated species rewire with nurses that are closely related to their preferred nurses in mild environments, while in harsh environments, facilitated species recruit preferentially beneath species with traits to overcome stressful conditions, which reduces the number of available nurses, and thus rewiring.

METHODS

Study site and sampling design

Gypsum outcrops in southeastern Spain are scattered in the landscape, surrounded by a different lithology. This generates a fragmented system for the edaphic specialist plants living on them that constitutes an excellent system to answer questions related to facilitation rewiring. The plant communities in these outcrops include well adapted specialist plants and stress-sensitive edaphic generalist species, and all of them face, in addition to water scarcity, critical edaphic limitations (Escudero et al., 2015; Palacio et al., 2007; Sánchez-Martín et al., 2021). Moreover, these outcrops are surrounded by other communities developed in less stressful substrates, avoiding harsh edaphic conditions but not semi-arid conditions. These two soil types generate contrasting stress levels, while maintaining plant communities under similar climatic conditions (see Appendix S1, Figure S1 to check basic community information differing between environments).

We developed the study in four sites in the Vinalopó valley, southeast Spain (38°29′39″ N, 0°47′00″ W; Figure 1). Here, plant communities grow under a semi-arid Mediterranean climate, with an average annual rainfall of ~360 mm, occurring in intense seasonal pulses, mainly in spring (March–June) and autumn (September–December). Plant communities are characterized by sparse vegetation, generally grouped in multispecific patches, mainly composed of camephytes and tiny shrubs. Within each site, we selected two contiguous subsites of 1 ha, one within a gypsum outcrop (stressful subsite hereafter) and another in the surrounding nongypsum lithology (limestones in our case; mild subsite hereafter). Stressful and mild subsites are in the four sites separated by a few meters to minimize changes in climatic conditions in each pair.
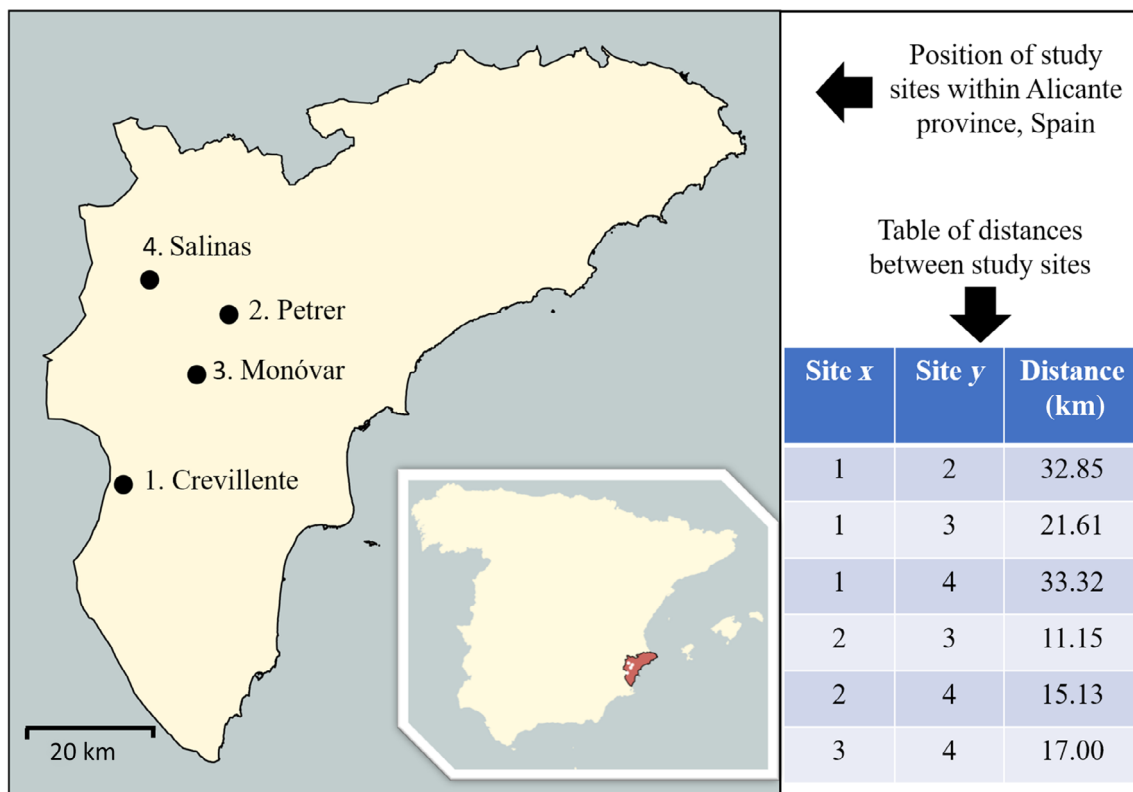

Site x	Site y	Distance (km)
1	2	32.85
1	3	21.61
1	4	33.32
2	3	11.15
2	4	15.13
3	4	17.00

FIGURE 1 Locations of the study sites in southeast Spain. Each point represents one site, including both a stressful and a mild subsite. The table on the right represents the distance between each pair (*xy*) of sites.

Our sampling design comprised 80 (150×150 cm) plots in each subsite, except for one site where the mild subsite had 79 plots. We randomly distributed the plots to occupy 1 ha entirely, avoiding places with difficult access. We sampled the four sites between April 2019 and February 2020. First, inside each plot, we identified all adult plants, independently whether they live isolated or in clumps, and measured the maximum and minimum diameter to approximate each plant cover using the ellipse equation:

$$\text{cover} = (\pi ab),$$

where (a) is the semi-major diameter and (b) is the semi-minor diameter. We also identified whether each plant grew alone (i.e., nonassociated) or in a patch with other individuals (i.e., associated). Moreover, the cover of each patch was estimated following the same method described for plants. Then, we calculated the bare ground cover by subtracting the surface occupied by patches and nonassociated plants from the sampled area. Second, we identified all recruits within the plots and identified whether they were recruiting on the bare ground or under an adult plant, identifying the species of the adult plant. When recruits inhabit patches with multiple species, we assign the recruit the closest adult plant whose canopy covers the recruit (Alcántara et al., 2019). We considered recruiting all plants ranging from seedlings (with at least the first two leaves) to tiny plants compared with adults (<15% in height compared with adults), showing neither signs of reproductive structures nor lignification at the stem base. All the species found in the adult stage are considered potential nurses independently whether they harbored recruits beneath their canopy or not, as far as they accounted for at least 0.5% of relative cover within each subsite. To assess whether they were actually acting as nurses or not, for each species of recruits, we tested for a significantly positive association among them, as explained in the *Analyses* section.

Analyses

The assemblage of facilitation networks

We constructed bipartite facilitation networks for the eight subsites (four sites × two edaphic environments), where species are classified as adults or recruits based on the size of the individuals in the sampling. Most species appeared in both roles, as we observed individuals in both ontogenetic stages (Alcántara et al., 2019). To reduce stochasticity associated with low sample size, we only included as adults species (i.e., potential nurses),

those with more than 0.5% of the relative coverage. Species absolute cover is available in "Adult species data" at Sánchez-Martín et al. (2022). As for recruit species, we only considered those with at least 20 recruits per subsite. Then, we defined the edges of the networks as the significant facilitative associations between recruit and nurse species, calculated as follows:

First, each interspecific interaction effect was calculated through the RII index (relative interaction index: Armas et al., 2004). We measured this metric for each interaction (i.e., RII of each interaction; recruit-nurse, hereafter RII_i) which we compared for each combination of recruit and nurse species in a subsite, the recruits density growing beneath the specific nurse species and the recruits density growing in the bare ground:

$$RII_i = \frac{\frac{R_i N_j}{CN_j} - \frac{R_i B}{CB}}{\frac{R_i N_j}{CN_j} + \frac{R_i B}{CB}},$$

where $R_i N_j$ is the number of recruits of a specific species (R_i) growing beneath a specific nurse (N_j), $R_i B$, is the number of recruits of the same species (R_i) growing in bare ground (B), CN_j is the cover occupied by the specific nurse (N_j), and CB is the bare ground cover. RII_i values range from -1 to 1, being positive when the density or recruits of a species under a given canopy is higher than in the bare ground, and negative when the opposite is true.

Second, we tested the significance of each observed RII_i by comparing it to a null model that randomly assigned, 1000 times, the number of recruits of each species to the available canopies in a given subsite, based on their relative cover. This redistribution considered that the nurse species are not equal in terms of cover, so we used the relative cover of each nurse species as a weighted element to be considered to obtain the weighted recruits' random distribution. Finally, all specific interactions whose observed RIIs were above 97.5% of the RIIs null model distribution were deemed significant and assigned a value of 1 in a matrix combining all possible pairwise interactions of recruits and nurse species (edges of the networks). Nonfacilitative interactions, including both nonsignificant (i.e., those between 2.5% and 97.5% of the RIIs null model distribution) and significant but negative interactions (i.e., those below 2.5% of the RIIs null model distribution), were set to zero as we were only interested in the facilitative interaction that constitutes the core of the significant interactions found in the interaction networks. Specifically, of 347 significant interactions, we found 325 positives (93.66%) and 22 negative interactions (6.34%). We also found 606 pairwise interactions that were not significant, which means that their

observed RIIs result from co-occurrence patterns that cannot be separated from the random expectation given the recruits abundance and nurse covers in the study community. All the interactions and significance tests can be checked in "Interactions data" at Sánchez-Martín et al. (2022).

Rewiring and abiotic conditions

To assess whether rewiring is more limited in stressful environments than in mild environments, we explored the dissimilarity of the networks by assessing the different components of the dissimilarity in each possible pair of sites segregated by edaphic environments (i.e., stressful and mild environments) ($N = 6$ pairs of sublocalities per edaphic setting). According to Poisot et al. (2012), the dissimilarity of interactions (i.e., interactions turnover; β_{WN}) can be decoupled into two components: (1) the dissimilarity due to species turnover (β_{ST}) and (2) the dissimilarity of interactions established between species common to both networks, also called the rewiring component (β_{OS}). That means that overall interaction dissimilarity (β_{WN}) equals the sum of the dissimilarity explained by species turnover and rewiring ($\beta_{ST} + \beta_{OS}$). Moreover, we calculated the dissimilarity in species composition (β_{S}) to assess how taxonomic changes in our communities could influence interaction dissimilarity. All these metrics were obtained by using the "network_betadiversity" function hosted in the *betalink/2.2.1* package of R (Poisot, 2016). Then, we assessed the differences between these metrics in the two contrasting edaphic environments. To do so, we conducted a generalized linear model with β_{WN}, β_{ST}, β_{OS}, or β_{S} as response variables and the edaphic setting (stressful/mild) as the predictor. We also included the identity of the pair sites as a random effect, but as it was not significant, it was not considered in further analyses. The information on the differences in species composition between stressful and mild subsites within each site and also the amount of positive interactions unique and shared between each pair of subsites is available in Appendix S1, Figure S2.

Fründ (2021) proposed an alternative normalization of dissimilarities to the Poisot partition that avoids overestimating rewiring. However, in a recent article, Poisot claims that the Fründ approach is inappropriate for measuring network diversity because rewiring is relative to the number of interactions in the global network (since considered unique interactions) and thus dependent on both rewiring probability and species turnover (Poisot, 2022). To ensure that our main conclusions were not the result of different methodological choices, we reanalyzed the data as mentioned above but following Fründ's approach.

Phylogenetic constraint to rewiring

We estimated the phylogenetic constraints to rewiring following the method described in Montesinos-Navarro et al. (2019). Using the information from the eight subsites, separately for stressful and mild soils, we calculated the number of potential interactions between nurse and recruit species by counting the number of times each interaction could potentially occur across sites (up to four times if both recruit and nurse were available at the four subsites of each soil). We only considered cases in which there were two or more potential interactions, avoiding extremely high or low stochastic percentages due to a small number of potential interactions. Then, for each recruit, we defined the preferred nurse species as the species that facilitated it in more than 50% of their potential interactions (i.e., times that both species are connected across facilitation networks). The rest of the nurse species that also facilitated the recruits in any of the subsites were considered nonpreferred nurse species (>0% and ≤50%) of their potential interactions. We also tested our analyses using other preferred/nonpreferred thresholds and checked the consistency of the results. The sensitivity test can be found in Appendix S1, Table S1. To calculate the phylogenetic distances between preferred and nonpreferred nurse species, we generated the phylogenetic relationships among all of the plant species found in the sampling using the "V.phylomaker" function from the *V.phylomaker/0.1.0* R package (Jin & Qian, 2019). This function matches a given species input with the "GBOTB.extended.tre" phylogeny that includes 74,533 species as a result of the combination of two previous mega-phylogenies (Smith & Brown, 2018; Zanne et al., 2014). The species from our input that did not appear in the mega-phylogeny were inserted following scenario.2 (S2 adds unknown species randomly to nodes below the genus or family basal nodes; Jin & Qian, 2019; Qian & Jin, 2016). The branch length of the resulting phylogeny is displayed in chronological time units, specifically in millions of years (myr). Finally, to calculate the phylogenetic distances between nonpreferred and preferred canopies, we used the "cophenetic" function hosted in the *ape/5.5* R package (Paradis & Schliep, 2019).

For each recruited species in each subsite, we calculated the minimum phylogenetic distance between the nonpreferred nurse that was actually facilitating it and its closest relative among the preferred nurses of the recruit species. Then we obtained the average distances per recruit species in each subsite.

Then, we developed a null model to compare the obtained average with a random expectation. The null model aims to randomly assign a nurse from the adult

plants present in a subsite. For this, for each recruit species at each site, the number of adult plants under which this species was found was counted. Then, that same number of plants was randomly selected from the total number of adult plants present at the site (excluding those belonging to nurse species preferred by the recruit species). Then, we used the nurses random selection to calculate the same phylogenetic distance described above. Finally, we assessed whether, for all recruit species at all subsites within each environment, the differences between the observed and expected values, were statistically different from 0 by using the "t.test" function hosted in R base (R Core Team, 2019). This comparison was performed separately for networks sampled in stressful environments and for networks in mild environments.

Functional constraint to rewiring

To identify whether recruit species tended to recruit beneath specialized species, we first measured the degree of gypsum affinity (g) as a functional proxy of the species' ability to respond to gypsum constraints (Sánchez-Martín et al., 2021). The metric g for each species is strictly the proportion of its cover found in the stressful subsite divided by its total cover in the site (sum of cover in the stressful and mild subsites) but only considering the cover of plants growing alone to reduce biotic interference:

$$g = \frac{Cs}{Cs + Cm},$$

where Cs is the species' cover in the stressful soil (i.e., gypsum) and Cm in the mild soil (i.e., limestones). Gypsum affinity (g) values range from 0 to 1, where 0 are species found in the limestone that never enter the gypsum and 1 represents strict gypsophytes restricted to gypsum. This metric is a good functional metric as it has been previously shown that the species' gypsum affinity in this community is positively related to harboring specific strategies to cope with harsh gypsum constraints, such as the ability of roots to penetrate hard gypsum layers and the accumulation of elements found in excess in those soils such as Ca, Mg and S (Sánchez-Martín et al., 2021). Species with g values close to 1 (high gypsum affinity) are those with the strategies mentioned above, while species with g values close to 0 (low gypsum affinity) do not show any specific response to survive in those soils (Sánchez-Martín et al., 2021). The g values calculated with few individuals may generate poor estimates of gypsum affinity due to stochasticity; therefore, we only calculated g for those species with a sufficient number of

adults (20 in both stressful and mild environments). Finally, we averaged the values of g for each species across sites.

Then, we compared the average g of the nonpreferred nurse species with the predicted by a null model that chose a set of nonpreferred nurses at random, which could have facilitated each recruit in each subsite. To do so, from the pool of nurses present in each subsite (excluding the preferred nurses for each recruit), we randomly selected the same number of observed nonpreferred nurses facilitating the recruits and calculated their average gypsum affinity. Finally, we assessed whether the differences between the actual and predicted values, based on the null model, were statistically different from 0 by using the "t.test" function hosted in R base (R Core Team, 2019). This comparison was performed separately for networks sampled in stressful and mild environments.

RESULTS

Facilitation networks capture the most prevalent interactions in the studied communities in both edaphic environments, the reliance on facilitation being more prominent in the stressful subsites, as shown by the higher average RII_i in these soils (Appendix S1, Figure S3). These networks contain 325 interactions in the four sites resulting from the analysis of the recruitment patterns of 11,929 recruits (4645 growing beneath a nurse species and 7284 on the bare ground). These interactions can be grouped in two metawebs that combine the facilitation patterns across communities in each edaphic environment (Figure 2a). Bringing together the networks of all the sites allows us to discern between interactions exclusive to one network from those that could potentially occur across networks (Figure 2b). From the latter, we can differentiate between those that occur with high frequency (i.e., preferred) and those that can potentially occur in many places but are only realized in a few (i.e., nonpreferred; Figure 2c). This distinction serves as the foundation for assessing limitations in the rewiring of interactions. For detailed facilitation networks of each subsite, see Appendix S1, Figure S4.

Rewiring and abiotic conditions

Network dissimilarity analyses suggested a differentiated pattern between networks in different edaphic environments. Networks from mild environments showed higher dissimilarity of interactions (mean $\beta_{WN} \pm SE$; 0.855 ± 0.033) than networks in stressful environments (0.734 ± 0.033) ($F = 6.796$, $p = 0.026$; Figure 3a,b).
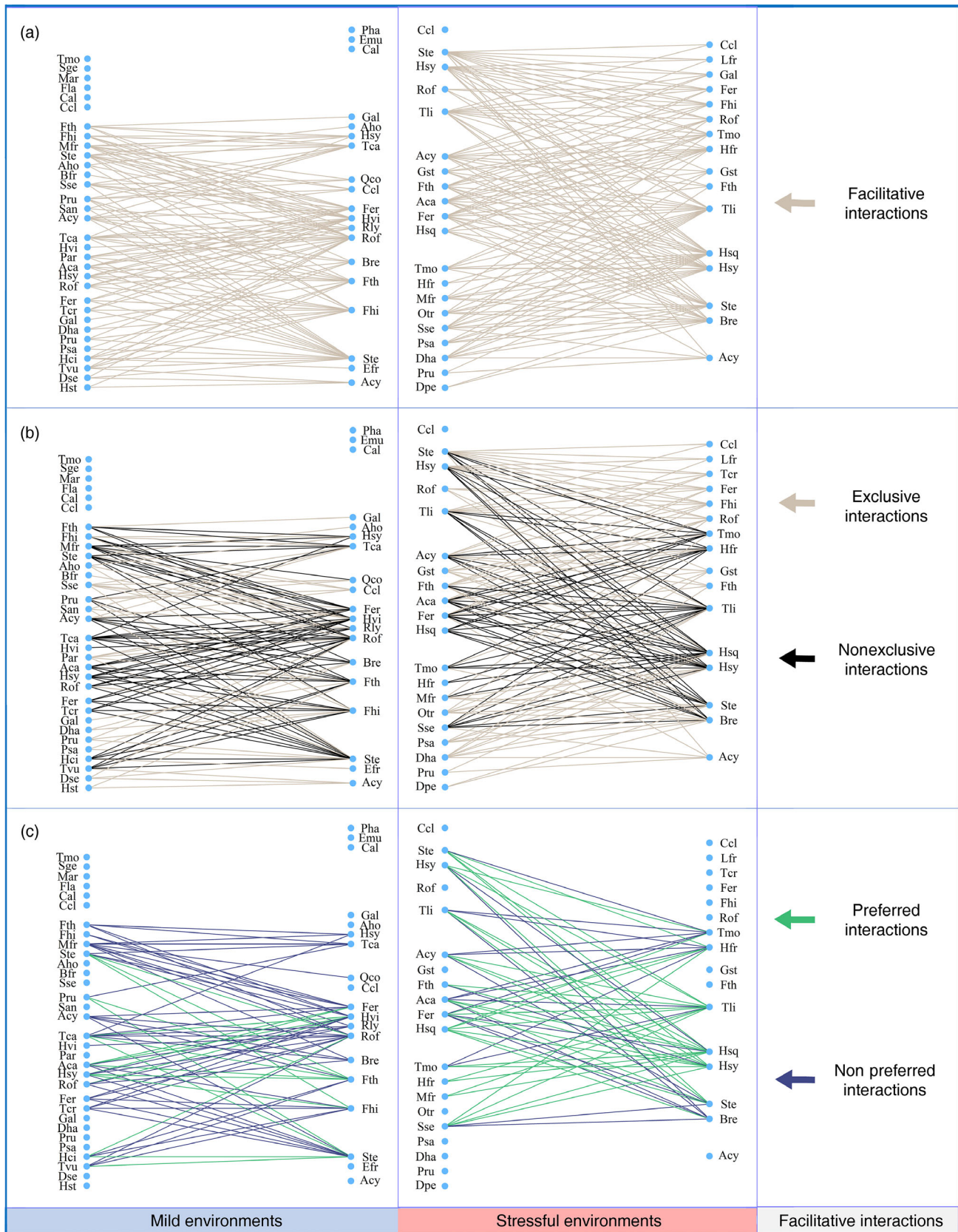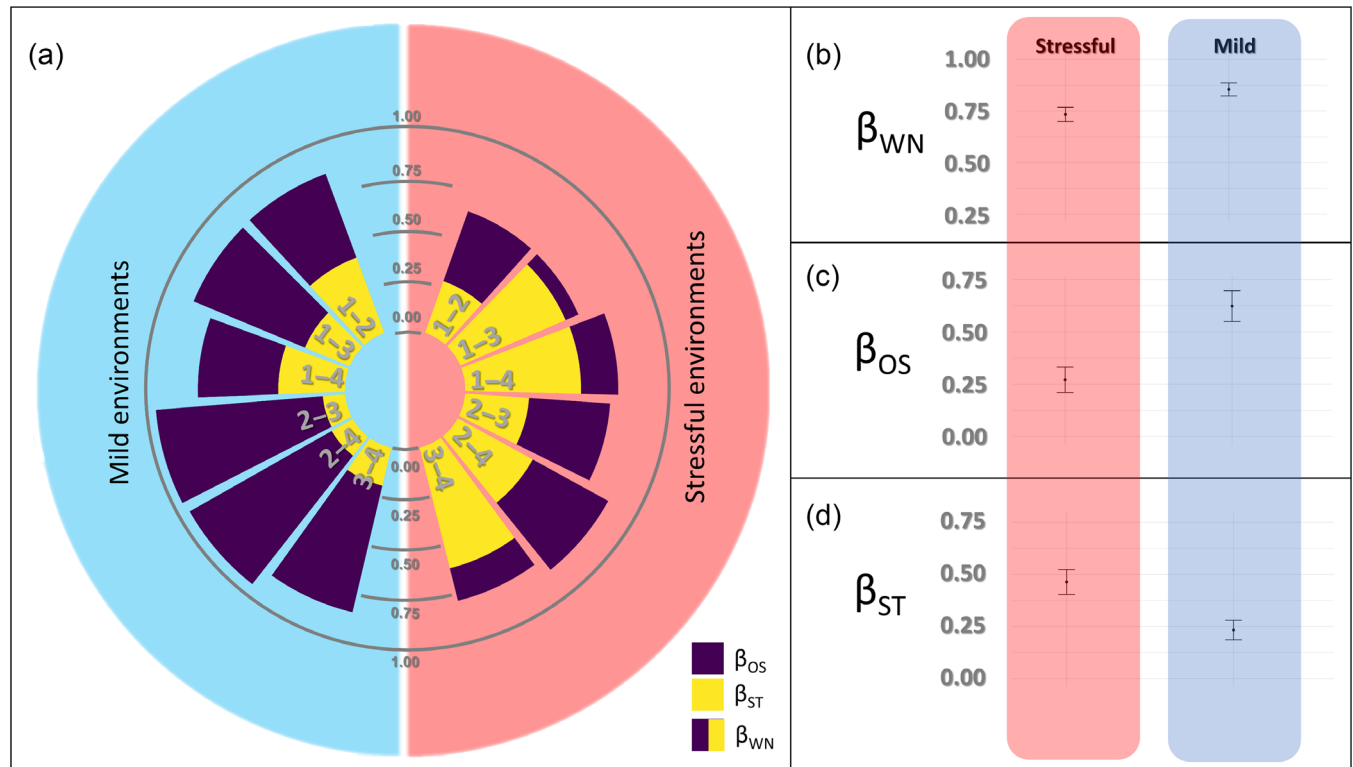
FIGURE 2 Legend on next page.

FIGURE 3 Results of network comparisons across sites in two contrasting edaphic environments. The circle bar plot (a) summarizes the dissimilarity of interactions decoupled in rewiring and species turnover ($\beta_{WN} = \beta_{OS} + \beta_{ST}$), being the numbers within each bar the specific pair of sites being compared, (b) shows the overall dissimilarity of interactions (β_{WN}) between mild and stressful environments, (c) shows differences between environments in the rewiring component (β_{OS}), while (d) refers to species turnover (β_{ST}) comparison between environments.

Interestingly, this greater dissimilarity of interactions was not equally distributed between rewiring (β_{OS}) and species turnover (β_{ST}). While rewiring (β_{OS}) was significantly lower in the stressful environments (0.270 ± 0.068) than in the mild environments (0.623 ± 0.068) ($F = 13.613$; $p = 0.004$; Figure 3a,c), and species turnover (β_{ST}) was higher in stressful (0.463 ± 0.054) than in mild environments (0.232 ± 0.054) ($F = 9.189$; $p = 0.013$; Figure 3a,d). Markedly, this occurred even though the dissimilarity in species composition (β_{S}) did not differ among environments ($F = 3.783$; $p = 0.080$) and, in any case, showed a tendency to be greater in mild (0.441 ± 0.023) than in stressful (0.378 ± 0.023) environments. Similar results

were obtained with Fründ's alternative approach. See Appendix S1, Figure S5 for details.

Constraints to rewiring

Rewiring is phylogenetically constrained in mild communities, that is, recruits rewire preferentially beneath nonpreferred canopies that are phylogenetically closer to the preferred ones than expected by the null model ($t = -3.635$; $df = 16$; $p = 0.002$; CI 95% (-104.814, -27.588); Figure 4a left). By contrast, this phylogenetic constraint does not occur in communities from

FIGURE 2 (a) A meta web representation combining the facilitation patterns detected in the four studied sites in mild (left) and stressful (right) environments. Nodes in the left column represent recruit species, whereas nodes in the right column are the nurse species. Lines connecting nurse and recruit species represent significant facilitative interactions. (b) Interactions dissimilarity patterns in the meta web can be due to interactions between unique species of local networks, so all the changes in these interactions among networks are due to species turnover (gray arrows). Conversely, we also found interactions that can occur in more than one local network (black arrows). (c) Among the latter, we can identify interactions occurring in more (preferred ones; green arrows) or in less (nonpreferred ones; fuchsia arrows) than half of its possibilities, being the latter those identified as rewiring cases. Species' full names related to codes are listed in Appendix S1, Table S2.
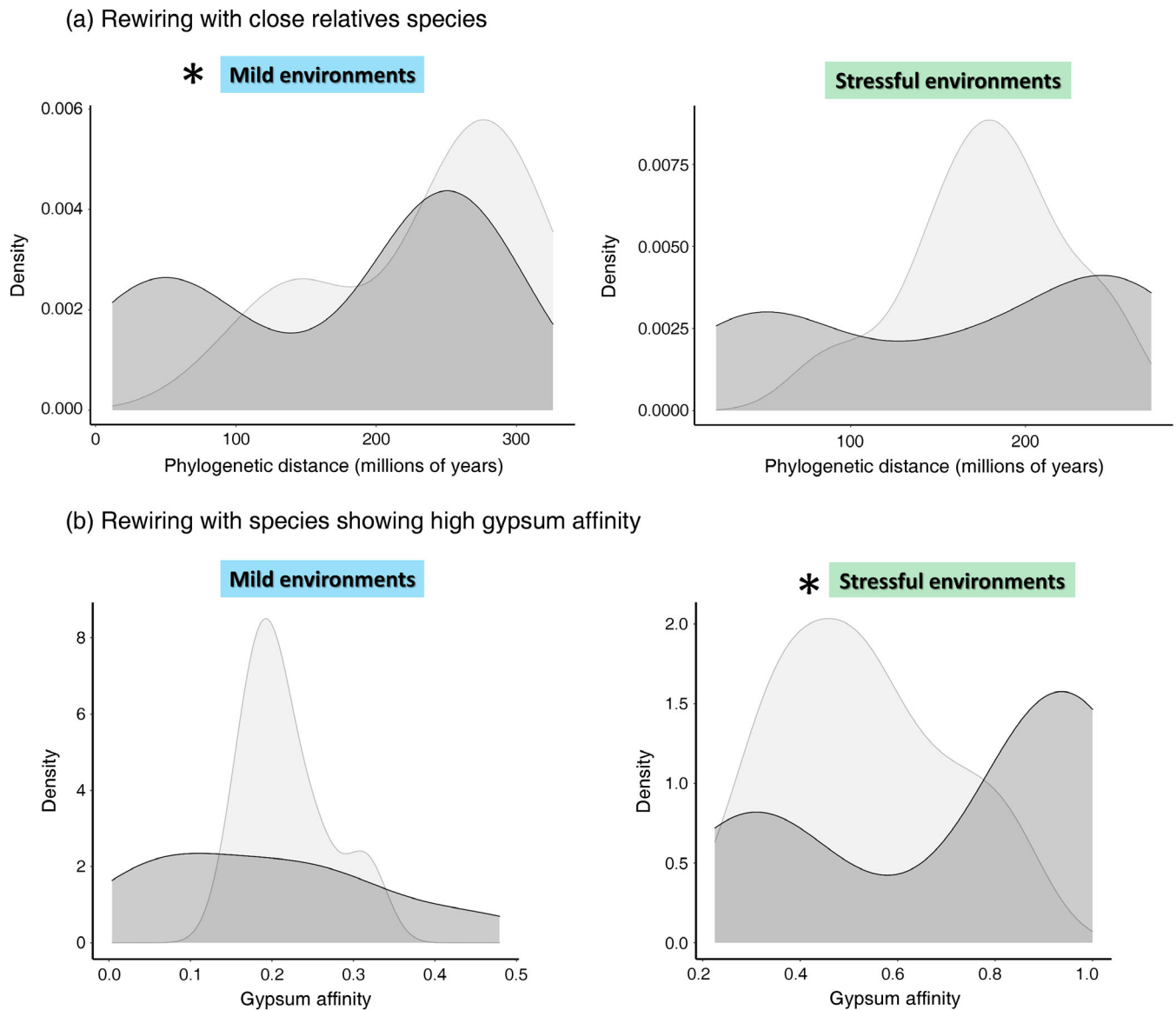
(a) Rewiring with close relatives species

(b) Rewiring with species showing high gypsum affinity

FIGURE 4 (a) Density plots comparing the observed (dark gray) and expected (light gray) distribution of the minimum phylogenetic distances between nonpreferred and their closest preferred nurse species. (b) Density plots comparing the observed (dark gray) and expected (light gray) distribution of the average gypsum affinity of nonpreferred nurses. *The observed distribution is significantly different from the expected by the null model.

stressful environments ($t = -1.188$; $df = 19$; $p = 0.249$, CI 95% (-55.891, 15.411), Figure 4a right). Conversely, the rewiring constraints in stressful environments are governed by the gypsum affinity of the nurses, that is, facilitated plants rewire with nurse species with higher levels of gypsum affinity than expected by chance ($t = 2.608$; $df = 19$, $p = 0.017$; CI 95% (0.038, 0.344); Figure 4b right). In contrast, this functional limitation does not seem to apply in communities from mild environments ($t = -0.718$; $df = 13$; $p = 0.486$; CI 95% (-0.102, 0.051); Figure 4b left). These results show consistency when checked with other preference thresholds. See Appendix S1, Table S1 for results of a sensitivity test checking multiple thresholds.

DISCUSSION

The observed dissimilarity pattern of interactions sheds light on how these communities subjected to different stress levels may respond to changes in community composition. In both environments, interaction dissimilarity was high, suggesting that the facilitative interactions can shift with high freedom across sites. Our results showed that interaction dissimilarity was slightly but significantly lower in stressful than in mild environments. However, much of this dissimilarity is explained by species turnover across communities, causing the appearance and disappearance of multiple interactions, a common

pattern in our networks of stressful systems. Conversely, the dynamics reversed when we focused on the pool of shared species across sites, showing that rewiring was of less magnitude in stressful environments than in the mild ones. These spatial variations have implications for understanding how the structure of these communities will vary under a species loss scenario.

On the one hand, we found a higher turnover in stressful environments even though species composition dissimilarities between mild and stressful environments did not differ. The higher reliance on facilitation of the recruiting species in stressful environments results in concomitant changes in interactions with the gain or loss of nurse species. Conversely, rewiring was low in stressful environments. Below we discuss that, in addition to stressful conditions, other phylogenetic and functional specific patterns may explain the limitations to rewiring patterns.

Limitations on rewiring patterns

Despite the high rewiring capacity found in mild environments, we still identified constraints to the establishment of interactions with nonpreferred nurse species. Specifically, we observed a pattern in which the recruiting species interacted with the nonpreferred nurse species that were close relatives of their preferred nurse species. That seems logical under the assumption that closely related species tend to share similar traits, so the traits that make a nurse suitable for certain species could also apply to similar species (Gómez et al., 2010). Indeed, this phylogenetic restriction to rewiring seems to apply to other mutualistic networks such as those established between plants and fungi (Montesinos-Navarro et al., 2019), suggesting that it could be a pattern widely distributed in nature. Conversely, we found no functional limitations related to gypsum affinity for rewiring in mild environments, which is logical, as the specific traits that sustain facilitative interactions in stressful environmental contexts may be meaningless in these milder environments (Butterfield & Callaway, 2013).

In contrast, we did not find any phylogenetic constraint to rewiring in stressful environments. In these systems, the harshness of the abiotic conditions has shaped a plant community harboring species with specific adaptations (Palacio et al., 2007). These specialized traits have emerged at different points in evolutionary history (Escudero et al., 2015; Moore et al., 2014), which prevents finding phylogenetic constraints to rewiring because species with varying gypsum affinity levels can be found within the same clades of the community (Appendix S1, Figure S6). Indeed, in these systems, rewiring occurred with nonpreferred species showing higher gypsum affinity levels than expected independently of the phylogenetic relatedness. Among the potential mechanisms underlying this pattern might be the fact that some gypsum-specialized species seem to be better nurses than stress-sensitive species (Foronda et al., 2019; Saiz et al., 2014), which may promote the situation that many species depend on the presence of these nurses to survive (Verdú & Valiente-Banuet, 2008).

Ecological implications

This paper emphasizes the critical role that well adapted species play in the stability of plant communities. When communities are subjected to high-intensity stressors and recruitment on bare soil is highly undermined, facilitative interactions are established with those species that have mechanisms to deal adequately with this stressful condition (Foronda et al., 2019; Saiz et al., 2014). This fact fosters the appearance of benefactor species facilitating multiple species (Verdú & Valiente-Banuet, 2008), a role that the gypsum specialists assumes as they are the only ones that can guarantee the survival of facilitated species. However, this limits rewiring with other less specialized species, as they may not provide the needed benefits. For this reason, retaining these specialist nurse species is vital for preserving the system's stability, as their disappearance could be catastrophic for the entire community (Valiente-Banuet & Verdú, 2013). This is especially relevant in fragmented stressful edaphic environments in which many specialized species are endemisms whose isolation makes them more vulnerable to extinction (Corlett & Tomlinson, 2020).

In contrast, in mild environments where the reliance on facilitation is less prominent, the rewiring capacity seems limited by nurse traits that must be phylogenetically conserved. It is worth noticing that the phylogenetically constrained rewiring found in these environments does not respond to recruits' necessity for particular traits as those found in the stressful environments, but to other general traits evolutionary conserved that are not homogeneous for all recruit species necessarily. These less stringent facilitation requirements could open up a gap for a more prominent contribution for rewiring in structuring these communities, as facilitative effects are not shaped by the traits of specific taxa.

Nevertheless, these results should be interpreted with caution, as our results are based on a space-by-time substitution approach, using multiple site snapshots. Ideally, it would be interesting to monitor this process over time within each subsite. However, assessing biological interactions in the field requires intense sampling, so conducting these studies over the long term under field conditions might become unfeasible.

CONCLUSIONS

We provide evidence for a distinct pattern in the rewiring of facilitation-driven communities at different stress levels. In highly stressful environments where plants strongly depend on facilitation, rewiring is limited to growth beneath habitat-specialized species. However, when environments are milder, rewiring, although of a lesser magnitude, is still limited to occur with nurse species relatively close to their preferred ones.

CONFLICT OF INTEREST
The authors report no conflict of interest.

DATA AVAILABILITY STATEMENT
Data (Sánchez Martín et al., 2022) are available in Zenodo at https://doi.org/10.5281/zenodo.7035834.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.