Global Ecology and Biogeography

WILEY

Global Ecology and Biogeography
A Journal of Macroecology

RESEARCH ARTICLE OPEN ACCESS

Plant Trait Matching Occurs in Facilitative Interactions Across Global Drylands

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Received: 26 May 2025 | **Accepted:** 10 November 2025

Handling Editor: Franziska Schrodt

Funding: This work was supported by the Ernest Oppenheimer Memorial Trust, 2023-2176. European Research Council, 647038. Fondo Europeo de Desarrollo Regional. South African Association of Botanists. King Abdullah University of Science and Technology.

Keywords: aridity | drylands | facilitation | functional traits | grazing | plant–plant interactions

ABSTRACT

Aim: Plant functional traits can influence interaction outcomes between nurse and target plants through a "functional trait match", which occurs when the traits of nurse plants ameliorate their environment, and target plants possess traits that allow them to benefit from this ameliorated environment. We investigated how the traits of putative nurse species affect interaction outcomes across global drylands and determined the functional match that promotes facilitation. We also investigated how grazing pressure and global climatic and edaphic gradients affected this trait match.
Location: Global drylands.
Time Period: 2016–2019.
Major Taxa Studied: Vascular plants.
Methods: We used a collaborative survey conducted across 29 sites from five continents, where we gathered in situ co-occurrences of dominant species ('nurses') and other vascular plant species, as well as their functional traits [plant height and leaf dry matter content (LDMC)]. Climate, edaphic variables and grazing pressure were measured in situ or extracted from databases. We used a model building approach to determine the effect of dominant plant traits on interaction outcomes, and how the functional trait match between nurse and target species is affected by environmental variables.
Results: Tall dominant plants with conservative leaves generally had a greater positive effect on species richness and cover beneath their canopies, but these effects were strongly modulated by grazing pressure and soil pH. Target plants that were significantly associated with dominant plants tended to be shorter, and have more acquisitive leaves than dominant plants, regardless

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https://doi.org/10.1111/geb.70158

of environmental conditions. However, the difference in height and LDMC between dominant plants and negatively associated target plants was strongly affected by environmental conditions.

Main Conclusions: Functional traits play a significant role in determining interaction outcomes between dryland plants. Facilitation in drylands is driven by a conservative-acquisitive trait match, a pattern observed regardless of grazing pressure, climate and soil conditions.

1 | Introduction

Plant–plant interactions are an important community structuring force (Bruno et al. 2003; Gotzenberger et al. 2012), especially in drylands, where more than 25% of species are more closely associated with nurse plants than expected by chance (Soliveres and Maestre 2014). It is, therefore, important to understand how the outcome of plant–plant interactions can vary through space and time, particularly since plant–plant interactions influence how communities respond to global environmental change (McCluney et al. 2012). The most prominent theory regarding spatio-temporal variation in the outcome of such interactions is the Stress Gradient Hypothesis (SGH), which predicts that greater environmental severity (more arid climates or higher herbivore pressure) leads to an increase in the frequency of positive plant–plant interactions (Bertness and Callaway 1994). While many studies support this hypothesis (see Adams et al. 2022; He et al. 2013; Soliveres et al. 2015 for reviews), many contradicting trends have also been reported (e.g., hump-shaped trends, Cui et al. 2023; Liancourt et al. 2017; Lopez et al. 2013). Furthermore, some studies report that environmental gradients do not have a strong effect on plant–plant interactions, and that interaction outcomes are contingent on species' characteristics (Liancourt et al. 2005; Maestre et al. 2009; Soliveres et al. 2014; Yang et al. 2022).

Species differ in their ecophysiological adaptations and tolerances and may not be equally stressed despite growing in the same environment (i.e., the idea of "individual strain"; Gross et al. 2010; Liancourt et al. 2017). Therefore, co-occurring species may not be equally likely to experience facilitation. Considering functional traits can aid in accounting for the species specificity of interaction outcomes, as plant functional traits are more informative of species environmental requirements and effects than growth forms or life history classifications (Schöb et al. 2013, 2017; Thomas et al. 2019). The traits of putative nurse plants determine how they affect the local environment under their canopy and can thus be expected to influence interaction outcomes (Schöb et al. 2013, 2017). For example, the canopy compactness of *Arenaria tetraquerta* cushion plants affected their ability to ameliorate temperature and water stress, with more compact cushions improving soil water content and soil organic matter to a greater degree, resulting in a stronger facilitative effect (Schöb et al. 2013). Depending on their functional traits, different nurse species may vary in the magnitude of their facilitative effect (e.g., Catorci et al. 2016; Fagundes et al. 2018), and host different communities of target species (e.g., Catorci et al. 2016; O'Brien et al. 2019; Schöb et al. 2017). In addition to being useful for predicting which species are likely to facilitate others, quantifying which nurse traits promote facilitation can also provide insights into the ameliorative mechanisms that are important for facilitation in drylands, and help select species for introduction in restoration projects (Gómez-Aparicio 2009; Navarro-Cano et al. 2019).

While the traits of nurse plants may be important in determining the ameliorative or protective effect, there are many instances in which target species do not benefit equally from the same nurse species (e.g., Fagundes et al. 2018; Filazzola et al. 2020; Liancourt et al. 2005). This suggests that the traits of target species also play a role in determining interaction outcomes (Gross et al. 2009). For example, in a watering and fertilisation experiment in China, the shrub *Artemisia ordosica* facilitated tall species but competed with short species (Bai et al. 2021). Schöb et al. (2017) suggested that the varying responses of target species to the presence of a neighbour can be explained by the effect and response traits of the nurse and target species. They suggested that facilitation is likely to occur between two plants when the effect traits of one plant are "compatible" with the response traits of another (Schöb et al. 2017). In other words, for a plant to have facilitative effects, it must possess effect traits that enable it to relieve stressful conditions (Schöb et al. 2017). In turn, the target species (the species experiencing the effects of the nurse plant) must possess response traits that enable it to take advantage of the environment created by the nurse (i.e., a compatible match of nurse effect traits and target species response traits; Schöb et al. 2017). For example, facilitation between trees and seedlings in a Brazilian dry forest was highest between trees with a low specific leaf area (SLA) and seedlings with a high apical growth rate (Fagundes et al. 2022). This trait match reflects how trees with low SLA allowed light to penetrate the canopy and acquired resources slowly, which had a positive effect on seedlings with a high apical growth rate who benefitted from the availability of light and soil resources (Fagundes et al. 2022). The relative importance of such trait matching in driving plant–plant interactions across broad environmental gradients, regarding the effect of the environment itself, or interactions between the environment and nurse-target functional traits, remains, however poorly understood.

The environmental drivers of facilitation are well researched, with aridity and grazing pressure regarded as key factors influencing the frequency of facilitation in dryland communities (Maestre et al. 2005; Rey et al. 2016; Smit et al. 2009). However, how these environmental drivers relate to trait-based predictions of plant–plant interactions is unclear. Will the compatible trait matches that promote facilitation shift as environmental conditions change the trait distributions of communities (Gross et al. 2024; Le Bagousse-Pinguet et al. 2017)? To address this unsolved question, we used a unique coordinated distributed study (Fraser et al. 2013) conducted across 29 sites from 10 countries to evaluate interactive effects of functional traits and environmental factors in driving plant–plant interactions across global drylands. We investigated the effects of well-researched drivers of facilitation such as grazing pressure and aridity, but also less well-known environmental factors that are known to be important in dryland ecosystem functioning (Le Bagousse-Pinguet et al. 2017; Maestre, Le Bagousse-Pinguet, et al. 2022). These include annual mean temperature, rainfall seasonality, soil pH and soil sand content. The multiplicity of potential drivers of plant–plant interaction outcomes, including climate characteristics and grazing pressure, but also soil characteristics and the functional traits of the species involved have, to the best of our knowledge, never been considered simultaneously and across a global scale. This could aid our understanding of the relative importance of contrasting environmental conditions and species-specific adaptations as drivers of plant–plant interaction outcomes. Specifically, we aimed to test: (i) the relative importance of grazing pressure, climate and soil characteristics in driving plant facilitation, (ii) whether a compatible trait match is required for facilitation to occur and (iii) whether the compatible nurse-target trait match is affected by grazing pressure, climate and soil characteristics.

2 | Methods

This study was conducted across 29 dryland sites from 10 countries (Algeria, Argentina, Australia, Chile, China, Iran, Israel, Namibia, South Africa and Spain) and five continents (Figure 1). Each site consisted of three to four 45 × 45 m plots, located along a grazing pressure gradient ranging from ungrazed or low grazing pressure to medium and high grazing pressure (see Maestre, Eldridge, et al. 2022 and Maestre, Le Bagousse-Pinguet, et al. 2022 for additional information and validation of the local grazing gradients surveyed). A total of 97 plots were surveyed (14 ungrazed, 26 low, 29 medium and 28 high grazing pressure plots). The aridity of the plots (1-FAO's aridity index, ranging from 0 [wettest] to 1 [driest]) surveyed ranged from 0.50 to 0.94, annual mean temperature ranged between 5°C and 22.3°C and mean annual rainfall ranged from 89 mm

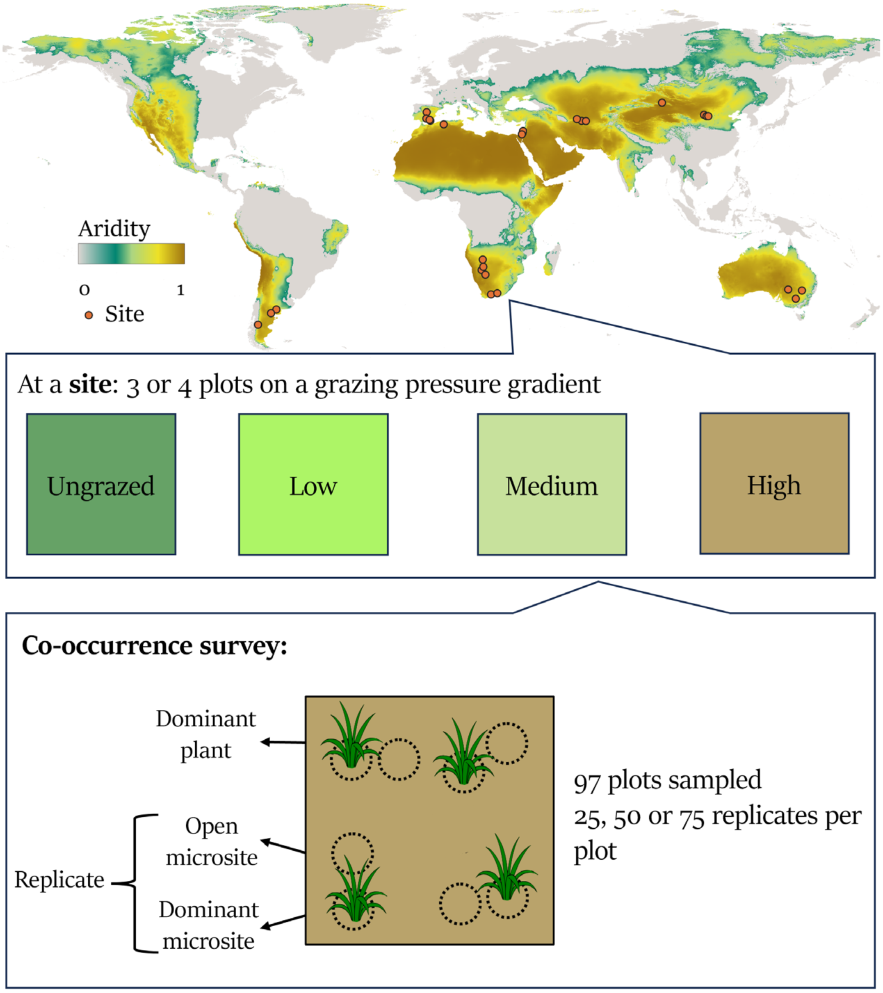

FIGURE 1 | Sampling design used in this study. Twenty-nine sites were sampled that each consisted of three to four plots arranged on a grazing pressure gradient. Each plot was subjected to a co-occurrence survey (in total 97 plots were sampled), in which vascular plant cover and species richness were sampled in 25, 50 or 75 replicates depending on whether one, two or three dominant species were present in the plot (for simplicity, only four replicates are shown on the figure).

to 606 mm. Soil sand content ranged from 13.7% to 98.3%, and pH ranged between 5.5 and 9.9. The vegetation of the plots surveyed included the main vegetation types that can be found in drylands (grasslands, shrublands, open forests, and savannas). Thus, our survey captured a wide range of vegetation and soil conditions, as well as hot and cold ecosystems that ranged from semi-arid to hyper-arid, as well as systems with highly seasonal and regular rainfall.

2.1 | Co-Occurrence Dataset

Plant–plant interactions were inferred from fine-scale spatial associations between dominant perennial plants and other target (plants growing under or away from dominant plant canopies) vascular species (following e.g., Liancourt et al. 2017). This approach is not without limitations, as co-occurrence patterns are influenced by the scale of data collection (Delalandre and Montesinos-Navarro 2018), and other processes besides facilitation (e.g., shared microhabitat requirements) can also give rise to aggregated spatial patterns (Steinbauer et al. 2016). However, the use of co-occurrence data allows plant–plant interactions to be studied between many species in the community, and across broader environmental gradients. Furthermore, spatial associations are often tightly linked to the outcome of plant–plant interactions and are a useful approach to study interaction outcomes at the community level (Alados et al. 2017; Tirado and Pugnaire 2005).

In each plot, 25 dominant plant patches (a patch could consist of more than one individual) were selected to form 25 "dominant microsites" (Figure 1). Species forming the dominant microsites were selected based only on their size and abundance (i.e., large, abundant perennial species), and not on any a priori knowledge of facilitative effects. Each dominant microsite was paired with an "open microsite", created by emulating the canopy area of the dominant microsite with a wire ring, and placing the ring at least one microsite radius away from the dominant plant's canopy edge in an area lacking the dominant plant. Together, a dominant-open microsite pair forms a replicate. If more than one dominant species were present in the plot, 25 additional replicates were surveyed around each dominant species to form 50 or 75 replicates if the plot had two or three dominant species, respectively. The richness and cover of all perennial vascular plant species growing in open and dominant microsites (i.e., target species) were recorded. Co-occurrence data were collected from 3789 replicates (each replicate is a paired dominant-open microsite).

2.2 | Grazing, Climate and Edaphic Data

Each site consisted of three to four 45 × 45 m plots, located at increasing distances from an artificial waterpoint to form a grazing pressure gradient (except for one site in China, where a grazing pressure gradient was created with grazing exclosures). Where possible, a plot in an ungrazed area was also surveyed. Four categories of grazing pressure were, therefore, defined: ungrazed, low, medium and high. To ensure that the plots placed at different distances from a watering point corresponded to a gradient in grazing pressure, a heuristic assessment of grazing pressure was conducted by local experts, making use of historic records and specialist knowledge. Additionally, in each plot, the dung mass per hectare for each herbivore species was calculated, and the depth and width of livestock tracks were measured. These three measures of grazing pressure (distance from water points, heuristic assessment, and dung mass) were found to correspond well, and to accurately predict the four different categories of grazing pressure. Increases in grazing pressure between plots (based on distance from artificial water sources) were correlated with increasing dung mass and area of livestock tracks. See Maestre, Eldridge, et al. (2022) and the supplementary text in Maestre, Le Bagousse-Pinguet, et al. (2022) for additional information and further validation of the local grazing gradients surveyed in a subset of sites that had stocking data available.

The following climate and soil variables were selected to test for their effect on plant–plant interactions: aridity (1—precipitation/potential evapotranspiration), annual mean temperature (AMT, measured in °C), rainfall seasonality (the coefficient of variation of precipitation, RASE), soil pH and soil sand content (SAC, the percentage mass of soil consisting of sand). Aridity was retrieved from the Global Aridity Index and Potential Evapotranspiration Climate Database v3 (Zomer et al. 2022), while AMT and RASE were extracted from WorldClim 2.0 (Fick and Hijmans 2017). The mean soil pH and SAC for each plot were estimated from soil samples collected at five sampling points, randomly placed in areas devoid of vascular plant cover, within each plot. At each sampling point, a composite sample was collected from four soil cores (7.5 cm depth) which were bulked and homogenised in the field. Soil pH was measured with a pH meter in a 1:1 soil to water mix, and sand content was measured following Kettler et al. (2001). See Maestre, Eldridge, et al. (2022) for additional details on the soil survey and laboratory analyses conducted.

2.3 | Functional Trait Dataset

We measured functional traits of multiple individuals ($N = 5–10$) of most species present in our sites following standardised protocols detailed in Perez-Harguindeguy et al. (2013) and as described in Gross et al. (2024). The following functional traits were measured: maximum vegetative height (cm), lateral spread (LS, the product of the width of the plant at its widest point and the width perpendicular to that, cm^2), leaf length (LL, cm), leaf area (LA, cm^2), specific leaf area (SLA, cm^2/g), leaf dry matter content (LDMC, %), and leaf C:N ratio (C:N, elemental concentration of C divided by the elemental concentration of N). These traits are informative of the shading effect (Violle et al. 2009), palatability (Pontes et al. 2007), and resource-use strategy of plants (Díaz et al. 2016; Reich 2014), and are therefore likely to be related to plant–plant interactions.

In each plot, the average (LL, LA, SLA, LDMC, C:N) or maximum (height, LS) value of each trait for each species was calculated. Five hundred forty-six species were sampled in both the co-occurrence and functional trait survey (comprising a mean of 80.6% of the species richness and 86.0% of the cover in each plot in the co-occurrence dataset). Due to logistic constraints, 181 species (24.9%) were not sampled for functional traits. However, these species were rare and only made up 8.6% of the total vegetation cover represented in our dataset. For some of these cases (an additional 2.5% more species × plot combinations), we imputed data from the same species in another site with similar environmental characteristics using the traitstrap package (Maitner et al. 2023), to achieve the most complete trait dataset for the species in the co-occurrence data.

2.4 | Data Analysis

2.4.1 | Quantifying Plant–Plant Interactions

We used two approaches to quantify plant–plant interaction outcomes: χ^2 tests of species' associations (species-level analysis) and the Neighbour-effect Intensity index with commutative symmetry ($NInt_C$, Díaz-Sierra et al. 2017; community-level analysis). χ^2 tests on species occurrences were performed to determine whether each species was significantly associated with open or dominant microsites. Yates's continuity correction for small sample sizes was applied. Species with expected values (i.e., the product of the row and column total divided by the grand total of the contingency table) lower than five due to low occurrence were excluded from this analysis. All species were classified as being significantly associated with dominant microsites, significantly associated with open microsites, or not significantly associated with either microsite (i.e., neutral association).

The Neighbour-effect Intensity index quantifies whether species richness or cover is higher or lower in the dominant microsite than in the open microsite. It is calculated as follows:

$$NIntC = 2\frac{\left(P_D - P_O\right)}{P_D + P_O + \left|P_D - P_O\right|}$$

where P_D and P_O indicate community metrics in the dominant and open microsite, respectively. Here, vascular plant species richness, total cover and the Shannon diversity index (calculated with species cover) were used as community metrics (resulting in $NInt_C$ richness, $NInt_C$ cover and $NInt_C$ Shannon, respectively). $NInt_C$ has commutative symmetry, that is, it assigns equal but opposite values when the community metric with and without a dominant are exchanged. $NInt_C$ ranges from −1 (indicating competitive exclusion, that is, species only present in the open microsite), to +1 (indicating obligate facilitation, that is, species only present in the dominant microsite). No further analyses were performed with $NInt_C$ Shannon because it was highly correlated with $NInt_C$ richness (Pearson's $r > 0.8$, Figure A1).

2.4.2 | Trait Selection

We first performed a principal component analysis on the traits of dominant and target plants from all sites. The first principal component was defined by traits related to resource use, and was positively related to LDMC, and negatively related to SLA. The second principal component was positively related to height and LS and thus represented a size axis. The trait with the highest loading on the first principal component was LDMC, and the trait with the highest loading on the second principal component was height (Figure A2 and Table A1). Therefore, height and LDMC were selected to be used in all further analyses. Higher plant height is associated with greater light interception by the plant canopy, and less transmission of light below the canopy (Violle et al. 2009). Height is thus informative of the shading effect of dominant plants but is also positively associated with the fertile island effect, which describes the phenomenon of concentrated nutrients and improved soil conditions beneath perennial patches in drylands (Eldridge et al. 2024). LDMC is related to the density of leaf tissues and is thus positively correlated with the toughness and longevity of leaves. High LDMC is indicative of a more conservative resource-use strategy, characterised by low rates of nutrient and water uptake, and a slow growth rate (Díaz et al. 2016; Reich 2014). Instead of investing in growth, plants with high LDMC invest more in the structural strength and longevity of leaves (Perez-Harguindeguy et al. 2013). Leaves with high LDMC are less palatable and less digestible to herbivores (Pontes et al. 2007) and are also more resistant to drought (Stears et al. 2022; Wilcox et al. 2021).

2.4.3 | Model Selection to Determine Drivers of Plant–Plant Interactions

To determine whether dominant plant traits affect interaction outcomes, and how environmental conditions modulate this effect, a best subset model building approach was used. The full model was a generalised linear mixed-effect model (GLMM) comprising grazing pressure, climate variables (aridity, AMT, RASE), soil variables (soil pH and sand content) and dominant plant traits (height and LDMC, log transformed) as fixed effects. The model also included grazing × climate, grazing × soil, grazing × trait, climate × trait and soil × trait interactions. The modelling procedure was repeated with $NInt_C$ richness and $NInt_C$ cover as response variables. $NInt_C$ values were rescaled to range from 0 to 1 prior to modelling. The binomial distribution was used because the response variables had many values near their limits and to prevent the models from estimating values beyond the limits of the interaction indices. To control for possible spatial autocorrelation, the latitude and longitude of each plot were also included in the full model (the sine of coordinates were used to make them linear). The identity of dominant species was included as a random effect. Sixty-four dominant plant species from 2501 replicates (from 74 plots) had height and LDMC data, amounting to 67% of replicates being included in this analysis. Models were constructed with all possible combinations of predictor variables from the full model and ranked by Akaike Information Criterion (AIC). Latitude, longitude, and dominant species identity were included in all candidate models. We retained the best fitting models with a difference in AIC less than two from the lowest AIC and averaged their coefficients. We calculated the importance of each variable in the averaged model by summing the model Akaike weights of each model the variable was included in.

2.4.4 | Model Selection to Determine the Functional Trait Match and Environmental Drivers Thereof

To determine the functional trait match between dominant and target species, we calculated the difference in height and LDMC between the dominant and open-associated species

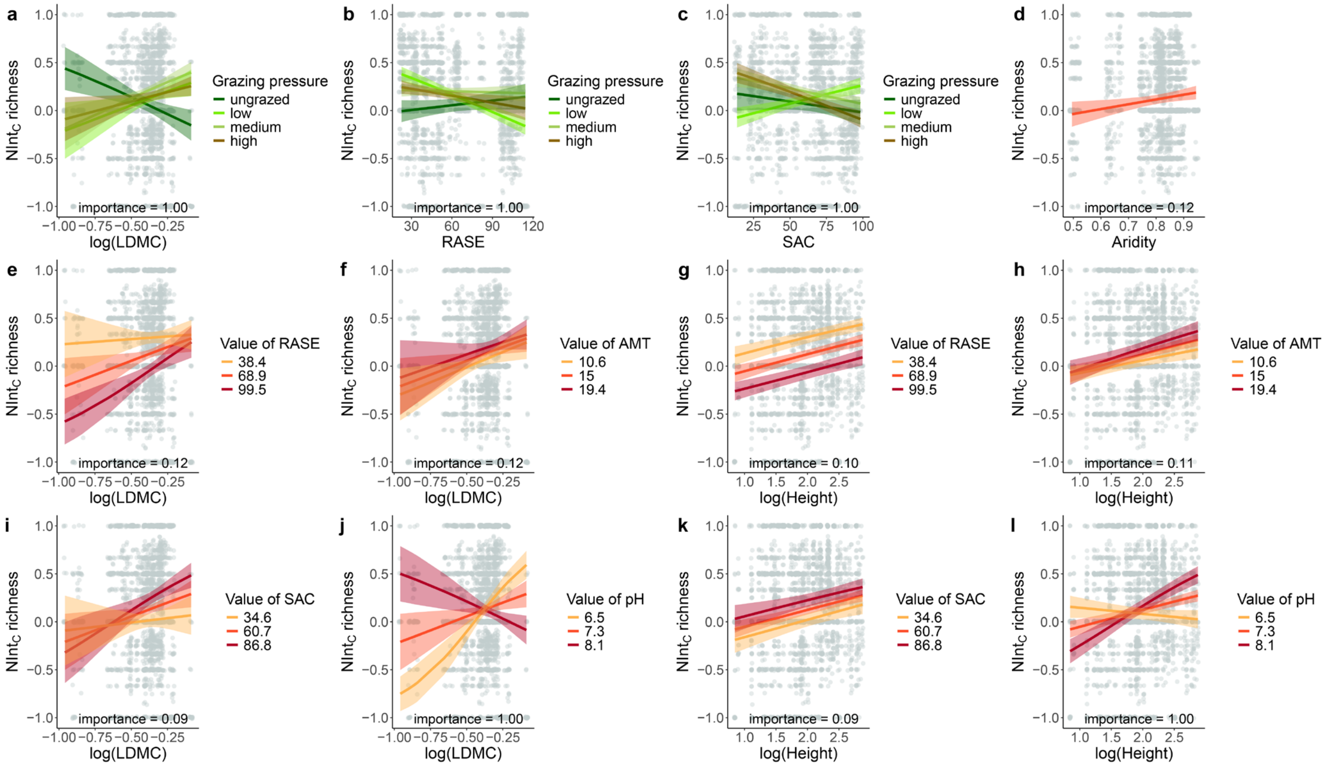

FIGURE 2 | The effects of interaction terms included in the summarised model of NInt$_C$ richness. Lines illustrate the predicted relationship between NInt$_C$ richness and plant traits, dependent on environmental variables. Transparent ribbons around the lines represent one standard error of the predictions. Grey points show the NInt$_C$ richness and dominant plant trait value of a replicate. Darker grey points indicate replicates with overlapping NInt$_C$ richness and trait values. Where there are interactions between continuous variables, three levels of the continuous variables (mean − standard deviation, mean, mean + standard deviation) are shown to illustrate the interaction. The importance of each interaction term in the summarised model is at the bottom of each figure. The variable importance is calculated as the sum of the Akaike weight of each model containing the variable. log(LDMC), dominant plant leaf dry matter content (log transformed); log(height), dominant plant height (log transformed); RASE, rainfall seasonality; AMT, annual mean temperature; Aridity, 1-potential precipitation/potential evapotranspiration; SAC, soil sand content; pH, soil pH.

in the replicate (Δ_{Do}, difference in trait value between dominant [D] and open-associated [o] species, with one value per species per replicate in each site) and the difference in height and LDMC between the dominant and dominant-associated species in the replicate (Δ_{Dd}, difference in trait value between dominant [D] and dominant-associated [d] species). If Δ_{Do} (Δ_{Dd}) < 0, it means that the trait value of open-associated (dominant-associated) species is higher than the trait value of the dominant species in the replicate. To determine whether dominant-associated target species were more or less similar to dominant plants than open-associated target species, and whether this functional trait match was mediated by environmental conditions, we used a best-subset model building approach. The association of the target species (open or dominant-associated), climate (aridity, AMT, RASE), soil (pH, SAC), and grazing pressure, as well as the association × climate, association × soil and association × grazing pressure interactions were included in the full model. The sine of latitude and longitude, as well as a random effect of dominant species identity, were included in every candidate model. 1412 replicates from 49 plots were included in this model. The same model averaging procedure as described above was followed. All GLMMs were built with the glmmTMB package (Brooks et al. 2017). Model selection and model averaging were done with functions from the MuMIn package (Bartoń 2023). Nakagawa's R^2 values for models were calculated with the performance package (Lüdecke et al. 2021). All analyses were done using R 4.4.2 (R Core Team 2024).

3 | Results

The richness and cover of target species were significantly higher in dominant than in open microsites (mean NInt$_C$ richness ± SE = 0.13 ± 0.01, $t = 14.37$, Df = 3788, $p < 0.001$; mean NInt$_C$ cover ± SE = 0.15 ± 0.01, $t = 13.25$, Df = 3735, $p < 0.001$). NInt$_C$ values varied greatly within plots (see grey dots in Figures 2 and 3). A total of 720 target species were recorded, with 305 species adequately sampled for χ^2 analyses. Of these species, 27.9% (85 species) were associated with dominant plants, 12.4% (38 species) were associated with open microsites, and 79.0% (241 species) showed no significant association with either microsite (species that occurred in multiple plots could show different associations in each plot).

Environmental conditions and dominant plant traits affected plant–plant interactions, with their effects often dependent on one another (Figures 2 and 3; Tables A2 and A3). All environmental predictors (climate, grazing and soils) played a role in determining NInt$_C$ richness and NInt$_C$ cover, either individually or

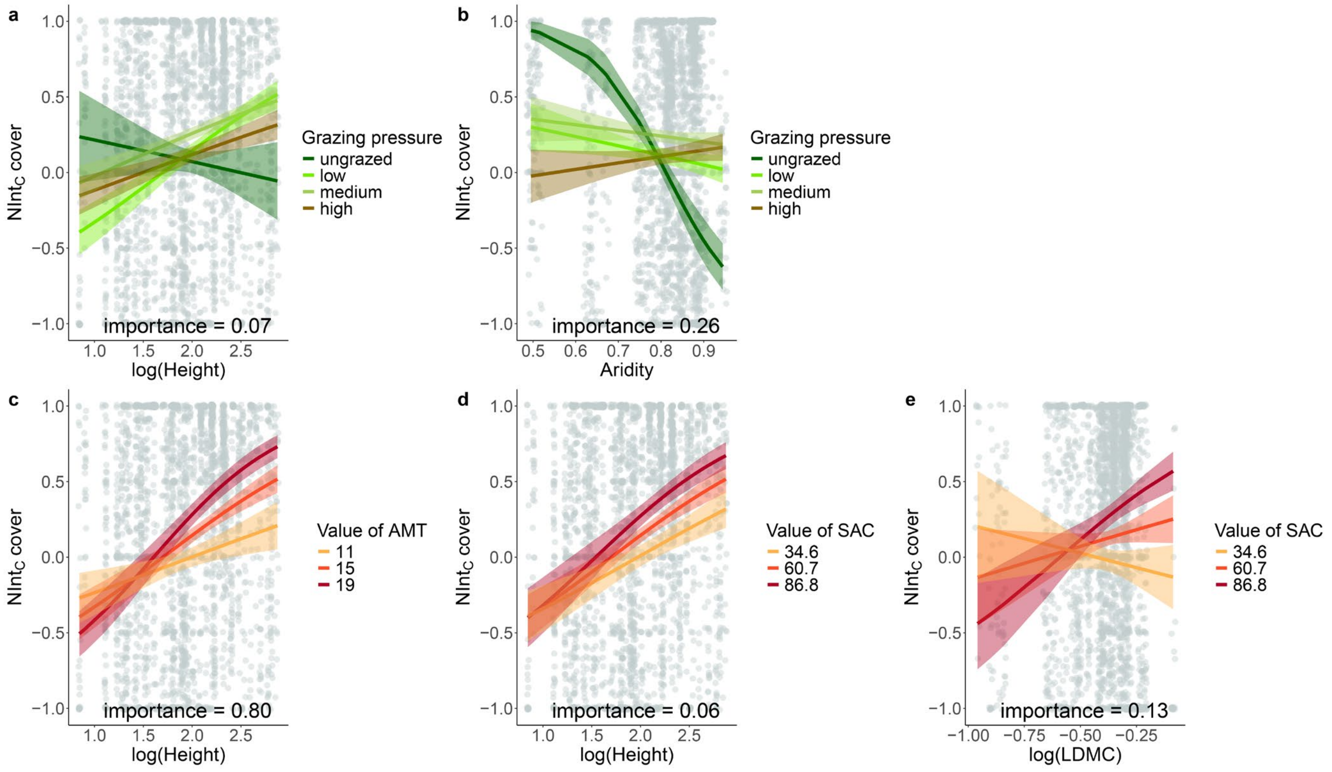

FIGURE 3 | The effects of interaction terms included in the summarised model of NInt$_C$ cover. Only interaction terms with relationships that differ from those with NInt$_C$ richness are shown (See Figure A3 for the rest of the interaction terms). Lines illustrate the predicted relationship between NInt$_C$ cover and plant traits, dependent on environmental variables. Transparent ribbons around the lines represent one standard error of the predictions. Grey points show the NInt$_C$ richness and dominant plant trait value of a replicate. Darker grey points indicate replicates with overlapping NInt$_C$ richness and trait values. Where there are interactions between continuous variables, three levels of the continuous variables (mean − standard deviation, mean, mean + standard deviation) are shown to illustrate the interaction. The importance of each interaction term in the summarised model is shown to the left of each figure. The variable importance is calculated as the sum of the Akaike weight of each model containing the variable. log(LDMC), dominant plant leaf dry matter content (log transformed); log(height), dominant plant height (log transformed); RASE, rainfall seasonality; AMT, annual mean temperature; Aridity, 1-potential precipitation/potential evapotranspiration; SAC, soil sand content; pH, soil pH.

via their influence on the effect of dominant plant traits. The effect of dominant plant traits on interaction outcomes was modulated strongly by grazing pressure and soil pH, and to a lesser degree by aridity, AMT, RASE and SAC (Figures 2 and 3). The LDMC and height of dominant plants were generally positively related to NInt$_C$ richness and NInt$_C$ cover, although negative effects of LDMC occurred under ungrazed conditions (Figures 2a and 3a) and high pH (Figures 2j and 3k); and negative effects of height occurred at low pH (Figure 2l).

NInt$_C$ richness and NInt$_C$ cover generally increased with harsher climatic conditions (high AMT, RASE aridity) and in soils with higher SAC and pH (Figures 2 and 3). However, differences in grazing pressure caused deviations from this trend. The effect of RASE on NInt$_C$ richness and NInt$_C$ cover was only positive in ungrazed conditions (Figures 2b and A3b), and the effect of aridity on NInt$_C$ cover was only positive at high grazing pressure (Figure 3b). The effect of SAC on NInt$_C$ richness and NInt$_C$ cover was only positive in low grazing or ungrazed conditions (Figures 2c and A3c). While all environmental predictors were included in the averaged models for NInt$_C$ richness and NInt$_C$ cover, aridity had a markedly lower importance than the other variables (Tables A2 and A3; Figures 2d and 3b). A large amount of variation remained unexplained by the averaged models of NInt$_C$ richness (marginal $R^2 = 4.2\%$) and NInt$_C$ cover (marginal $R^2 = 8.1\%$).

The analysis of the difference in height and LDMC between dominant and target plants showed that the functional match between dominant and target plants also plays a role in determining interaction outcomes. Dominant-associated and open-associated target plants differed in their similarity to the dominant plant (Tables A4 and A5), and this was modulated by environmental conditions (Figures 4 and 5). The difference in height and LDMC between dominant and open-associated plants was strongly affected by grazing pressure, climate and soil conditions, often shifting from having a higher trait value than the dominant plant to having a low value under harsher conditions (e.g., Figures 4b and 5e). However, the functional match between dominant and dominant-associated species was not strongly influenced by grazing pressure, climate and soil conditions (Figures 4 and 5). Regardless of differences in broad-scale climate or local grazing and soil factors, plants that were shorter, with lower LDMC than dominant plants (ΔDd was generally greater than zero) were more likely to benefit from association with dominant plants. Thus, while the compatible match in traits that promoted facilitation stayed relatively consistent across gradients of climate, grazing pressure and soil, incompatible trait syndromes varied.

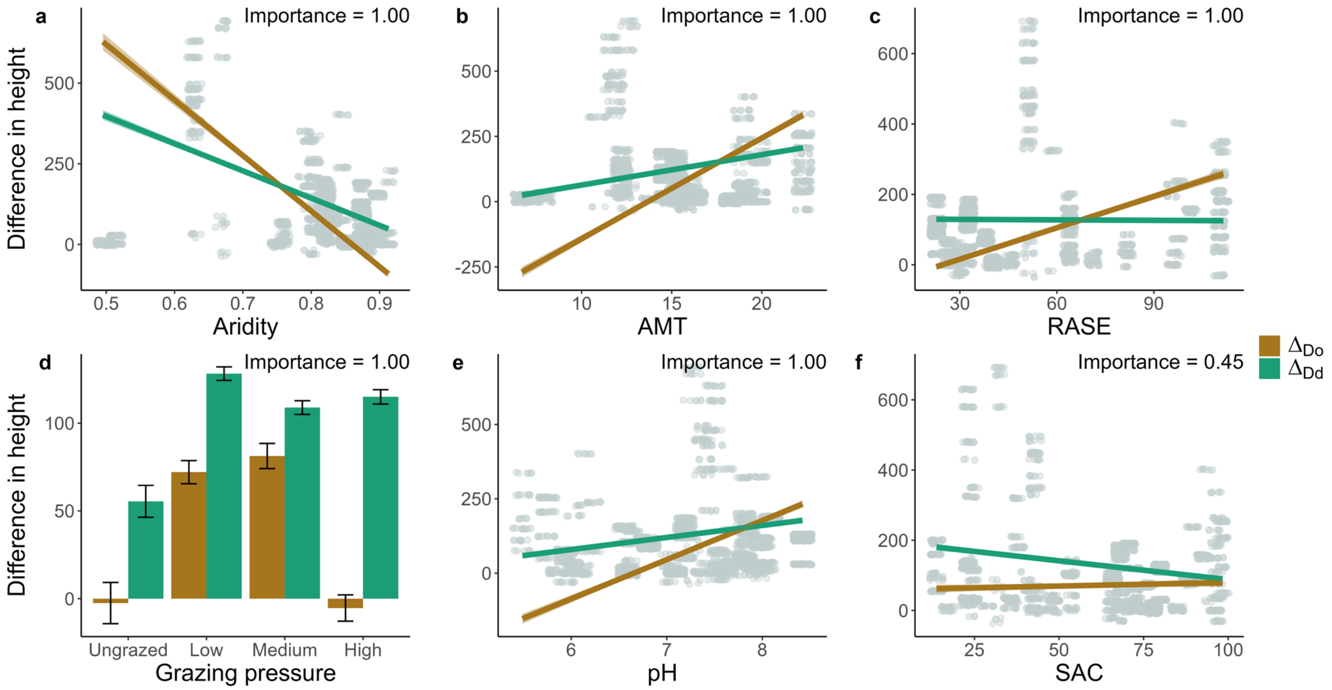

FIGURE 4 | The effects of interaction terms included in the summarised model predicting the difference in height between dominant and target plants. ΔD_o, Difference in height between dominant and open-associated plants. ΔD_d, Difference in height between dominant and dominant-associated plants. Ribbons around the fitted lines represent standard errors but are often very small due to the large sample size. RASE, rainfall seasonality; AMT, annual mean temperature; Aridity,1-potential precipitation/potential evapotranspiration; SAC, soil sand content; pH, soil pH.

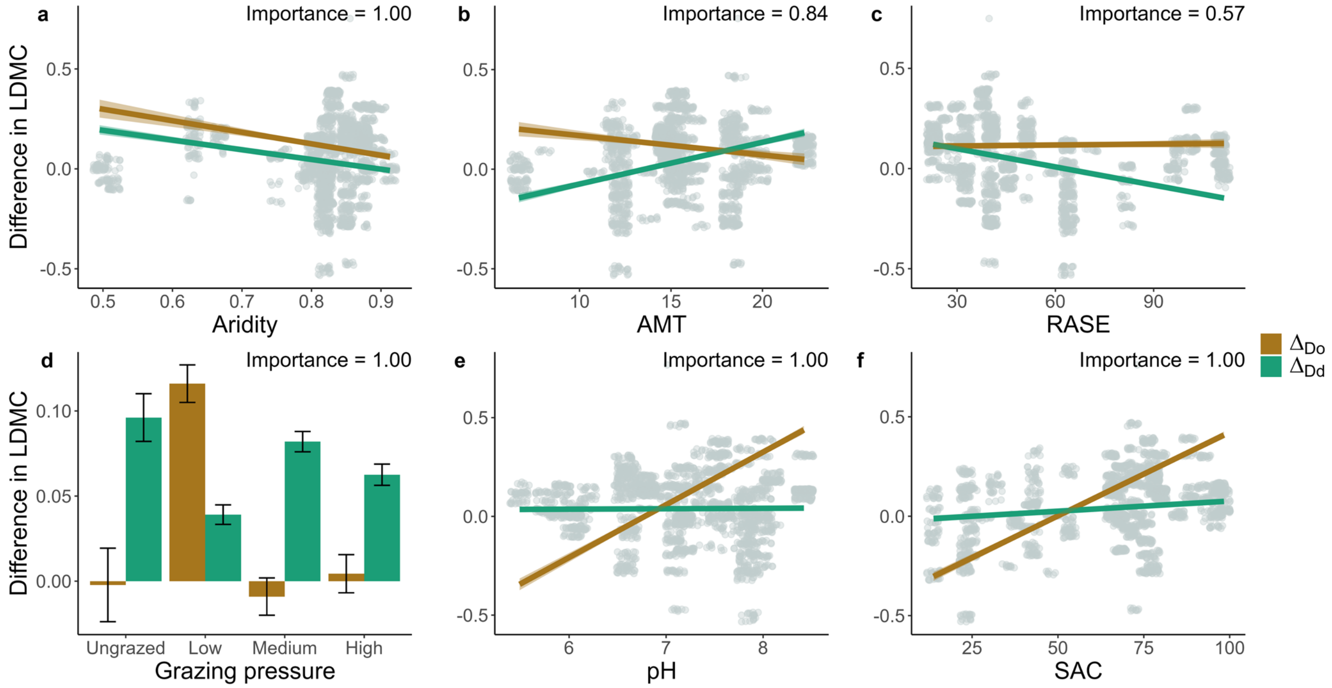

FIGURE 5 | The effects of interaction terms included in the summarised model predicting the difference in LDMC between dominant and target plants. ΔD_o, ifference in LDMC between dominant and open-associated plants. ΔD_d, Difference in LDMC between dominant and dominant-associated plants. Ribbons around the fitted lines represent standard errors but are often very small due to the large sample size. RASE, rainfall seasonality; AMT, annual mean temperature; Aridity, 1-potential precipitation/potential evapotranspiration; SAC, soil sand content; pH, soil pH.

4 | Discussion

We analyzed a comprehensive co-occurrence dataset covering global drylands to explore how plant functional traits influence interaction outcomes and how their effects are modulated by grazing pressure, climate, and soil conditions. Our study shows the prevalence of plant functional traits as drivers of the outcome of plant–plant interactions in drylands. Dominant plants with higher LDMC and plant height generally had a greater positive effect on vascular plant species richness and cover. However, it was not only the traits of the dominant plant that affected interaction outcomes, but also the traits of the target species and the relation between the trait syndromes of these two groups. Here, a conservative-acquisitive functional trait match between dominant and target plants promoted facilitation. Target plants that were associated with dominant plants tended to be smaller and have less conservative leaves than dominant plants, and this remained true under a large range of environmental conditions. While the nurse-target functional match was not strongly affected by changes in grazing pressure, climate or soil conditions, the competitive trait mismatch (dominant vs. open-associated species) was highly dependent on such environmental conditions, suggesting that competitive interactions are more sensitive to the environment than facilitative ones.

The conservative-acquisitive trait match that increased the probability of plant–plant facilitation in drylands is likely driven by associational resistance and the fertile island effect (Eldridge et al. 2024; Fagundes et al. 2022; Ochoa-Hueso et al. 2018; Smit et al. 2009). Dominant plants with conservative leaves (characterised by high LDMC) are less palatable and digestible (Perez-Harguindeguy et al. 2013; Pontes et al. 2007), making them less likely to be grazed, and thus able to offer herbivore protection to plants growing beneath their canopies. Species with conservative leaf traits are typically slow growing and have a low photosynthetic rate, meaning that they do not take up large quantities of water or nutrients (Díaz et al. 2016; Reich 2014), thus reducing their potential competitive effect on neighbouring plants. Large, conservative species also enhance the fertile island effect by adding more persistent leaf litter to the soil (Eldridge et al. 2024; Ochoa-Hueso et al. 2018), which decomposes more slowly than litter from short-lived, acquisitive leaves, and can, therefore, decrease evaporative water loss and improve soil fertility to a greater degree (Ochoa-Hueso et al. 2018). In contrast, species with acquisitive leaf traits (i.e., low LDMC) are faster growing and require more water and nutrients (Díaz et al. 2016; Reich 2014; Stears et al. 2022). Such species will benefit from the higher water and nutrient availability under a large, conservative species, while suffering minimal competition owing to the low resource requirements of the conservative species. Our findings align with studies conducted across smaller extents that found that less well adapted (i.e., more "strained", sensu Liancourt et al. 2017) species benefit more from the presence of a neighbour than species that are better adapted to the prevailing environmental stressors (e.g., Filazzola et al. 2020; Graff and Aguiar 2017; Liancourt et al. 2005; Soliveres, Eldridge, et al. 2011). In drylands, specifically, species with low LDMC are assumed to be more strained, because they are less resistant to drought (Stears et al. 2022; Wilcox et al. 2021).

Although high LDMC and plant height in dominant plants generally promoted facilitative interactions, exceptions occurred when grazing was absent, or soil pH was high. The reason why LDMC was no longer positively related to facilitation at high soil pH is difficult to understand. It is possible that more acquisitive dominant plants had greater nurse effects at high soil pH due to their ability to add leaf litter that can decompose quickly and improve the low phosphorus and micronutrient values typically found in alkaline soils (Diaz et al. 2004; Whitford 2002). The LDMC and height of dominant plants were positively related to NInt_C richness and NInt_C cover, except in ungrazed plots. This may be due to the decreased benefit of associational resistance from plants with high LDMC when herbivores are absent (Pontes et al. 2007; Smit et al. 2009). The higher plant cover in ungrazed plots may also mean that the shading effect of tall plants is less desirable, as drought-adapted target species are often intolerant of heavy shading (Soliveres, Garcia-Palacios, et al. 2011). Thus, without herbivore pressure, shorter, more acquisitive species may be able to offer the same advantage as tall conservative species in grazed plots, and may even be preferred due to their lower shading effect.

The difference in LDMC and height between dominant and dominant-associated species stayed relatively constant across gradients of grazing pressure, climate and soil conditions. However, the trait syndrome enabling survival without a neighbour changed along the environmental gradients. This is likely due to environmental filtering, whereby only those species that possess traits conferring tolerance to environmental conditions can survive (Kraft et al. 2015; Le Bagousse-Pinguet et al. 2017). Dominant plants can relax this environmental filter by improving microclimatic and soil conditions beneath their canopies, enabling species with less well-adapted trait syndromes to survive (McIntire and Fajardo 2014; O'Brien et al. 2019; Schöb et al. 2013). Our results suggest that the ameliorative effect of dominant species on their environment stays relatively constant, benefitting target species with the same trait syndrome (shorter species with more acquisitive leaves) across broad environmental gradients. However, the trait syndrome of open-associated species is the result of the interplay between environmental filtering and net competition and therefore seems more sensitive to changing environmental conditions (McIntire and Fajardo 2014).

Despite the significant effect of plant traits and some of the environmental characteristics included in our study, we were only able to explain a small proportion of the variance in plant–plant interactions. Other potential drivers of such interactions could be the evolutionary relationships between the interacting species (e.g., Soliveres et al. 2012; Valiente-Banuet and Verdú 2007; Verdú et al. 2009), or the different grazing history characterizing our sites (Price et al. 2022). Regarding the former, evolutionary relationships can implicitly include species characteristics not easy to address with commonly measured functional traits, such as the regeneration niche that can drastically determine their preferred microsites (Valiente-Banuet and Verdú 2007), or the presence of allelochemicals and plant-defence compounds, which could alter plant–plant interactions (Ehlers and Thompson 2004). Regarding the latter, more recent impacts of extensive livestock grazing by sheep and cattle, such as that in Australia or South America could drive weaker grazing-adaptation syndromes in these areas (Milchunas et al. 1988), and therefore a higher proportion of facilitated species (if target species are less adapted) or a weaker nurse effect of the dominant species (if dominant species are less adapted and therefore provide weaker associational resistance).

These evolutionary drivers should be further considered together with the environmental and species-specific drivers addressed here, in order to enhance our explanatory power regarding the outcome of plant–plant interactions in drylands.

From a theoretical perspective, our findings may explain the high variability in interaction outcomes that can occur within communities. Drylands are characterised by high functional diversity, especially in the most arid regions where trait covariation is reduced (Gross et al. 2024). While such variation exists in the size and leaf traits of plants, there will be plants that are relatively more acquisitive and will benefit from increased resource and water availability, and there will also be plants with incompatible trait syndromes that prefer to grow away from such effects. Thus, in drylands, irrespective of the climate or grazing conditions, there will always likely be species that are facilitated by, and compete with, large dominant plants due to the high plant functional diversity in these habitats (Gross et al. 2024). Practically, functional traits also provide a way to predict the outcome between pairs of species, where, at least within drylands, a conservative-acquisitive functional match promotes facilitation between dominant and target vascular plants.

Author Contributions

The BIODESERT global survey was designed and coordinated by F.T.M. Data were collected by the BIODESERT consortium. I.C.S. cleaned and standardised the data from the co-occurrence survey and harmonised it with the functional trait dataset. I.C.S. conceived the study and analysed the data with input from P.C.L.R., S.S., Y.L.B.-P. and N.G. P.C.L.R., N.G., Y.L.B.-P., H.S. and S.S. gave suggestions on the interpretation and presentation of the results. I.C.S. wrote the manuscript with inputs from P.C.L.R., S.S., N.G., Y.L.B.-P. and F.T.M. All other authors contributed data and were involved in the final editing of the manuscript.

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Acknowledgements

The BIODESERT survey was funded by the European Research Council (ERC Grant agreement 647038), awarded to F.T.M. I.C.S. was supported by a Master's bursary from the South African Association of Botanists as well as a Master's scholarship from the Oppenheimer Memorial Trust (grant number 2023-2176). F.T.M. acknowledges support by the King Abdullah University of Science and Technology (KAUST) and the KAUST Climate and Livability Initiative. P.J.R. and A.J.M. acknowledge support by Fondo Europeo de Desarrollo Regional through the FEDER Andalucía operative programme, FEDER-UJA 1261180 project.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data and R scripts that support the findings of this study are available on Dryad at https://doi.org/10.5061/dryad.9cnp5hqx5.

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Appendix A

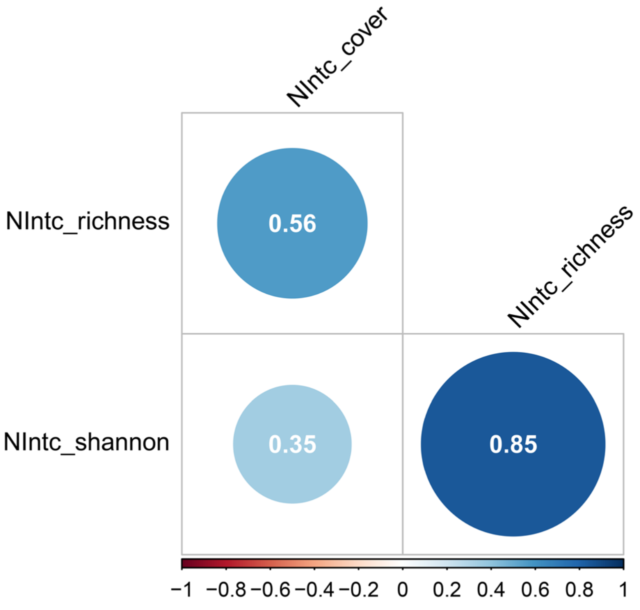

FIGURE A1 | Pearson's r correlation coefficients between interaction intensity indices. Darker shading represents stronger correlations; all correlations are significant.

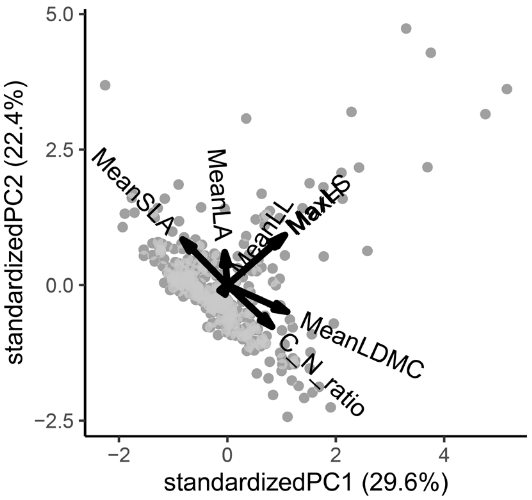

FIGURE A2 | The traits of dominant and target species plotted along the first and second principal components calculated by principal component analysis. The arrows represent the eigenvectors of each trait along the first and second principal components. The first principal component (standardizedPC1) encompasses 29.6% of the variation in traits, while the second principal component (standardizedPC2) describes 22.4% of the variation in the traits of dominant and target species. MaxH, plant height; MaxLS, lateral spread; MeanLA, leaf area; MeanLDMC, leaf dry matter content; MeanLL, leaf length; MeanSLA, specific leaf area; C_N_ratio, leaf carbon to nitrogen ratio.

TABLE A1 | Loadings of each trait on the principal components retrieved from principal component analysis on the traits of dominant and target species.

	PC 1	PC 2	PC3	PC 4	PC 5	PC 6	PC 7
Height	0.489	0.488					0.713
LS	0.464	0.478	0.183		−0.114	−0.286	−0.652
LA		0.320	−0.598	−0.690	−0.127	0.207	
LDMC	0.506	−0.260			0.430	0.662	−0.211
LL			−0.715	0.666	−0.195		
SLA	−0.380	0.444		0.123	0.790		
C:N	0.379	−0.406	−0.288	−0.221	0.350	−0.654	0.101

Abbreviations: C:N, leaf carbon to nitrogen ratio; Height, plant height; LA, leaf area; LDMC, leaf dry matter content; LL, leaf length; LS, lateral spread; SLA, specific leaf area.

TABLE A2 | Predictors included in the best models (there were eight best models with $\Delta\text{AIC} < 2$) for NInt_C richness.

Predictors selected	Estimate	Standard error	*p*	*n*	Variable importance (sum of weights)	Whole model R^2c and R^2m
Latitude (sin)	−0.042	0.162	0.796	8	1.00	R^2m = 0.042, R^2c = 0.071
Longitude (sin)	−0.014	0.142	0.920	8	1.00	
AMT	0.045	0.039	0.248	8	1.00	
aridity	0.086	0.436	0.844	1	0.12	
RASE	0.007	0.007	0.356	8	1.00	
graz1	1.512	0.758	0.011	8	1.00	
graz2	2.149	0.714	0.683			
graz3	1.846	0.723	0.802			
pH	−2.601	0.739	< 0.001	8	1.00	
SAC	−0.008	0.009	0.405	8	1.00	
Height	−3.958	1.584	0.012	8	1.00	
LDMC	28.340	9.347	0.002	8	1.00	
graz1:RASE	−0.017	0.006	0.004	8	1.00	
graz2:RASE	−0.006	0.006	0.300			
graz3:RASE	−0.009	0.006	0.153			
graz1:SAC	0.020	0.008	0.011	8	1.00	
graz2:SAC	0.003	0.008	0.683			
graz3:SAC	−0.002	0.008	0.802			
AMT:Height	0.002	0.014	0.859	1	0.11	
AMT:LDMC	0.011	0.060	0.849	1	0.12	
Height:RASE	< 0.001	0.002	0.896	1	0.10	
LDMC:RASE	0.002	0.009	0.845	1	0.12	
graz1:LDMC	3.395	1.457	0.020	8	1.00	
graz2:LDMC	4.170	1.209	< 0.001			
graz3:LDMC	2.274	1.024	0.026			
Height:pH	0.562	0.212	0.008	8	1.00	
LDMC:pH	−4.235	1.254	< 0.001	8	1.00	
Height:SAC	< −0.001	0.002	0.982	1	0.09	
LDMC:SAC	< 0.001	0.009	0.981	1	0.09	

Note: n is the number of times the variable was included in the set of best models. The variable importance is the sum of the Akaike weights over all models including each explanatory variable.

Abbreviations: AMT, annual mean temperature, °C; aridity, 1-precipitation/potential evapotranspiration; graz1, low grazing pressure; graz2, medium grazing pressure; graz3, high grazing pressure; Height, plant height, cm; LDMC, leaf dry matter content, %; pH, soil pH; R^2c, conditional R^2, that is, the fraction of variation explained by the model including the random effect; R^2m, marginal R^2, that is, the fraction of variation explained by the model not including random effects; RASE, rainfall seasonality, the coefficient of variation of monthly precipitation; SAC, soil sand content, %.

TABLE A3 | Predictors included in the best models (there were 13 best models with ΔAIC < 2) for $\mathrm{NInt}_{\mathrm{C}}$ cover.

Predictors selected	Estimate	Standard error	*p*	*n*	Variable importance (sum of weights)	Whole model R^2c and R^2m
Latitude (sin)	−0.019	0.199	0.925	13	1.00	R^2m = 0.081, R^2c = 0.146
Longitude (sin)	−0.038	0.173	0.827	13	1.00	
AMT	−0.077	0.096	0.420	12	0.94	
Aridity	−2.642	4.521	0.559	5	0.41	
RASE	0.010	0.008	0.212	13	1.00	
graz1	0.724	3.765	0.848	13	1.00	
graz2	1.136	3.622	0.754			
graz3	0.695	3.974	0.861			
pH	−2.798	0.971	0.004	13	1.00	
SAC	−0.001	0.014	0.944	13	1.00	
Height	−5.400	2.705	0.046	12	0.94	
LDMC	31.140	11.440	0.007	13	1.00	
graz1:RASE	−0.023	0.007	< 0.001	13	1.00	
graz2:RASE	−0.010	0.007	0.137			
graz3:RASE	−0.019	0.007	0.009			
graz1:SAC	0.015	0.011	0.196	13	1.00	
graz2:SAC	−0.003	0.011	0.774			
graz3:SAC	−0.007	0.012	0.595			
graz1:aridity	1.834	3.782	0.628	3	0.26	
graz2:aridity	2.047	4.102	0.618			
graz3:aridity	2.428	4.633	0.603			
AMT:Height	0.072	0.056	0.200	10	0.80	
AMT:LDMC	0.004	0.048	0.927	1	0.06	
Height:RASE	< −0.001	0.002	0.962	1	0.06	
LDMC:RASE	< 0.001	0.007	0.947	1	0.06	
graz1:Height	0.124	0.502	0.806	1	0.07	
graz2:Height	0.088	0.386	0.819			
graz3:Height	0.100	0.423	0.813			
graz1:LDMC	3.766	1.738	0.030	13	1.00	
graz2:LDMC	4.336	1.405	0.002			
graz3:LDMC	2.325	1.225	0.058			
Height:pH	0.617	0.309	0.046	12	0.94	
LDMC:pH	−4.596	1.592	0.003	13	1.00	
Height:SAC	< −0.001	0.002	0.997	1	0.06	
LDMC:SAC	0.003	0.016	0.824	2	0.13	

Note: n is the number of times the variable was included in the set of best models. The variable importance is the sum of the Akaike weights over all models including each explanatory variable.

Abbreviations: AMT, annual mean temperature, °C; aridity, 1-precipitation/potential evapotranspiration; graz1, low grazing pressure; graz2, medium grazing pressure; graz3, high grazing pressure; Height, plant height, cm; LDMC, leaf dry matter content, %; pH, soil pH; R^2c, conditional R^2, that is, the fraction of variation explained by the model including the random effect; R^2m, marginal R^2, that is, the fraction of variation explained by the model not including random effects; RASE, rainfall seasonality, the coefficient of variation of monthly precipitation; SAC, soil sand content, %.

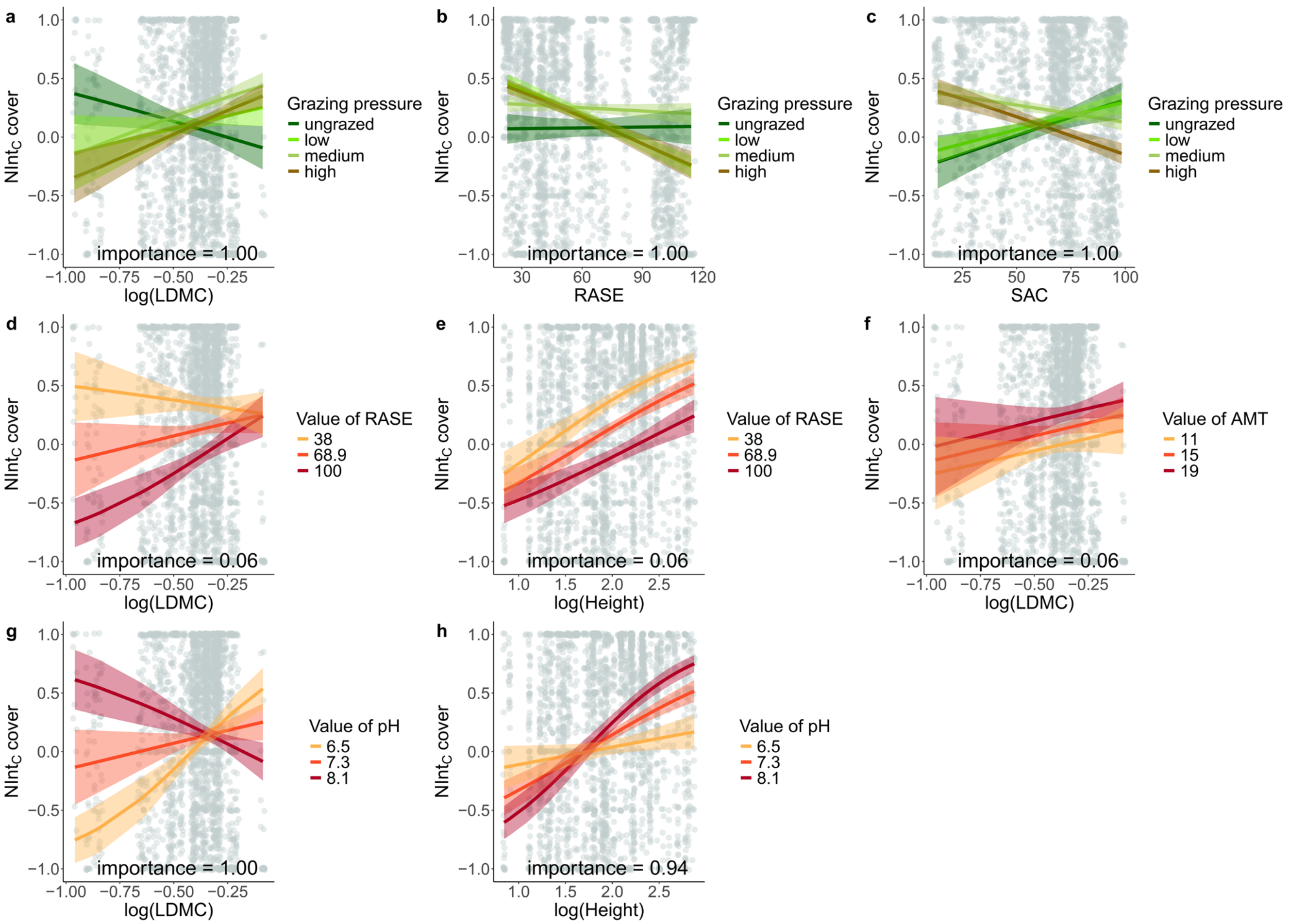

FIGURE A3 | The effects of interaction terms included in the summarised model of NInt$_C$ cover. The relationships between these interaction terms and NInt$_C$ cover do not differ from relationships with NInt$_C$ richness. Lines illustrate the predicted relationship between NInt$_C$ cover and plant traits, dependent on environmental variables. Where there are interactions between continuous variables, three levels of the continuous variables (mean, mean + standard deviation, mean − standard deviation) are shown to illustrate the interaction. The importance of each interaction term in the summarised model is shown to the left of each figure. The variable importance is calculated as the sum of the Akaike weight of each model containing the variable. log(LDMC), dominant plant leaf dry matter content (log transformed); log(Height), dominant plant height (log transformed); RASE, rainfall seasonality; AMT, annual mean temperature; Aridity, 1-potential precipitation/potential evapotranspiration; SAC, soil sand content; pH, soil pH.

TABLE A4 | Predictors included in the best models (there were two best models with ΔAIC < 2) for the difference in height between dominant and target species.

Predictors selected	Estimate	Standard error	p	n	Variable importance	Whole model R^2c and R^2m
Latitude (sin)	−17.380	24.3101	0.475	2	1.00	R2m = 0.306, R2c = 0.944
Longitude (sin)	56.742	12.594	< 0.001	2	1.00	
Association (dominant)	−7.463	47.8035	0.876	2	1.00	
AMT	3.460	4.014	0.389	2	1.00	
Aridity	−579.190	114.931	< 0.001	2	1.00	
RASE	3.064	0.700	< 0.001	2	1.00	
graz1	−3.374	9.154	0.713	2	1.00	
graz2	12.633	9.204	0.170			
graz3	16.081	8.696	0.065			
pH	36.197	7.660	< 0.001	2	1.00	
SAC	−1.555	0.259	< 0.001	2	1.00	
AMT:association	−14.562	1.614	< 0.001	2	1.00	
aridity:association	562.153	55.377	< 0.001	2	1.00	
RASE:association	−1.109	0.122	< 0.001	2	1.00	
graz1:association	−3.374	9.154	0.713	2	1.00	
graz2:association	12.633	9.204	0.170			
graz3:association	16.081	8.696	0.065			
pH:association	−24.822	6.801	< 0.001	2	1.00	
SAC:association	−0.1101	0.178	0.537	1	0.45	

Note: n is the number of times the variable was included in the set of best models. The variable importance is the sum of the Akaike weights over all models including each explanatory variable.

Abbreviations: AMT, annual mean temperature, °C; aridity, 1-precipitation/potential evapotranspiration; graz1, low grazing pressure; graz2, medium grazing pressure; graz3, high grazing pressure; Height, plant height, cm; LDMC, leaf dry matter content, %; pH, soil pH; R^2c, conditional R^2, that is, the fraction of variation explained by the model including the random effect; R^2m, marginal R^2, that is, the fraction of variation explained by the model not including random effects; RASE, rainfall seasonality, the coefficient of variation of monthly precipitation; SAC, soil sand content, %.

TABLE A5 | Predictors included in the best models (there were two best models with ΔAIC <2) for the difference in LDMC between dominant and target species.

Predictors selected	Estimate	Standard error	p	n	Variable importance	Whole model R^2c and R^2m
Latitude (sin)	0.010	0.085	0.902	3	1.00	R^2m = 0.280, R^2c = 0.890
Longitude (sin)	−0.022	0.063	0.731	3	1.00	
association (dominant)	1.342	0.177	< 0.001	3	1.00	
AMT	−0.070	0.012	< 0.001	3	1.00	
aridity	0.805	0.352	0.022	3	1.00	
RASE	0.003	0.002	0.040	3	1.00	
graz1	−0.285	0.036	< 0.001	3	1.00	
graz2	−0.076	0.032	0.019			
graz3	−0.236	0.029	< 0.001			
pH	0.201	0.027	< 0.001	3	1.00	
SAC	0.006	< 0.001	< 0.001	3	1.00	
AMT:association	−0.009	0.006	0.138	2	0.84	
aridity:association	1.338	0.185	< 0.001	3	1.00	
RASE:association	< 0.001	< 0.001	0.422	2	0.57	
graz1:association	−0.285	0.036	< 0.001	3	1.00	
graz2:association	−0.076	0.032	0.019			
graz3:association	−0.236	0.029	< 0.001			
pH:association	−0.239	0.023	< 0.001	3	1.00	
SAC:association	−0.004	< 0.001	< 0.001	3	1.00	

Note: n is the number of times the variable was included in the set of best models. The variable importance is the sum of the Akaike weights over all models including each explanatory variable.

Abbreviations: AMT, annual mean temperature, °C; aridity, 1-precipitation/potential evapotranspiration; graz1, low grazing pressure; graz2, medium grazing pressure; graz3, high grazing pressure; Height, plant height, cm; LDMC, leaf dry matter content, %; pH, soil pH; R^2c, conditional R^2, that is, the fraction of variation explained by the model including the random effect; R^2m, marginal R^2, that is, the fraction of variation explained by the model not including random effects; RASE, rainfall seasonality, the coefficient of variation of monthly precipitation; SAC, soil sand content, %.