RESEARCH ARTICLE

Global Ecology and Biogeography   A Journal of Macroecology   WILEY

Plant–plant interactions determine taxonomic, functional and phylogenetic diversity in severe ecosystems

Maral Bashirzadeh[1] | Santiago Soliveres[2,3] | Mohammad Farzam[4] | Hamid Ejtehadi[1]

[1]Quantitative Plant Ecology and Biodiversity Research Laboratory, Department of Biology, Faculty of Science, Ferdowsi University of Mashhad, Mashhad, Iran

[2]Instituto Multidisciplinar para el Estudio del Medio "Ramon Margalef", Universidad de Alicante, Alicante, Spain

[3]Departamento de Ecología, Universidad de Alicante, Alicante, Spain

[4]Department of Range and Watershed Management, Faculty of Natural Resources and Environment, Ferdowsi University of Mashhad, Mashhad, Iran

Correspondence
Hamid Ejtehadi, Quantitative Plant Ecology and Biodiversity Research Laboratory, Department of Biology, Faculty of Science, Ferdowsi University of Mashhad, PO Box 9177948974, Mashhad, Iran.
Email: hejtehadi@um.ac.ir

Funding information
Ferdowsi University of Mashhad

Editor: Volker Bahn

Abstract

Aim: Plant–plant interactions are an important factor in structuring plant biodiversity. However, most studies on the impacts of plant–plant interactions on biodiversity focus on species richness and to a lesser extent on other facets of diversity. When other facets of biodiversity are considered, studies often include a limited set of environmental conditions. We aimed to quantify the impacts of nurse plants on taxonomic, functional and phylogenetic facets of plant biodiversity and how these impacts change across environmental gradients.

Location: We report data on 28 alpine and 50 dryland sites, established in 11 countries.

Time period: 1998–2019.

Major taxa studied: Vascular plants.

Methods: We analysed plant–plant interactions using co-occurrence analyses and obtained information on the functional traits and phylogenetic relationships of the beneficiary species. We calculated the change in taxonomic, functional and phylogenetic diversity caused by the presence of nurse plants and environmental conditions.

Results: Nurse plants enhanced taxonomic and phylogenetic diversity in alpine communities and enhanced functional and phylogenetic diversity in dryland communities. However, they had a positive effect on functional and taxonomic diversity only in moderate environments in alpine and dryland communities, respectively. The effects of nurse plants were larger in drylands for functional and phylogenetic diversity and in alpine communities for taxonomic diversity. Interestingly, nurse plants induced non-linear changes in all facets of biodiversity across environmental gradients, whereas biodiversity tended to increase linearly toward more benign conditions in open interspaces.

Main conclusions: Facilitation is important in alpine environments to maximize taxonomic diversity and has a more consistent positive effect on the functional and phylogenetic diversity of drylands. In general, effects of facilitation on biodiversity peak in moderate environmental conditions, which suggests that nurse plants can protect biodiversity from impacts of climate change mostly in those places currently under low environmental stress and that will be likely to experience moderate stress levels in the future.

KEYWORDS
alpine communities, biodiversity facets, climatic gradients, competition, drylands, facilitation, stress gradient hypothesis

1 | INTRODUCTION

Multiple facets of biodiversity, including taxonomic, functional and phylogenetic diversity, are important to understand community assembly and the effect of biotic communities on ecosystem functioning (Butterfield & Briggs, 2011; Cadotte et al., 2013; Le Bagousse-Pinguet, et al., 2019; Valiente-Banuet et al., 2007). All these facets of biodiversity are likely to be influenced by plant–plant interactions. For example, the presence of nurse plants can enhance microclimatic conditions and soil fertility or provide protection from grazing, which might allow the recruitment and survival of species that would not be present otherwise, increasing as a result the taxonomic diversity of the community (Cavieres et al., 2013; Madrigal-Gonzalez et al., 2020; Soliveres & Maestre, 2014). Owing to the different microenvironments generated by nurse canopies (e.g., buffered temperature and radiation, higher soil organic matter), the plants growing beneath nurse species often show functional trait values different from those plants able to thrive in their absence, commonly presenting larger heights or specific leaf areas, typical of more competitive and less stress-tolerant strategies. Therefore, nurse plants can enhance the functional diversity of the community in addition to the taxonomic diversity (Butterfield & Briggs, 2011; Schöb et al., 2012). However, facilitation depends not only on the functional traits of the beneficiary species, but also on the relationship between nurse and beneficiary traits and on competition between beneficiary species (Greiner La Peyre et al., 2001; McIntire & Fajardo, 2013; Soliveres et al., 2014). Therefore, patterns of functional diversity driven by nurse plants might not match those of taxonomic diversity, because strong competition between beneficiary species beneath nurse canopies could hinder the overall positive effect on taxonomic diversity. In addition, facilitation of taxonomic diversity and facilitation of functional diversity can change in different ways across environmental gradients (Madrigal-Gonzalez et al., 2020), with facilitation of functional diversity responding monotonically and positively to increases in abiotic stress, whereas facilitation of taxonomic diversity shows more nuanced responses to environmental gradients (reviewed by Soliveres et al., 2015). In addition, nurse plants can facilitate the presence of phylogenetically distant species, although shared mutualisms could also render facilitatory effects for species closely related to their nurses (Butterfield et al., 2013; Pistón et al., 2016; Valiente-Banuet et al., 2007). Although the relationships between facilitation and phylogenetic diversity should mimic those found for facilitation and functional traits, these responses of phylogenetic diversity to nurse plants can differ from that of functional diversity if functional traits are not phylogenetically conserved (Valiente-Banuet & Verdú, 2013; Vega-Alvarez et al., 2019) or if phylogeny represents important functional traits, the details of these traits have not been measured [e.g., chemical defenses against herbivores or vulnerability to fungal pathogens, both of which show evidence of phylogenetic conservatism (Gilbert & Webb, 2007; Salazar et al., 2016), or root-related traits, all of which are rarely measured in the field]. Therefore, we still do not understand how consistent the effects of facilitation are for different facets of plant biodiversity or whether these effects change consistently across environmental gradients.

A large body of literature illustrates changes in plant–plant interactions across environmental gradients. Existing results can, arguably, be summarized in the following three main categories: (1) those showing increases in the frequency, intensity or importance of facilitation with environmental harshness, because the more stressful an environment becomes, the more likely it is that facilitatory interactions will gain importance, whereas competitive interactions should prevail in more benign conditions (the stress gradient hypothesis; Bertness & Callaway, 1994); (2) if the microclimatic amelioration does not suffice to sustain the growth and survival of beneficiary species, facilitation can collapse when the environment becomes too harsh, therefore showing a hump-shaped relationship for facilitation across an environmental gradient (Maestre & Cortina, 2004; Michalet et al., 2006); and (3) if facilitation–environment relationships depend on the species-specific adaptations to the environment of each beneficiary species, the overall community responses to facilitation could show a rather neutral relationship between facilitation and plant biodiversity across environmental gradients (reviewed by Michalet et al., 2014; Soliveres et al., 2015). Previous studies looking at the relationship between plant–plant interactions and environmental gradients have focused mostly on the effects of these interactions on taxonomic diversity (or other attributes of the vegetation, such as biomass, survival, seed production and growth). However, there are few studies addressing how the effects of plant–plant interactions on evolutionary relatedness and functional trait distribution vary across such environmental gradients (Butterfield & Callaway, 2013; Butterfield et al., 2013; García-Camacho et al., 2017; Le Bagousse-Pinguet, et al., 2018; Schöb et al., 2013; Soliveres et al., 2012, 2014). From the available information, it seems that the responses of these facets of biodiversity to plant–plant interactions can differ strongly from those found on taxonomic diversity in their dependence on the environmental conditions.

In drylands, for example, species that evolved during the Tertiary, in wetter conditions, are generally dependent on nurse plants to recruit (Valiente-Banuet et al., 2007), and this seems generally true regardless of how harsh the environment is, which generates neutral facilitation–environment relationships (García-Camacho et al., 2017; Soliveres et al., 2012). In alpine environments, however, there is no parallel to the Tertiary–Quaternary division in plant regeneration syndromes found in drylands, and facilitation intensifies with environmental stress for those taxa more distantly related to their nurse (Duarte et al., 2021). Plant functional traits, instead, respond strongly to both environmental gradients and the presence of nurse plants (e.g., Butterfield & Briggs, 2011; Schöb et al., 2013), and this could generate more clear and monotonic relationships of increasing facilitation with environmental stress than those found for taxonomic or phylogenetic diversity. Hence, it is likely that strong differences arise in the relationships between the effects of plant–plant interactions on biodiversity across environmental gradients depending on the biodiversity facets on which we focus. Given that these different

facets of biodiversity interact in driving ecosystem functioning (Le Bagousse-Pinguet, et al., 2019) and that they show contrasting responses to the presence of nurse plants across environmental gradients (e.g., Vega-Alvarez et al., 2019), this could explain, in part, the conflicting results sometimes reported regarding associations between facilitation and ecosystem functioning (Maestre et al., 2010; Wright et al., 2017, 2021).

Here, we re-analysed a large dataset of species co-occurrences together with new data to assess plant–plant interactions in alpine and dryland sites, where facilitation is a major driver of community assembly (Callaway, 2007). Although missing important alpine (e.g., Alps, Scandes and Rocky mountains) and dryland locations (e.g., sub-Saharan Africa and Asia), our database includes sites covering a large variety of environmental conditions and plant compositions and should therefore be representative of plant biodiversity responses to facilitation across environmental gradients in harsh environments. We obtained information on functional trait values and phylogenetic relationships for the most common species and addressed the following hypotheses: (1) facilitation consistently enhances taxonomic, functional and phylogenetic diversity in alpine and dryland environments and (2) facilitation–diversity relationships across environmental gradients differ depending on the biodiversity facet, the biome and the environmental conditions, showing significant relationships for taxonomic diversity and more monotonic and positive responses to environmental stress for functional and phylogenetic diversity.

2 | MATERIALS AND METHODS

2.1 | Study area and data collection

We used an existing dataset complemented by an additional field study (Soliveres & Maestre, 2014; Soliveres et al., 2014; Supporting Information Table S1). Our data come from community-level studies, in which plant–plant interactions were inferred from co-occurrence analyses and which were conducted in alpine and dryland ecosystems, where a large proportion of the studies focusing on plant–plant interactions are developed (Callaway, 2007). Therefore, data were collected from reported empirical data on the dominant(s) nurse species and all their neighbours (i.e., paired microsites of nurse/open) with the same methodology in drylands and alpine studies (Soliveres & Maestre, 2014). We found 15 study cases, including 28 and 50 sites located in alpine and dryland areas, respectively. Alpine sites were in five countries (Chile, Ecuador, India, Spain and USA), whereas dryland sites were in eight countries (Australia, Ecuador, Iran, Morocco, Palestine, Spain, Tunisia and Venezuela) (see details in Supporting Information Table S1). From all these sites, we obtained comparable data on elevation and 19 bioclimatic variables from the WorldClim dataset (http://www.worldclim.org; Hijmans et al., 2005) at a 30″ resolution. The use of WorldClim provided us with a standardized and common climatic dataset for all our sites, while accurately reflecting

local climatic conditions measured *in situ* at several of the study locations (correlations between WorldClim and local climatic data > .8; for details, see Soliveres & Maestre, 2014). These sites varied widely in their vegetation and climatic conditions, with elevations ranging from 0 to 6,000 m a.s.l., average annual precipitation from 76 to 1,300 mm and mean annual temperature from −10.5 to 28.4°C. We included nurse species with different life-forms, such as trees, shrubs and grass tussocks. For each site, we used the number of individuals found for plant species in the open interspaces and beneath nurse microsites (i.e., two microsites were located in each site) as the observed values. Open interspaces refer to places beyond the influence of the canopies of nurses, as opposed to nurse microsites, which are those beneath nurse canopies. We obtained 2,685 pairwise combinations from these 15 study cases, from which we selected only those species occurring in at least four sites in the dataset (45 species accounting for 320 occurrences in total) for further analyses. This ensured that we covered enough range in environmental conditions to be able to disentangle nurse–environment interactions in determining diversity, while minimizing potential confounding effects of strong changes in species composition in these responses. In any case, the diversity metrics reported (please see 2.4 section in material and methods) are abundance weighted, which should minimize the effect of ignoring the least abundant species in our selection of pairwise interactions. Finally, functional trait information was not available for the rarest species in most of our study sites, which prevented us from including those species in our analyses.

Inferring plant–plant interactions from co-occurrence data can have some issues, widely recognized in the literature (e.g., Blanchet et al., 2020; Delalandre & Montesinos-Navarro, 2018). However, given that the sampling procedure across all sites was consistent, these issues should not bias facilitation–environment relationships, which is what we are focusing on here. Furthermore, and although with many exceptions, species co-occurrence can indicate net plant–plant interaction outcomes (Tirado & Pugnaire, 2003), and this is particularly true for abundant species (Rajala et al., 2019), such as the ones we considered in our analyses. Finally, nurse species could select more favorable microsites to establish in the first place, which could overestimate their facilitatory effects later on. However, nurse plants improve soil and microclimatic conditions as they age, therefore contributing to the improved microhabitats beneath their canopies beyond any initial effect of establishing in more benign microsites (e.g., Navarro-Cano et al., 2015; Pugnaire et al., 1996). Thus, by sampling beyond (relatively) large individuals of the nurse species, we should be including this nurse-mediated microclimatic improvement.

2.2 | Functional trait information

Plant functional traits generally influence ecosystem properties via their effects on plant growth, tissue quality and resource use. These effects can depend on environmental conditions and

biotic interactions (Lavorel, 2013; Lienin & Kleyer, 2012; Meng et al., 2015). Many studies have suggested that a robust image of the functional profile of a species can be obtained by considering traits related to resource acquisition, resource limitation and reproductive investment (Douma et al., 2012; Drenovsky et al., 2012; Ostertag et al., 2014; Sonnier et al., 2012). Leaf dry matter content (LDMC), specific leaf area (SLA), leaf nitrogen, phosphorous and carbon content and C/N ratio are related to leaf structural properties, fast to slow strategies and leaf quality, which affect growth rate and litter quality (Cortez et al., 2009; DeChaine et al., 2014; Kazakou et al., 2006). Plant height is strongly related to the ability of plants to compete for light, growth rate and demographic features, such as longevity and time to reproduction (Cornelissen et al., 2003; Moles et al., 2009). Seed mass is related to dispersal, longevity and survival (Ostertag et al., 2014). Leaf fresh matter content (LFMC) is an important trait, especially in species whose leaf shape is narrow, where it might be a better surrogate of leaf photosynthesis and respiration than leaf dry mass (Huang et al., 2019). Therefore, we obtained information on these 10 plant functional traits (plant height, LFMC, LDMC, seed mass, leaf carbon content, leaf nitrogen content, leaf phosphorus content, leaf thickness, SLA and C:N) for plant species occurring in the alpine and dryland communities, either from field measurements, for c. 10% of plant species, or from publicly available trait datasets [BIEN package in R (Maitner et al., 2018), TRY (Kattge et al., 2011), LEDA (Kleyer et al., 2008) and TR8 (Bocci, 2015)]. When multiple measurements per species were available in these databases, we averaged observations to create a species mean trait value. For some plant species, we used genus-level means when either species-level data were not available or plants were identified only to genus level (Lamanna et al., 2014) (for details, see Supporting Information Table S2.

2.3 | Phylogenetic information

We obtained a phylogeny of species based on the most up-to-date megaphylogeny for seed plants (Smith & Brown, 2018), which comprises 79,881 taxa. We standardized the species names in our dataset according to The Plant List using the R package "Taxonstand" (Cayuela et al., 2012). We then used the R function V.PhyloMaker (Jin & Qian, 2019) to link the species names in our dataset with those in the megaphylogeny, and the scenario 3 approach (Qian & Jin, 2016) to add species to the phylogeny. Scenario 3 adds missing taxa (e.g., genus or species) to the phylogeny within the taxa with known branch lengths, in a similar way to the approach implemented in Phylomatic and BLADJ (Webb et al., 2008). We pruned our complete phylogeny to create two trees, which included either (1) only 30 (most abundant, occurring in at least four sites) plant species recorded in the alpine environments or (2) only 34 (most abundant) plant species recorded in the dryland communities in our dataset. These trees were then used as reference lists, from which phylogenetic diversity could be calculated for alpine and dryland communities in the dataset.

2.4 | Measures of taxonomic, functional and phylogenetic diversity

To measure the contribution of nurse plants to the different biodiversity facets, we considered communities with and without the presence of nurse plants (i.e., PN factor). In this regard, we considered communities including nurse plants as PN=YES (communities accounting for nurse and open interspaces) and PN=NO (communities with only open microsites). The PN=YES communities were created by randomly replacing 50% of the quadrats sampled in open microsites per site with the same amount of randomly selected quadrats sampled at the same site beneath nurse microsites. Although this does not consider the relative proportion of nurse/open microsites at each location, using this standard proportion allowed us to compare our results across the two different biomes and their environmental gradients. To measure taxonomic diversity, we used the first three Hill numbers (Chao et al., 2014) to estimate species richness ($q = 0$), the exponential of Shannon's entropy ($q = 1$; referring to Shannon diversity) and the inverse of Simpson's concentration ($q = 2$; referring to Simpson diversity) of alpine and dryland communities (Hsieh et al., 2016). The exponential of Shannon's entropy and the inverse of Simpson's concentration capture important facets of taxonomic diversity weighted by abundances of rare and dominant plant species in community, respectively (Chao et al., 2014). The calculation was based on the number of species, which is less affected by differences in total sampling effort than other methods (Chao & Jost, 2012). However, it must be noted that species richness is underestimated in our dataset, because we focused on only those species occurring in at least in four sites and, for the same reason, Shannon's and Simpson's indices could be overestimated, although all these metrics should remain comparable across sites. Given that $q = 2$ was highly correlated with the other Hill numbers ($\rho > 0.9$ in both alpine and dryland communities), this measure of taxonomic diversity was not considered further in our analyses.

To assess functional and phylogenetic diversity, we chose the mean pairwise distance (MPD) (Tucker et al., 2017; Webb et al., 2002) among the many metrics of functional and phylogenetic diversity, given that MPD is one of the most robust measures for computing the phylogenetic and functional relatedness between pairs of species belonging to a given group in each community (Webb et al., 2002) and, in the abundance-weighted case, is equivalent to Rao's Q and Hill numbers (Tucker et al., 2017). To produce a phylogenetic and functional index of diversity that is independent of species richness, we calculated the standardized effect sizes (SESs) of abundance-weighted mean pairwise distance for functional (FSES.mpd) and phylogenetic (PSES.mpd) diversity by comparing the observed community diversity with the null distribution of randomly assembled communities. We used the independent-swap algorithm to draw a null distribution based on 999 randomizations, which retains the species richness within each plot and the relative frequency of species occurrences, but changes species co-occurrences. SES values > 1.96 or < −1.96

indicate significant functional/phylogenetic overdispersion and clustering in the community, respectively (Webb et al., 2002). We calculated SES.mpd with the "ses.mpd" function in the R package picante (Kembel et al., 2010).

2.5 | Statistical analyses

The degree to which the studied traits of alpine and dryland species showed a phylogenetic signal was assessed by the *K*-statistic of Blomberg et al. (2003) to estimate the strength of phylogenetic conservatism for different traits of dryland and alpine communities using the "multiPhylosignal" function in R package picante. The *K*-statistic was compared with randomized *K* values, and significant *p*-values indicate non-random correspondences between traits and phylogeny. Values of *K* higher than one indicate that traits are more conserved than expected by a Brownian motion evolutionary model (Swenson, 2014). Values lower than one indicate that traits are less conserved along the phylogeny than expected according to this model. In addition, we analysed the relationships between the different facets of biodiversity by conducting Spearman's rank correlations between our community-level biodiversity metrics (q_0, q_1, FSES.mpd and PSES.mpd). We considered the influence of the presence of nurse plants (i.e., PN factor) in these relationships by performing them separately for PN=NO and PN=YES communities.

Some of the environmental predictors were highly correlated with each other and could induce multicollinearity in our models. To avoid this, environmental variables with |r| > 0.7 were considered highly correlated (Wheeler & Tiefelsdorf, 2005), and one of the variables was removed from our dataset before performing any further analyses to avoid multicollinearity among environmental variables. To select among pairs of highly correlated variables, we favoured those more plausibly related to macroclimatic parameters known to determine the plant species distribution and plant–plant interactions in alpine and drylands (e.g., Callaway et al., 2002; Cavieres et al., 2013; Vallejo et al., 2012; Xiao et al., 2019). Furthermore, we analysed multicollinearity amongst the remaining variables using variance inflation factors (VIFs) [function *vif()* in the package "car" (Fox &Weisberg, 2011], and variables with VIF scores > 10 were considered to be highly collinear and removed from our list of predictors. For alpine communities, five variables [elevation, maximum temperature of warmest quarter (MTWaQ), precipitation of warmest quarter (PWaQ), precipitation seasonality (PS) and maximum temperature of wettest quarter (MTWeQ)] were selected and used in subsequent analyses. They are related to environmental conditions during the growing season in alpine environments (MTWaQ, PWaQ and MTWeQ) and also to the general harshness, length of the growing season and general climatic unpredictability of the environment (elevation and PS). They have been identified previously as important determinants of plant–plant interactions in these environments (e.g., Callaway et al., 2002; Cavieres et al., 2013; Körner & Hiltbrunner, 2018). Annual precipitation (PP), elevation, mean diurnal ranges of temperature (MDR), maximum temperature during the coldest quarter (MTCQ), precipitation during the coldest quarter (PDQ), precipitation during the warmest quarter (PWaQ) and precipitation seasonality (PS) were selected as non-correlated variables for dryland communities. These climatic variables reflect the general harshness in dryland environments (PP), water availability during the driest period, a major bottleneck of seedling recruitment in drylands (PDQ), and temperature and other environmental oscillations that could cause additional physiological stress (MDR, MTCQ, TS, elevation and PS). Most of these climatic variables have been identified previously as major drivers of plant distributions and plant–plant interactions in drylands (e.g., Soliveres & Maestre, 2014; Whitford, 2002; Xiao et al., 2019).

Hence, we analysed the response of taxonomic, functional and phylogenetic diversity (using separate analyses for each) relative to the presence/absence of nurse plants in communities and environmental factors described above using multi-model inference based on information theory (Burnham & Anderson, 2004) using the function "dredge" provided in the "MuMIn" R package (Barton, 2013). From all possible models, we kept only those with ΔAIC (difference in AIC between a focal model and the model with the lowest AIC) < 2, which included elevation and PWaQ in alpine environments, and MDR and PWaQ in drylands (for details, see Supporting Information Table S3).

When plotting the data, nonlinear trends between the different facets of biodiversity and climatic predictors emerged. Thus, we also included quadratic terms for these climatic predictors in our models. Then, we compared models with and without the quadratic term, using second-order Akaike information criteria (AIC) and R^2_{adj} values in both biomes (for details, see Supporting Information Table S4). Finally, the best models were plotted, and their marginal R^2 values were obtained using the function "r.squaredGLMM" provided in the package "MuMIn" (Barton, 2013). Marginal R^2 is the proportion of variance explained solely by our fixed factors (the climatic variables and the presence of nurse plants).

To examine the relative importance of environment and the presence of nurse plants in explaining variation in each diversity index, we performed variation partitioning based on partial linear regression using the "varpart" function (Oksanen et al., 2016). The total percentage of variation explained was divided into a unique and shared contribution for two sets of predictors: (1) environment (i.e., elevation and PWaQ in alpine communities, and MDR and PWaQ in drylands); and (2) PN.

3 | RESULTS

3.1 | Relationships between facets of biodiversity

We found a significant phylogenetic conservatism for plant height and LDMC in both alpine and dryland species. In addition, other resource-use traits were phylogenetically conserved in alpine (LFMC and leaf thickness) or dryland (leaf C, N, P and C:N ratio, and SLA) communities. Generally, phylogenetic conservatism was

much higher in dryland species than in alpine ones, with 8 of 10 traits showing significant conservatism in drylands, versus 4 of 10 in alpine plants (Table 1). According to this, our metrics of functional and phylogenetic diversity exhibited strong and positive correlations with each other ($\rho > 0.68$) in drylands, but this relationship was much weaker in alpine communities (Figure 1).

Our different biodiversity indices showed contrasting degrees of correlation depending on the biome studied and the presence of nurse plants. In alpine environments, all biodiversity metrics (except phylogenetic vs. functional diversity) exhibited strong and positive correlations, and these relationships did not differ substantially when considering the presence of nurse plants. However, in dryland communities the different facets of biodiversity showed weaker correlations (except phylogenetic vs. functional diversity, as stated above), and the strength of correlations between functional and taxonomic diversity decreased when including the presence of nurse plants (Figure 1).

3.2 | Impacts of plant–plant interactions and environmental factors on biodiversity

All biodiversity facets responded significantly to environmental conditions and the presence of nurse plants in both alpine and dryland environments (Figure 2). A common pattern across all biodiversity facets and biomes was that biodiversity showed linear relationships

TABLE 1 Phylogenetic signal for the functional traits in alpine and dryland plants (Blomberg's *K* for individual trait levels)

| All functional traits | Blomberg's *K* | | | |
| | Alpine | | Dryland | |
	K	*p*-value	*K*	*p*-value
Seed mass	0.37	.33 ns	0.48	.19 ns
Plant height	**0.95**	**.02***	**0.63**	**.01***
Specific leaf area (SLA)	0.08	.62	0.38	.03*
Leaf fresh matter content (LFMC)	**0.091**	**.03***	0.27	.10 ns
Leaf dry matter content (LDMC)	**0.93**	**.04***	**0.68**	**.01***
Leaf carbon content	0.07	.77 ns	**0.41**	**.05***
Leaf nitrogen content	0.27	.11 ns	**0.92**	**.001****
Leaf phosphorus content	0.23	.10 ns	**0.94**	**.001****
Leaf C:N ratio	0.02	.62 ns	**0.82**	**.005****
Leaf thickness	**0.55**	**.03***	**0.63**	**.001****

Note: Significant results are shown in bold (**p* < .05; ***p* < .01; ns: these traits do not show phylogenetic conservatism).

with climate when considering only open interspaces (Figure 2, PN=NO), whereas these biodiversity patterns became nonlinear when including the presence of nurse plants (Figure 2, PN=YES; for further details, see Supporting Information Table S4). Nurse plants enhanced taxonomic (q_0 and q_1), functional (FSES.mpd) and phylogenetic (PSES.mpd) diversity in alpine environments, mainly in moderate environments (at an elevation of *c*. 4,000 m a.s.l.), with lower diversity in open + nurse versus open-only communities across the remaining gradient [particularly for taxonomic (q_0 and q_1) and functional (FSES.mpd) diversity; Figure 2a]. Biodiversity patterns in drylands and alpine environments changed in a similar manner across climatic gradients when including nurse plants (i.e., in open + nurse communities) compared with their open interspaces (Figure 2b). However, stronger increases for both functional and phylogenetic diversity were found in drylands than in alpine environments (Figure 2b, marginal R^2_{adj} for FSES.mpd and PSES.mpd in alpine and dryland environments), whereas taxonomic diversity showed a stronger response to nurse plants in the alpine environments. Increases in plant biodiversity facets beneath nurse plants peaked in moderate environments, with a reduction in biodiversity values at both ends of the environmental gradients.

The amount of variance explained for all facets of diversity increased when considering the presence of nurse plants in both biomes (Figure 3). This was particularly true for taxonomic (q_0 and q_1) and phylogenetic (PSES.mpd) diversity in alpine communities (Figure 3) and for functional (FSES.mpd) and phylogenetic diversity indices in drylands (Figure 3). The presence of nurse species explained almost twice the amount of the variation of the latter biodiversity facets compared with environmental factors (Figure 3). In addition, the interactions between nurse presence and climate were also particularly strong predictors of variation in phylogenetic and functional diversity compared with pure climate fraction (Figure 3, drylands), suggesting that the effects of plant–plant interactions on these facets of biodiversity are relatively sensitive to environmental changes and are more predictable. This is consistent with the large R^2 registered for functional and phylogenetic diversity as a response to nurse presence across our environmental gradients, much larger than that found for taxonomic diversity (Figure 2).

4 | DISCUSSION

The influences of positive plant–plant interactions on diversity have received considerable attention, with reported increases in taxonomic (e.g., Cavieres et al., 2005), phylogenetic (e.g., Valiente-Banu et al., 2007) and functional (e.g., Butterfield & Briggs, 2011) diversity. However, we do not know whether the positive effects of nurse plants on these different facets of biodiversity are of similar magnitude (but see Vega-Alvarez et al., 2019) or whether they respond consistently across environmental gradients. Here, we have analysed a global co-occurrence database to address these research gaps and have found that the effects of nurse plants on facets of biodiversity are biome dependent, being particularly beneficial for taxonomic
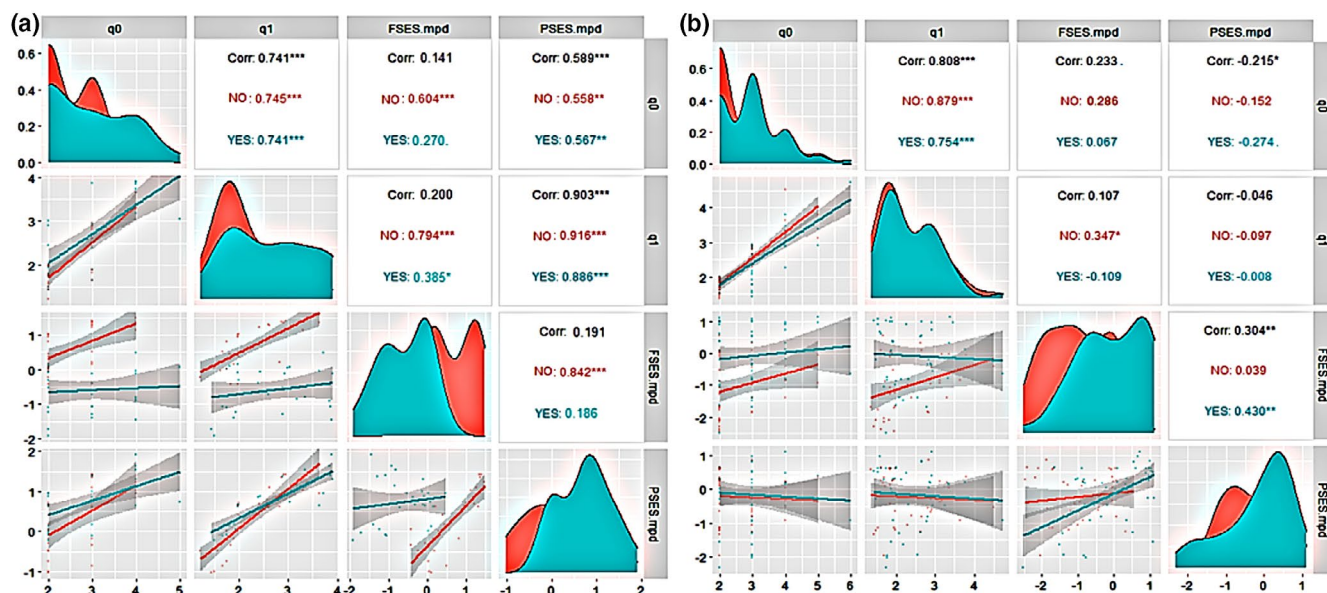
FIGURE 1 Correlations between different biodiversity indices in (a) alpine and (b) dryland communities. Spearman rank correlation coefficients are shown for communities when including presence of nurse plants (i.e., PN=YES, in blue) and communities when considering only open microsites (i.e., PN=NO, in red) in both the biomes. $^*p < .05$; $^{**}p < .01$; $^{***}p < .001$

and phylogenetic diversity in alpine environments, but for functional and phylogenetic diversity in drylands. The effects of nurse plants on these facets of biodiversity were as strong or stronger than those of environmental conditions, and triggered nonlinear responses of plant biodiversity to environmental gradients, showing their major importance as drivers of community assembly in harsh environments. It is important to notice that, by focusing solely on the most abundant species, our results could have underestimated the importance of the positive effects of nurse plants on biodiversity, because rare and subdominant species account for a major proportion of species richness and functional diversity in any community (Magurran & Henderson, 2003; Violle et al., 2017), and they are particularly favoured by the presence of nurse species (Soliveres et al., 2015).

4.1 | Nurse plants enhance all facets of biodiversity, albeit in a different manner in alpine and dryland communities

In addition to fostering recruitment of the rarest species, nurse plants modify understorey plant communities by shifting the relative abundances of the dominant ones (Berdugo et al., 2018; Vega-Álvarez et al., 2019). The latter effect would explain the relatively strong effects we found of nurse plants on biodiversity despite focusing solely on the most abundant species. Our results are also consistent with previous analyses using the complete species list, showing that the effect of nurse plants on the taxonomic richness of the beneficiary community are stronger and more predictable in alpine ecosystems than in dryland ecosystems (Soliveres & Maestre, 2014). Furthermore, our work goes beyond taxonomic richness and shows that nurses have a stronger influence on functional and phylogenetic

plant diversity with respect to environment in drylands than in alpine ecosystems. Why do these results depend on the plant diversity facet, if all of them are, to some degree, correlated? The fact that taxonomic and functional richness are less well correlated in drylands than in alpine environments, when including the nurse effect, suggests competitive exclusion between the beneficiary species (McIntire & Fajardo, 2013; Soliveres et al., 2014). This weak (or nonsignificant) correlation suggests that fewer, and more functionally divergent, species are able to coexist in intermediate levels of climatic conditions found beneath nurse canopies. This would explain not only the weaker effect of dryland nurse plants on taxonomic diversity (in comparison to alpine environments), but also their stronger and more consistent effect on functional diversity. If only fewer and more competitive (or functionally divergent) species can coexist beneath nurse plants, their presence will always contribute to the functional diversity of the entire community (Butterfield & Briggs, 2011; Schöb et al., 2012), regardless of the prevalent environmental conditions outside nurse canopies. Contrary to other communities growing in harsh environments (Tomas and Bjorkman, 2020), dryland communities have a large functional diversity despite the harsh conditions they withstand (Le Bagousse-Pinguet et al., 2017; Maestre et al., 2021). The strong effect we found of dryland nurse plants on functional diversity could explain, in part, the "functional paradox", in which dryland communities have a much larger functional diversity than one would expect (Maestre et al., 2021). The strong competition between beneficiary species could be less prevalent under the tight cushion shape of many alpine nurse species, or simply because of the direct impacts of low temperatures in the recruitment and survival of beneficiary species. Either tight cushions or limiting environments could foster a larger spatial separation in between beneficiary species (lower species density within than outside cushion plants;
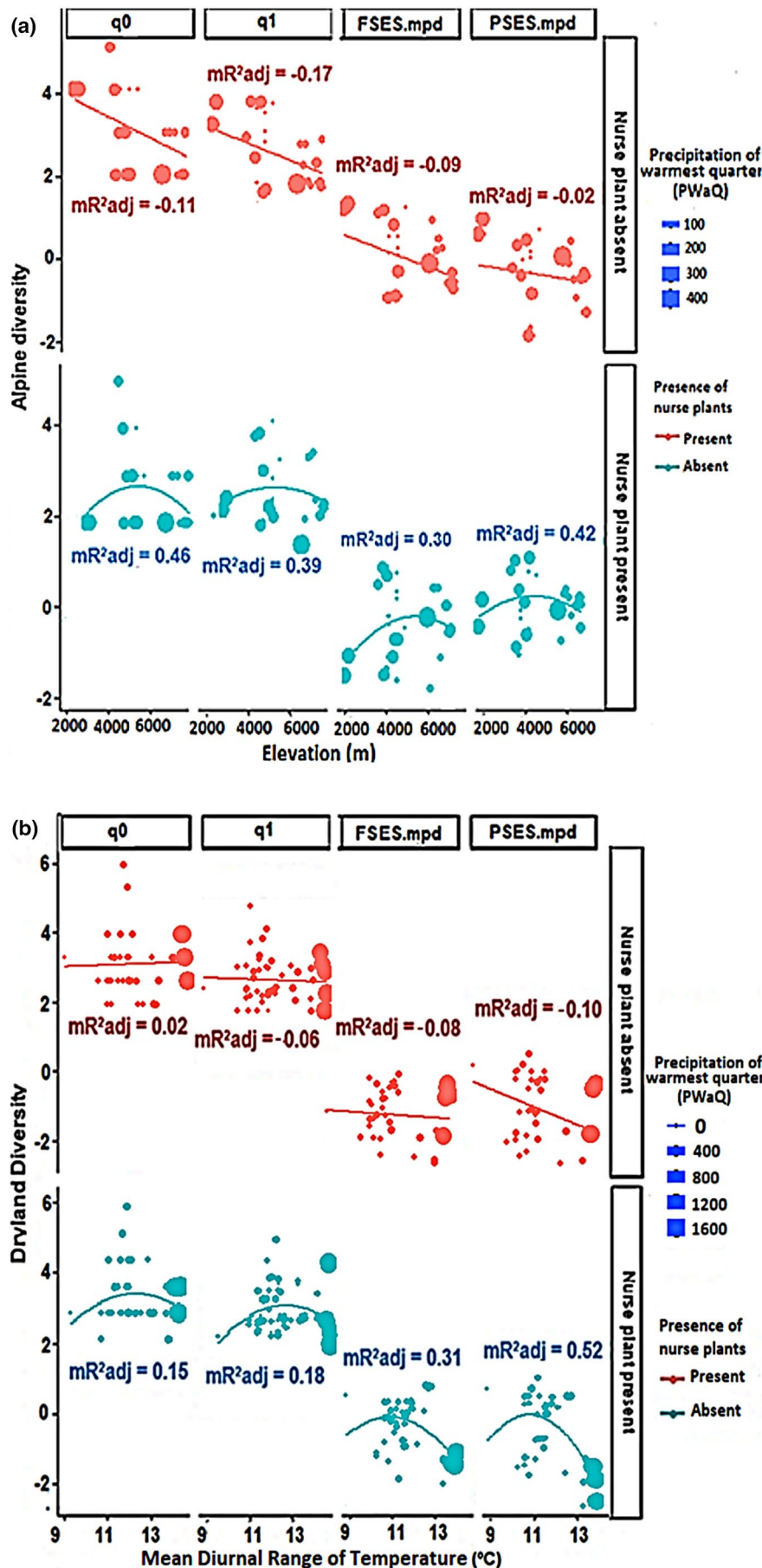
FIGURE 2 Relationships between taxonomic, functional and phylogenetic diversity relative to environmental factors and presence of nurse plants in (a) alpine and (b) dryland communities. From left to right, panels show results on taxonomic diversity (q_0 and q_1), functional diversity (FSES.mpd) and phylogenetic diversity (PSES.mpd) within communities with and without the presence of nurse plants across the studied gradients [i.e., elevation and mean diurnal range of temperature (MDR)] in alpine and dryland communities. Circles of different sizes show variation in the second most important climatic driver of plant diversity, which was precipitation of the warmest quarter (PWaQ) in both alpine and dryland communities. The adjusted R^2 explained by the fixed factors in our statistical models (marginal adjusted R^2, mR^2_{adj}) is shown in each case
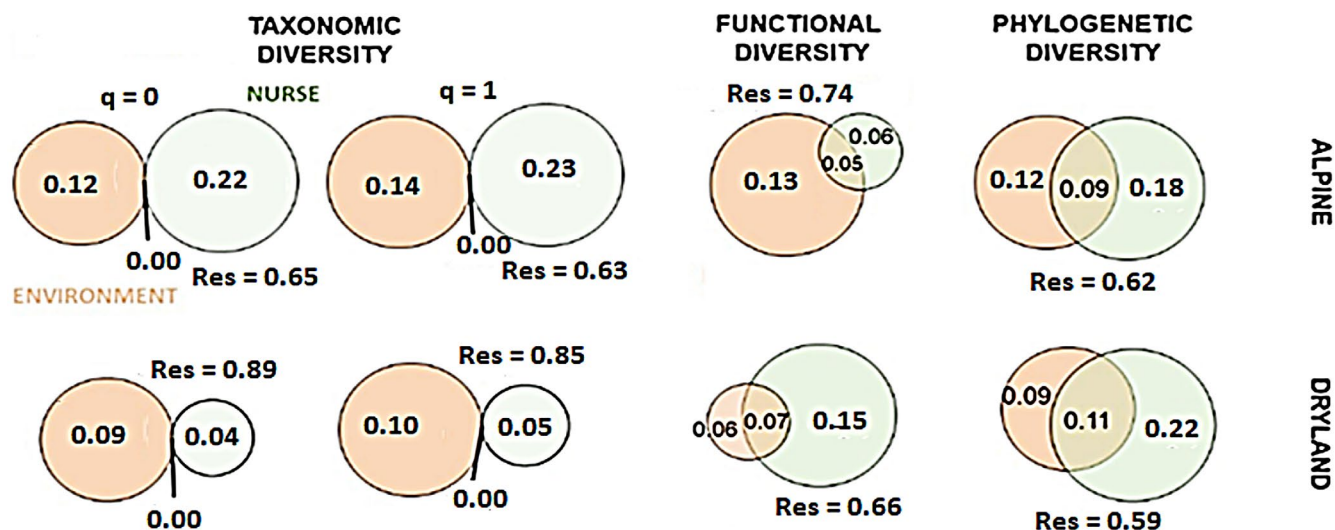
FIGURE 3 The relative contribution of the environment [in pink; i.e., elevation + precipitation of warmest quarter (PWaQ) for alpine communities; mean diurnal range of temperature (MDR) + precipitation of warmest quarter (PWaQ) for drylands] and presence of nurse plants (in blue) to taxonomic (q_0 and q_1 indices), functional (FSES.mpd) and phylogenetic (PSES.mpd) diversity in alpine (up) and dryland (down) communities. Values represent the adjusted R^2 values

Cavieres et al., 2016), avoiding opportunities for strong competition in between them. In this regard, cushion plants might allow more complex interaction networks within their canopies, which could enhance coexistence without the need for strong differences in traits between interacting species (Losapio et al., 2021). This could explain the stronger effect of alpine nurses on taxonomic but not functional diversity, suggesting that facilitation mechanisms, or else interaction networks between beneficiary plants, could be fundamentally different between alpine and dryland environments, rendering strong differences in how nurse plants affect different biodiversity facets. However, it is also possible that the weaker effect of nurse plants on functional diversity in alpine environments, compared with taxonomic and phylogenetic diversity, is related to the very limited trait information available for our alpine species (many extrapolated from genus-level means, which can include species with very diverse and different trait values). Thus, our results regarding the effects of plant–plant interactions on the functional diversity of alpine communities should be considered with caution and interpreted more as a working hypothesis to be evaluated with a more complete and larger database in the future.

The larger amount of variance explained for phylogenetic diversity by nurse plants in dryland than in alpine communities was somewhat expected, although positive effects of alpine nurse plants on phylogenetic diversity are also commonplace (e.g., Butterfield et al., 2013). Dryland species show a strong phylogenetic conservatism in their regeneration niches, related to those lineages that evolved during the wetter conditions of the Tertiary versus those that emerged during the drier Quaternary period (Valiente-Banuet et al., 2007). This leaves a strong fingerprint on current phylogenetic patterns and would explain the stronger effects of nurse plants on this facet of biodiversity in drylands than in alpine environments (see variance partitioning analyses in Figure 3), with the latter lacking

such a strong phylogenetic fingerprint. However, the effect of nurse plants on the phylogenetic diversity of alpine communities was only slightly weaker, and indeed more positive (see SES in Figure 2) than that found in drylands. This could be explained, in part, by: (1) the direct effect of the improved microenvironments beneath nurse plants, known to dampen reductions of phylogenetic diversity in unproductive conditions in alpine communities (Butterfield et al., 2013), whereas the response to environmental productivity is less consistent in drylands (García-Camacho et al., 2017; Soliveres et al., 2012); or (2) the strong facilitatory effect of alpine nurses on species richness, which could, via a sampling effect, enhance phylogenetic diversity (these were strongly correlated; Figure 1). Regardless of the underlying mechanisms, our results clearly show that effects on phylogenetic diversity are the strongest effects of nurse plants of all the biodiversity facets we studied, but also the most dependent on climate, judging by the large intersections between nurse and environmental effects on this facet (Figure 3).

4.2 | Nurse plants trigger hump-shaped relationships of plant biodiversity across environmental gradients

The responses of plant–plant interactions to environmental gradients offer conflicting results, with positive, neutral or hump-shaped relationships found across environmental gradients (reviewed by Michalet et al., 2014; Soliveres et al., 2015). Most of these previous studies have focused on the effect of plant–plant interactions on species richness, and to a less extent on other individual facets of plant diversity (but see Butterfield et al., 2013; Pistón et al., 2016; Schöb et al., 2012; Vega-Álvarez et al., 2019). By looking simultaneously at three major plant biodiversity facets (taxonomic, functional

and phylogenetic) across a wide range of environments and two contrasting biomes, we found that positive effects of nurse plants on understorey plant diversity generally peaked in moderate environmental conditions (e.g., at a mean annual temperature of *c.* 5°C in alpine environments; Figure 2). This provides empirical support for the hump-shaped model (e.g., Maestre & Cortina, 2004; Michalet et al., 2006), in which effects of facilitative interactions on the dominant species peak in moderately harsh environments, collapsing at the more severe end of environmental gradients and perhaps being outweighed by competition at the more productive end (i.e., less harsh environments) (also see Berdugo et al., 2018; Vega-Álvarez et al., 2019). This suggests that nurse plants can inhibit the loss of plant biodiversity when stress increases (Brooker et al., 2006; Butterfield et al., 2013), but only up to certain levels of harshness. Although these patterns hold true for effects of nurse plants on dominant beneficiary species, they do not necessarily follow for subordinate species, which can benefit through different mechanisms, and for which the response to nurse plants follows less predictable changes across environmental gradients (e.g., Soliveres & Maestre, 2014). Analysing collectively the response to nurse plants of the diversity of common and rare species offers great potential to link plant–plant interactions to ecosystem functioning, because these multiple plant biodiversity facets have contrasting effects on functioning (Craven et al., 2018; Le Bagousse-Pinguet, et al., 2019; Mahaut et al., 2019) and seemingly hold contrasting responses to nurse plants too.

A substantial body of work has addressed the importance of plant–plant interactions across environmental gradients (i.e., change in the sign, strength or importance of plant–plant interactions in response to environmental changes). However, there is still little quantitative evidence of the relative importance of environmental conditions versus plant–plant interactions as drivers of plant biodiversity, with most studies either reporting changes in the sign, strength or importance of plant–plant interactions across environmental gradients or reporting the effects of plant–plant interactions on biodiversity in a specific location (but see Cavieres et al., 2013). We found that the relative importance of plant–plant interactions versus environmental conditions varies greatly depending on the biodiversity facet and the biome on which we focus. Consistent with recent reports, plant–plant interactions were of lower importance than environmental conditions in defining taxonomic richness in drylands (see Maestre et al., 2021; Xie et al., 2021), but they were as important or more important than the environment in defining alpine taxonomic diversity. These results are somewhat at odds with a previous global analysis that found a greater importance of the environment than plant–plant interactions on alpine taxonomic diversity (Cavieres et al., 2013). This could be explained by our focus on dominant beneficiary species, leaving out the rarest species that could be more sensitive to such environmental conditions. In addition, our alpine database was limited in geographical coverage, and it was restricted mostly to mountains at lower latitudes. This could have led to an underestimation of the relative importance of the environment in our alpine dataset. Notwithstanding the disagreements with

previous reports, our results show that nurse plants can effectively buffer the impacts of climate change on plant taxonomic diversity in alpine environments (Anthelme et al., 2014), but might not suffice to buffer the impacts of climate change on the species richness of drylands.

Interestingly, the relative importance of plant–plant interactions versus the environment in determining plant biodiversity increased drastically when looking at functional diversity and, especially, at phylogenetic diversity (Figure 3). Nurse plants were the strongest predictors of plant phylogenetic diversity in both alpine and dryland communities, suggesting that the "safety net" effect (*sensu* Butterfield et al., 2013; Cavieres et al., 2013) of plant–plant interactions in buffering impacts of climate change on plant biodiversity might be particularly important for this facet of biodiversity, and this also extended to functional diversity in drylands. Contrary to taxonomic richness, the interactions between nurse presence and climate were also strong predictors of the variation in phylogenetic and functional diversity in dryland environments (Figure 3). This suggests that the effects of plant–plant interactions on these facets of biodiversity are most sensitive to environmental changes and, to some degree, more predictable (Thuiller et al., 2014). This is consistent with the larger R^2 registered for functional and phylogenetic diversity than for their taxonomic counterparts (Figure 2). Although the debate on how plant–plant interactions change across environmental gradients has focused mostly on their effects on taxonomic diversity, we argue that perhaps more consistent outcomes could be obtained if focusing this debate on the functional and phylogenetic facets of plant diversity. These biodiversity facets are of major importance for ecosystem functioning (Le Bagousse-Pinguet, et al., 2019) and could perhaps provide better mechanistic explanations of the role of plant–plant interactions in community assembly across contrasting environments.

4.3 | Conclusion

Nurse plants generally enhanced taxonomic and phylogenetic diversity in alpine communities and enhanced functional and phylogenetic diversity in dryland communities across environmental gradients. These effects peaked in moderate stress conditions, inducing nonlinear changes of the three plant biodiversity facets across environmental gradients. Assuming that ongoing climate change will exacerbate environmental stress in many alpine and dryland communities world-wide, our results suggest that nurse plants can protect plant biodiversity from the impacts of climate change on these communities, but only in places that are currently undergoing low to moderate environmental stress, because the positive effect of nurse plants on biodiversity is likely to collapse from moderate to high environmental harshness. Our study helps to improve our understanding of the effects of plant–plant interactions on plant biodiversity in severe ecosystems and how these effects will be likely to change with ongoing climate change.

CONFLICT OF INTERESTS

The authors declare that they have no conflict of interests.

AUTHOR CONTRIBUTIONS

M.B., S.S. and M.F. provided the data; H.E. and S.S. designed the study; data analyses were done by M.B.; the paper was written by M.B., assisted by S.S.; and all authors contributed substantially to the subsequent drafts.

DATA AVAILABILITY STATEMENT

All data supporting this study are available at: https://datadryad.org/stash/dataset/doi:10.5061/dryad.70rxwdbzr

ORCID

Maral Bashirzadeh https://orcid.org/0000-0001-6213-1020

REFERENCES

Anthelme, F., Cavieres, L. A., & Dangles, O. (2014). Facilitation among plants in alpine environments in the face of climate change. *Frontiers in Plant Science*, 5, 387. https://doi.org/10.3389/fpls.2014.00387

Barton, K. (2013). Package 'MuMIn'. Model Selection and Model Averaging Based on Information Criteria. R package version 1.15.11. http://CRAN.R-project.org/package=MuMIn

Berdugo, M., Maestre, F. T., Kefi, S., Gross, N., Le Bagousse-Pinguet, Y., & Soliveres, S. (2018). Aridity preferences alter the relative importance of abiotic and biotic drivers on plant species abundance in global drylands. *Journal of Ecology*, 107(1), 190–202.

Bertness, M. D., & Callaway, R. (1994). Positive interactions in communities. *Trends in Ecology & Evolution*, 9(5), 191–193. https://doi.org/10.1016/0169-5347(94)90088-4

Blanchet, F. G., Cazelles, K., & Gravel, D. (2020). Co-occurrence is not evidence of ecological interactions. *Ecology Letters*, 23(7), 1050–1063. https://doi.org/10.1111/ele.13525

Blomberg, S. P., Garland, T. Jr, & Ives, A. R. (2003). Testing for phylogenetic signal in comparative data: Behavioral traits are more labile. *Evolution*, 57(4), 717–745. https://doi.org/10.1111/j.0014-3820.2003.tb00285.x

Bocci, G. (2015). TR8: An R package for easily retrieving plant species traits. *Methods in Ecology and Evolution*, 6(3), 347–450. https://doi.org/10.1111/2041-210X.12327

Brooker, R. W., Maestre, F. T., Callaway, R. M., Lortie, C. L., Cavieres, L. A., Kunstler, G., Liancourt, P., Tielbörger, K., Travis, J. M. J., Anthelme, F., Armas, C., Coll, L., Corcket, E., Delzon, S., Forey, E., Kikvidze, Z., Olofsson, J., Pugnaire, F., Quiroz, C. L., ... Michalet, R. (2006). Facilitation in plant communities: The past, the present, and the future. *Journal of Ecology*, 96(1), 18–34.

Burnham, K. P., & Anderson, D. R. (2004). Multimodel inference: Understanding AIC and BIC in model selection. *Sociological Methods and Research*, 33(2), 261–304. https://doi.org/10.1177/0049124104268644

Butterfield, B. J., & Briggs, J. M. (2011). Regeneration niche differentiates functional strategies of desert woody plant species. *Oecologia*, 165(2), 477–487. https://doi.org/10.1007/s00442-010-1741-y

Butterfield, B. J., & Callaway, R. M. (2013). A functional comparative approach to facilitation and its context dependence. *Functional Ecology*, 22(4), 907–917. https://doi.org/10.1111/1365-2435.12019

Butterfield, B. J., Cavieres, L. A., Callaway, R. M., Cook, B. J., Kikvidze, Z., Lortie, C. J., Michalet, R., Pugnaire, F. I., Schöb, C., Xiao, S., Zaitchek, B., Anthelme, F., Björk, R. G., Dickinson, K., Gavilán, R., Kanka, R., Maalouf, J.-P., Noroozi, J., Parajuli, R., ... Brooker, R. W. (2013). Alpine cushion plants inhibit the loss of phylogenetic diversity in severe environments. *Ecology Letters*, 16(4), 478–486. https://doi.org/10.1111/ele.12070

Cadotte, M., Albert, C. H., & Walker, S. C. (2013). The ecology of differences: Assessing community assembly with trait and evolutionary distances. *Ecology Letters*, 16(10), 1234–1244. https://doi.org/10.1111/ele.12161

Callaway, R. M. (2007). *Positive interactions and interdependence in plant communities*. Springer.

Callaway, R. M., Brooker, R. W., Choler, P., Kikvidze, Z., Lortie, C. J., Michalet, R., Paolini, L., Pugnaire, F. I., Newingham, B., Aschehoug, E. T., Armas, C., Kikodze, D., & Cook, B. J. (2002). Positive interactions among alpine plants increase with stress. *Nature*, 417(6891), 844–888. https://doi.org/10.1038/nature00812

Cavieres, L. A., Badano, E. I., Sierra-Almeria, A., Gomez-Gonzalez, S., & Molina-Montenegro, M. A. (2005). Positive interactions between alpine plant species and the nurse cushion plant *Laretia acaulis* do not increase with elevation in the Andes of central Chile. *New Phytologist*, 196(1), 59–69.

Cavieres, L. A., Brooker, R. W., Butterfield, B. J., Cook, B. J., Kikvidze, Z., Lortie, C. J., Michalet, R., Pugnaire, F. I., Schöb, C., Xiao, S., Anthelme, F., Björk, R. G., Dickinson, K. J. M., Cranston, B. H., Gavilán, R., Gutiérrez-Girón, A., Kanka, R., Maalouf, J.-P., Mark, A. F., ... Callaway, R. M. (2013). Facilitative plant interactions and climate simultaneously drive alpine plant diversity. *Ecology Letters*, 17(2), 193–202.

Cavieres, L. A., Hernandez-Fuentez, C., Sierra-Almeida, A., & Kikvidze, Z. (2016). Facilitation among plants as an insurance policy for diversity in Alpine communities. *Functional Ecology*, 30(1), 52–59. https://doi.org/10.1111/1365-2435.12545

Cayuela, L., Granzow-de la Cerda, Í., Albuquerque, F. S., & Golicher, D. J. (2012). taxonstand: An r package for species names standardization in vegetation databases. *Methods in Ecology and Evolution*, 3(6), 1078–1083.

Chao, A., Gotelli, N. J., Hsieh, T. C., Sander, E. L., Ma, K. H., Colwell, R. K., & Ellison, A. M. (2014). Rarefaction and extrapolation with Hill numbers: A framework for sampling and estimation in species diversity studies. *Ecological Monographs*, 84(1), 45–67. https://doi.org/10.1890/13-0133.1

Chao, A., & Jost, L. (2012). Coverage-based rarefaction and extrapolation: Standardizing samples by completeness rather than size. *Ecology*, 93(12), 2533–2547. https://doi.org/10.1890/11-1952.1

Cornelissen, J. H., Lavorel, S., Diaz, S., & Garnier, E. B. (2003). A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. *Australian Journal of Botany*, 51(4), 335–380.

Cortez, M. C., Silva, F., & Areal, N. (2009). Socially responsible investing in the global market: The performance of US and European funds. *International Journal of Finance & Economics*, 17(3), 1–37. https://doi.org/10.2139/ssrn.1342469

Craven, D., Eisenhauer, N., Pearse, W. D., Hautier, Y., Isbell, F., Roscher, C., Bahn, M., Beierkuhnlein, C., Bönisch, G., Buchmann, N., Byun, C., Catford, J. A., Cerabolini, B. E. L., Cornelissen, J. H. C., Craine, J. M., De Luca, E., Ebeling, A., Griffin, J. N., Hector, A., ... Manning, P. (2018). Multiple facets of biodiversity drive the diversity–stability relationship. *Nature Ecology and Evolution*, 2(10), 1579–2158. https://doi.org/10.1038/s41559-018-0647-7

DeChaine, E. G., Wendling, B. M., & Forester, B. R. (2014). Integrating environmental, molecular, and morphological data to unravel an

ice-age radiation of arctic-alpine *Campanula* in western North America. *Ecology and Evolution*, *4*(20), 3940–3959.

Delalandre, L., & Montesinos-Navarro, A. (2018). Can co-occurrence networks predict plant-plant interactions in a semi-arid gypsum community. *Perspectives in Plant Ecology, Evolution and Systematics*, *31*, 36–43. https://doi.org/10.1016/j.ppees.2018.01.001

Douma, J. C., Bardin, V., Bartholomeus, R. P., & Bodegom, P. M. (2012). Quantifying the functional responses of vegetation to drought and oxygen stress in temperate ecosystems. *Functional Ecology*, *26*(6), 1355–1365. https://doi.org/10.1111/j.1365-2435.2012.02054.x

Drenovsky, R. E., Grewell, B. J., Dantanio, C. M., & Funk, J. L. (2012). A functional trait perspective on plant invasion. *Annals of Botany*, *110*(1), 141–153.

Duarte, M., Verdú, M., Cavieres, L. A., & Bustamante, R. O. (2021). Plant–plant facilitation increases with reduced phylogenetic relatedness along an elevation gradient. *Oikos*, *130*(2), 248–259. https://doi.org/10.1111/oik.07680

Fox, J., & Weisberg, S. (2011). *An R companion to applied regression*. Sage.

García-Camacho, R., Metz, J., Tielborger, K., & Bilton, M. C. (2017). Phylogenetic structure of annual plant communities along an aridity gradient. Interacting effects of habitat filtering and shifting plant–plant interactions. *Israel Journal of Plant Science*, *64*(1), 122–134.

Gilbert, G. S., & Webb, C. O. (2007). Phylogenetic signal in plant pathogen–host range. *Proceedings of the National Academy of Sciences of the United States of America*, *104*(12), 4979–4983. https://doi.org/10.1073/pnas.0607968104

Greiner La Peyre, M. K., Grace, J. B., Hahn, E., & Mendelssohn, I. A. (2001). The importance of competition in regulating plant species abundance along a salinity gradient. *Ecology*, *82*(1), 62–69. https://doi.org/10.2307/2680086

Hijmans, R. J., Cameron, S. E., Parra, J. L., Jones, P. G., & Jarvis, A. (2005). Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology*, *25*(15), 1965–1978. https://doi.org/10.1002/joc.1276

Hsieh, T. C., Ma, K. H., Chao, A., & McInerny, G. (2016). iNEXT: An R package for rarefaction and extrapolation of species diversity (Hill numbers). *Methods in Ecology and Evolution*, *7*(12), 1451–1456.

Huang, W., Ratkowsky, D., Hui, C., Wang, P., Su, J., & Shi, P. (2019). Leaf fresh weight versus dry weight: Which is better for describing the scaling relationship between leaf biomass and leaf area for broad-leaved plants? *Forests*, *10*(3), 256. https://doi.org/10.3390/f10030256

Jin, Y., & Qian, H. (2019). V.PhyloMaker: An R package that can generate very large phylogenies for vascular plants. *Ecography*, *42*(8), 1353–1359. https://doi.org/10.1111/ecog.04434

Kattge, J., Díaz, S., Lavorel, S., Prentice, I. C., Leadley, P., Bönisch, G., Garnier, E., Westoby, M., Reich, P. B., Wright, I. J., Cornelissen, J. H. C., Violle, C., Harrison, S. P., Van Bodegom, P. M., Reichstein, M., Enquist, B. J., Soudzilovskaia, N. A., Ackerly, D. D., Anand, M., … Wirth, C. (2011). TRY – a global database of plant traits. *Global Change Biology*, *17*(9), 2905–2935. https://doi.org/10.1111/j.1365-2486.2011.02451.x

Kazakou, E., Vile, D., Shipley, B., Gallet, C., & Garnier, E. (2006). Co-variations in litter decomposition, leaf traits and plant growth in species from a Mediterranean old-field succession. *Functional Ecology*, *20*(1), 21–30. https://doi.org/10.1111/j.1365-2435.2006.01080.x

Kembel, S. W., Cowan, P. D., Helmus, M. R., Cornwell, W. K., Morlon, H., Ackerly, D. D., Blomberg, S. P., & Webb, C. O. (2010). Picante: R tools for integrating phylogenies and ecology. *Bioinformatics*, *26*(11), 1463–1464. https://doi.org/10.1093/bioinformatics/btq166

Kleyer, M., Bekker, R. M., Knevel, I. C., Bakker, J. P., Thompson, K., Sonnenschein, M., Poschlod, P., van Groenendael, J. M., Klimeš, L., Klimešová, J., Klotz, S., Rusch, G. M., Hermy, M., Adriaens, D., Boedeltje, G., Bossuyt, B., Dannemann, A., Endels, P., Götzenberger, L., … Peco, B. (2008). The LEDA Traitbase: A database of life-history

traits of the Northwest European flora. *Journal of Ecology*, *96*(6), 1266–1274. https://doi.org/10.1111/j.1365-2745.2008.01430.x

Korner, C., & Hiltbrunner, E. (2018). The 90 ways to describe plant temperature. *Perspectives in Plant Ecology Evolution and Systematics*, *30*, 16–21. https://doi.org/10.1016/j.ppees.2017.04.004

Lamanna, C., Blonder, B., Violle, C., Kraft, N. J. B., Sandel, B., Imova, I., Donoghue, J. C., Svenning, J.-C., McGill, B. J., Boyle, B., Buzzard, V., Dolins, S., Jorgensen, P. M., Marcuse-Kubitza, A., Morueta-Holme, N., Peet, R. K., Piel, W. H., Regetz, J., Schildhauer, M., … Enquist, B. J. (2014). Functional trait space and the latitudinal diversity gradient. *Proceedings of the National Academy of Sciences of the United States of America*, *111*(38), 13745–13750. https://doi.org/10.1073/pnas.1317722111

Lavorel, S. (2013). Plant functional effects on ecosystem services. *Journal of Ecology*, *101*(1), 4–8. https://doi.org/10.1111/1365-2745.12031

Le Bagousse-Pinguet, Y., Gross, N., Maestre, F. T., Maire, V., de Bello, F., Fonseca, C. R., Kattge, J., Valencia, E., Leps, J., & Liancourt, P. (2017). Testing the environmental filtering concept in global drylands. *Journal of Ecology*, *105*(4), 1058–1069.

Le Bagousse-Pinguet, Y., Liancourt, P., Götzenberger, L., de Bello, F., Altman, J., Brozova, V., Chlumska, Z., Dvorsky, M., Capkova, K., Kopecky, M., Rehakova, K., Riha, P., Leps, J., & Dolezal, J. (2018). A multi-scale approach reveals random phylogenetic patterns at the edge of vascular plant life. *Perspectives in Plant Ecology, Evolution and Systematics*, *30*, 22–30. https://doi.org/10.1016/j.ppees.2017.10.002

Le Bagousse-Pinguet, Y., Soliveres, S., Gross, N., Torices, R., Berdugo, M., & Maestre, F. T. (2019). Phylogenetic, functional, and taxonomic richness have both positive and negative effects on ecosystem multifunctionality. *Proceedings of the National Academy of Sciences of the United States of America*, *116*(17), 8419–8424. https://doi.org/10.1073/pnas.1815727116

Lienin, P., & Kleyer, M. (2012). Plant trait responses to the environment and effects on ecosystem properties. *Basic and Applied Ecology*, *13*(4), 301–311. https://doi.org/10.1016/j.baae.2012.05.002

Losapio, G., Schöb, C., Staniczenko, P. P. A., Carrara, F., Palamara, G. M., De Moraes, C. M., Mescher, M. C., Brooker, R. W., Butterfield, B. J., Callaway, R. M., Cavieres, L. A., Kikvidze, Z., Lortie, C. J., Michalet, R., Pugnaire, F. I., & Bascompte, J. (2021). Network motifs involving both competition and facilitation predict biodiversity in alpine plant communities. *Proceedings of the National Academy of Sciences of the United States of America*, *118*(6), e2005759118. https://doi.org/10.1073/pnas.2005759118

Madrigal-Gonzalez, J., Cano-Barbacil, C., Kigel, J., Ferrandis, P., & Luzuriaga, A. L. (2020). Nurse plants promote taxonomic and functional diversity in an arid Mediterranean annual plant community. *Journal of Vegetation Science*, *31*(4), 658–666. https://doi.org/10.1111/jvs.12876

Maestre, F. T., Benito, B. M., Berdugo, M. et al (2021). Biogeography global drylands. *New Phytologist*, *231*(2), 540–558.

Maestre, F. T., Bowker, M. A., Escolar, C., Puche, M. D., Soliveres, S., Maltez-Mouro, S., Garcia-Palacios, P., Castillo-Monroy, A. P., Martinez, I., & Escudero, A. (2010). Do biotic interactions modulate ecosystem functioning along stress gradients? Insights from semi-arid plant and biological soil crust communities. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *365*(1549), 2057–2070. https://doi.org/10.1098/rstb.2010.0016

Maestre, F. T., & Cortina, J. (2004). Do positive interactions increase with abiotic stress? A test from a semi-arid steppe. *Proceedings of the Royal Society B: Biological Sciences*, *271*, S331–S333.

Magurran, A. E., & Henderson, P. A. (2003). Explaining the excess of rare species in natural species abundance distributions. *Nature*, *422*(6933), 714–716. https://doi.org/10.1038/nature01547

Mahaut, L., Fort, F., Violle, C., & Freschet, G. T. (2019). Multiple facets of diversity effects on plant productivity: Species richness, functional

diversity, species identity and intraspecific competition. *Functional Ecology*, 34(1), 287–298. https://doi.org/10.1111/1365-2435.13473

Maitner, B. S., Boyle, B., Casler, N., Condit, R., Donoghue, J., II, Durán, S. M., Guaderrama, D., Hinchliff, C. E., Jørgensen, P. M., Kraft, N. J. B., McGill, B., Merow, C., Morueta-Holme, N., Peet, R. K., Sandel, B., Schildhauer, M., Smith, S. A., Svenning, J.-C., Thiers, B., ... Enquist, B. J. (2018). The BIEN R package: A tool to access the Botanical Information and Ecology Network (BIEN) database. *Methods in Ecology and Evolution*, 9(2), 373–379.

McIntire, E. J. C., & Fajardo, A. (2013). Facilitation as a ubiquitous driver of biodiversity. *New Phytologist*, 201(2), 403–416. https://doi.org/10.1111/nph.12478

Meng, X., Huang, Z., Di, J., Mu, D., Wang, Y., Zhao, X., Zhao, H., Zhu, W., Li, X., Kong, L., & Xing, L. (2015). Expression of Human epidermal growth factor receptor-2 in resected rectal cancer. *Medicine*, 94(47), 1–8. https://doi.org/10.1097/MD.0000000000002106

Michalet, R., Brooker, R. W., Cavieres, L. A., Kikvidze, Z., Lortie, C. J., Pugnaire, F. I., Valiente-Banuet, A., & Callaway, R. M. (2006). Do biotic interactions shape both sides of the humped-back model of species richness in plant communities? *Ecology Letters*, 9(7), 767–773. https://doi.org/10.1111/j.1461-0248.2006.00935.x

Michalet, R., Schöb, C., Lortie, C. J., Brooker, R. W., & Callaway, R. M. (2014). Partitioning net interactions among plants along altitudinal gradients to study community responses to climate change. *Functional Ecology*, 20(1), 75–86. https://doi.org/10.1111/1365-2435.12136

Moles, A. T., Warton, D. I., Warman, L., Swenson, N. G., Laffan, S. W., Zanne, A. E., Pitman, A., Hemmings, F. A., & Leishman, M. R. (2009). Global patterns in plant height. *Journal of Ecology*, 97(5), 923–932. https://doi.org/10.1111/j.1365-2745.2009.01526.x

Navarro-Cano, J. A., Verdú, M., Garcia, C., & Goberna, M. (2015). What nurse shrubs can do for barren soils: Rapid productivity shifts associated to a 40 year ontogenetic gradient. *Plant and Soil*, 388, 197–209.

Oksanen, J., Blanchet, F. G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P. R., O'Hara, R. B., Simpson, G. L., Solymos, P., Stevens, M. H. H., Szoecs, E., & Wagner, H. (2016). vegan: Community Ecology Package. R package version 2.4-1. https://CRAN.R-project.org/package=vegan

Ostertag, R., Inman-Narahari, F., Cordell, S., & Giardina, C. P. (2014). Forest structure in low-diversity tropical forests: A study of Hawaiian wet and dry forests. *PLoS One*, 9(8), e103268.

Pistón, N., Schöb, C., Armas, C., Prieto, I., & Pugnaire, F. I. (2016). Contribution of co-occurring shrub species to community richness and phylogenetic diversity along an environmental gradient. *Perspectives in Plant Ecology, Evolution and Systematics*, 19, 30–39. https://doi.org/10.1016/j.ppees.2016.02.002

Pugnaire, F. I., Haase, P., & Puigdefábregas, J. (1996). Facilitation between higher plant species in a semiarid environment. *Ecology*, 77(5), 1420–1426. https://doi.org/10.2307/2265539

Qian, H., & Jin, Y. (2016). An updated megaphylogeny of plants, a tool for generating plant phylogenies and an analysis of phylogenetic community structure. *Journal of Plant Ecology*, 9(2), 233–239. https://doi.org/10.1093/jpe/rtv047

Rajala, T., Olhede, S. C., & Murrell, D. J. (2019). When do we have the power to detect biological interactions 197 in spatial point patterns? *Journal of Ecology*, 107(2), 711–721.

Salazar, D., Jaramillo, M. A., & Marquis, R. J. (2016). Chemical similarity and local community assembly in the species rich tropical genus *Piper*. *Ecology*, 97(11), 3176–3183.

Schob, C., Armas, C., Guler, M., Prieto, I., & Pugnaire, F. I. (2013). Variability in functional traits mediates plant interactions along stress gradients. *Journal of Ecology*, 101(3), 753–762. https://doi.org/10.1111/1365-2745.12062

Schob, C., Butterfield, B. J., & Pugnaire, F. I. (2012). Foundation species influence trait-based community assembly. *New Phytologist*, 196(3), 824–834. https://doi.org/10.1111/j.1469-8137.2012.04306.x

Smith, S. A., & Brown, J. W. (2018). Constructing a broadly inclusive seed plant phylogeny. *American Journal of Botany*, 105(3), 302–314.

Soliveres, S., & Maestre, F. T. (2014). Plant–plant interactions, environmental gradients and plant diversity: A global synthesis of community-level studies. *Perspectives in Plant Ecology, Evolution and Systematics*, 16(4), 154–163. https://doi.org/10.1016/j.ppees.2014.04.001

Soliveres, S., Maestre, F. T., Bowker, M. A., Torices, R., Quero, J. L., García-Gómez, M., Cabrer, O., Cea, A. P., Coaguila, D., Eldridge, D. J., Espinosa, C. I., Hemmings, F., Monerris, J. J., Tighe, M., Delgado-Baquerizo, M., García-Palacios, C. E. P., Gozalo, B., Ochoa, V., Blones, J., ... Noumi, Z. (2014). Functional traits determine plant co-occurrence more than environment or evolutionary elatedness in global drylands. *Perspectives in Plant Ecology, Evolution and Systematics*, 16(4), 164–173.

Soliveres, S., Smit, C., & Maestre, F. T. (2015). Moving forward on facilitation research: Response to changing environments and effects on the diversity, functioning and evolution of plant communities. *Biological Reviews*, 90(1), 297–313. https://doi.org/10.1111/brv.12110

Soliveres, S., Torices, R., & Maestre, F. T. (2012). Environmental conditions and biotic interactions acting together promote phylogenetic randomness in semi-arid plant communities: New methods help to avoid misleading conclusions. *Journal of Vegetation Science*, 23(5), 822–836. https://doi.org/10.1111/j.1654-1103.2012.01410.x

Sonnier, G. P., McAlister, L., & Rutz, O. (2012). A Dynamic model of the effect of online communications on firm sales. *Marketing Science*, 30(4), 702–716. https://doi.org/10.1287/mksc.1110.0642

Swenson, N. G. (2014). *Functional and phylogenetic ecology in R*. Springer.

Thomas, H. J. D., Bjorkman, A. D., Myers-Smith, I. H., Elmendorf, S. C., Kattge, J., Diaz, S., Vellend, M., Blok, D., Cornelissen, J. H. C., Forbes, B. C., Henry, G. H. R., Hollister, R. D., Normand, S., Prevéy, J. S., Rixen, C., Schaepman-Strub, G., Wilmking, M., Wipf, S., Cornwell, W. K., ... de Vries, F. T. (2020). Global plant trait relationships extend to the climatic extremes of the tundra biome. *Nature*, 11(1), 1351. https://doi.org/10.1038/s41467-020-15014-4

Thuiller, W., Guéguen, M., Georges, D., Bonet, R., Chalmandrier, L., Garraud, L., Renaud, J., Roquet, C., Van Es, J., Zimmermann, N. E., & Lavergne, S. (2014). Are different facets of plant diversity well protected against climate and land cover changes? A test study in the French Alps. *Ecography*, 37(12), 1254–1266. https://doi.org/10.1111/ecog.00670

Tirado, R., & Pugnaire, F. I. (2003). Shrub spatial aggregation and consequences for reproductive success. *Oecologia*, 136(2), 296–301. https://doi.org/10.1007/s00442-003-1264-x

Tucker, C. M., Cadotte, M. W., Carvalho, S. B., Davies, T. J., Ferrier, S., Fritz, S. A., Grenyer, R., Helmus, M. R., Jin, L. S., Mooers, A. O., Pavoine, S., Purschke, O., Redding, D. W., Rosauer, D. F., Winter, M., & Mazel, F. (2017). A guide to phylogenetic metrics for conservation, community ecology and macroecology. *Biological Reviews*, 92(2), 698–715. https://doi.org/10.1111/brv.12252

Valiente-Banuet, A., Gally, R. S., Arizmendi, M. C., & Casas, A. (2007). Pollination biology of the hemiepiphytic cactus *Hylocereus undatus* in the Tehuacán Valley, Mexico. *Journal of Arid Environments*, 68(1), 1–8. https://doi.org/10.1016/j.jaridenv.2006.04.001

Valiente-Banuet, A., & Verdú, M. (2013). Plant facilitation and phylogenies. *Annual Review of Ecology, Evolution, and Systematics*, 44, 347–366.

Vallejo, V. R., Smanis, A., Chirino, E., Fuentes, D., Valdecantos, A., & Vilagrosa, V. (2012). Perspectives in dryland restoration: Approaches for climate change adaptation. *New Forests*, 43, 561–579.

Vega-Alvarez, J., Garcia-Rodriguez, J., & Cayuela, L. (2019). Facilitation beyond species richness. *Journal of Ecology*, 107(2), 722–734.

Violle, C., Thuiller, W., Mouquet, N., Munoz, F., Kraft, N. J. B., Cadotte, M. W., Livingstone, S. W., & Mouillot, D. (2017). Functional rarity:

The ecology of outliers. *Trends in Ecology & Evolution, 32,* 356–367. https://doi.org/10.1016/j.tree.2017.02.002

Webb, C. O., Ackerly, D. D., McPeek, M. A., & Donoghue, M. J. (2002). Phylogenies and community ecology. *Annual Review of Ecology and Systematics, 33*(1), 475–505. https://doi.org/10.1146/annurev.ecolsys.33.010802.150448

Webb, C., Ackerly, D. D., & Kembel, S. W. (2008). Phylocom: Software for the analysis of phylogenetic community structure and character evolution. *Bioinformatics, 24*(18), 2098–2100.

Wheeler, D. C., & Tiefelsdorf, M. (2005). Multicollinearity and correlation among local regression coefficients in geographically weighted regression. *Journal of Geographical Systems, 7*(2), 161–187. https://doi.org/10.1007/s10109-005-0155-6

Whitford, W. G. (2002). *Ecology of desert systems.* Academic Press.

Wright, A. J., Barry, K. E., Lortie, C. L., & Callaway, R. M. (2021). Biodiversity and ecosystem functioning: Have our experiments and indices been underestimating the role of facilitation? *Journal of Ecology, 109*(5), 1962–1968. https://doi.org/10.1111/1365-2745.13665

Wright, J. S., Fu, R., Worden, J. R., Chakraborty, S., Clinton, N. E., Risi, C., Sun, Y., & Yin, L. (2017). Rainforest-initiated wet season onset over the southern Amazon. *Proceedings of the National Academy of Sciences of the United States of America, 114*(32), 8481–8486. https://doi.org/10.1073/pnas.1621516114

Xiao, J., Eziz, A., Zhang, H., Wang, Z., Tang, Z., & Fang, J. (2019). Responses of four dominant dryland plant species to climate change in the Junggar Basin, northwest China. *Ecology and Evolution, 9*(23), 13596–13607. https://doi.org/10.1002/ece3.5817

Xie, H., Tang, Y., Yu, M., & Wang, G. G. (2021). The effects of afforestation tree species mixing on soil organic carbon stock, nutrients accumulation, and understory vegetation diversity on reclaimed coastal lands in Eastern China. *Global Ecology and Conservation, 26,* e01478. https://doi.org/10.1016/j.gecco.2021.e01478

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.