Journal of Vegetation Science

Journal of Vegetation Science IAVS

SPECIAL ISSUE Island Plant Communities

RESEARCH ARTICLE OPEN ACCESS

Shrubs as Nurse Species for Plant Communities in Arid Environments: A Case Study From Socotra Island (Yemen)

Dario La Montagna[1] | Michele De Sanctis[1] | Petr Maděra[2] | Kay Van Damme[2,3] | Salem Hamdiah[2,4] | Fabio Attorre[1] | Luca Malatesta[1]

[1]Department of Environmental Biology, Sapienza University of Rome, Rome, Italy | [2]Department of Forest Botany, Dendrology and Geobiocoenology, Faculty of Forestry and Wood Technology, Mendel University in Brno, Brno, Czech Republic | [3]Centre for Academic Heritage and Archives and Ghent University Botanical Garden, Ghent University, Ghent, Belgium | [4]Biotechnical Faculty, University of Ljubljana, Ljubljana, Slovenia

Correspondence: Dario La Montagna (dario.lamontagna@uniroma1.it)

Received: 26 September 2024 | **Revised:** 1 January 2025 | **Accepted:** 9 February 2025

Co-ordinating Editor: Julian Schrader

Funding: This work was supported by Franklinia Foundation Projects: "Conservation of the endangered endemic *Boswellia* trees on Socotra Island (Yemen)" Phase I (2020-03) and Phase II (2023-03).

Keywords: biodiversity conservation | facilitative shrubs | insular ecosystems | natural tree regeneration | nature-based solutions | overgrazing | plant–plant interactions

ABSTRACT

Question: Plant–plant facilitation is a critical ecological mechanism in arid environments, influencing biodiversity and ecosystem resilience globally. Shrubs often serve as nurse species, enhancing tree regeneration and sheltering plant communities, particularly in overgrazed or degraded habitats. In this study, we examine the role of shrubs as nurse species in the Socotra Archipelago (Yemen), a biodiversity hotspot in which several endemic tree species, including the iconic frankincense (*Boswellia* spp.), myrrh (*Commiphora* spp.), and Socotran dragon's blood (*Dracaena cinnabari*) trees, are threatened. This is largely due to a lack of natural regeneration caused by the combined effects of overgrazing by goats, sheep, and climatic events such as extreme droughts and cyclones. To aid conservation of threatened trees in arid regions, nature-based solutions are urgently needed to help tree regeneration. Effective nurse plants have this potential, particularly in arid environments. We therefore examined the role of thorny, poisonous, and/or unpalatable shrubs as nurse plants in sheltering threatened plant communities, with a focus on woody species in an arid insular context.

Study Area: The Socotra Archipelago (Yemen) situated in the western Indian Ocean, east of the Horn of Africa. It is a biodiversity sanctuary and a UNESCO Natural World Heritage Site.

Methods: Vegetation surveys were conducted in 144 paired plots under six common shrub species and adjacent open areas. Community data, environmental variables, and functional traits were analysed using RLQ and fourth-corner analyses, while Linear Mixed Models (LMMs) evaluated the effects of environmental variables and nurse species on key functional traits based on Community Weighted Means (CWMs). Facilitation effects were quantified using the Relative Interaction Index (RII).

Results: Our analysis revealed significant variations in species composition and functional traits between under-canopy and open-area plots. Certain shrubs, such as *Cebatha balfourii*, facilitated significantly higher species richness under its canopy compared to open areas. Elevation and grazing pressure influenced these interactions, with notable effects on functional traits like

Island plant communities: natural experiments at the intersection of biogeography, conservation and global change ecology

This article is a part of the Special Issue "Island plant communities: natural experiments at the intersection of biogeography, conservation and global change ecology", edited by Alessandro Chiarucci, Jorge Capelo and Julian Schrader.

This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

© 2025 The Author(s). *Journal of Vegetation Science* published by John Wiley & Sons Ltd on behalf of International Association for Vegetation Science.

the occurrence of legumes and tree growth forms. *Buxus hildebrandtii* was less effective in supporting species richness, while *C. balfourii, Lycium sokotranum*, and two *Cissus* species exhibited significant positive facilitation. The LMMs confirmed the importance of environmental variables and nurse shrub characteristics in shaping plant community dynamics.

Conclusions: The results highlight differences in the facilitative potential of the studied species, with some showing a stronger ability to act as nurse shelters through microhabitat amelioration and protection from herbivory. The presence of tree species under shrubs is confirmed, and the role of these nurse species in supporting diverse plant communities provides critical insights for conservation strategies, supporting biodiversity resilience and sustainable management in degraded landscapes like Socotra Island and other arid environments. Future efforts should focus on leveraging nurse shrubs to mitigate environmental pressures and enhance ecological restoration, in particular to help conserve range-restricted and threatened plant species.

1 | Introduction

Plant–plant interactions are recognised as critical processes shaping the structure and dynamics of plant communities, particularly in arid and semi-arid ecosystems, with facilitation being one of the key interactions. The latter occurs when one species (the "nurse") ameliorates harsh environmental conditions, from which neighbouring or associated plants benefit (Bruno et al. 2003; Filazzola and Lortie 2014). Nurse plants provide essential shelter from abiotic stressors such as extreme temperatures, limited water availability, and high solar radiation. These facilitative effects are vital for maintaining biodiversity and ecosystem function, especially in areas subject to environmental degradation or climatic extremes (Padilla and Pugnaire 2006).

Nurse plants, particularly thorny, poisonous, or unpalatable shrubs, have been observed to provide critical shelter from environmental stressors in various arid and semi-arid environments (Aerts et al. 2006; Badano et al. 2016; Noumi 2020). Nurse plants can offer shade, reduce temperature extremes, and enhance soil moisture retention, all of which are crucial in harsh conditions (Padilla and Pugnaire 2006). Moreover, these interactions can often vary significantly depending on abiotic variables and/or grazing intensity, especially in arid environments. In fact, the association between plant communities and nurse species in arid and semi-arid regions depends on a balance between interference and facilitation effects (Callaway 2007; Butterfield et al. 2010).

While these interactions are well-documented in other regions, island ecosystems like the Socotra Archipelago (Yemen) provide unique opportunities to study plant–plant interactions due to distinct biodiversity, isolation, and environmental pressures. This archipelago is globally recognised as a hotspot of biodiversity, characterised by exceptional species richness and a high degree of endemism (Van Damme and Banfield 2011; Maděra and Van Damme 2022). Socotra Island, the largest in the archipelago, is home to several iconic endemic tree species, including frankincense (*Boswellia* spp.), myrrh (*Commiphora* spp.), and the Socotran dragon's blood tree (*Dracaena cinnabari* Balf.f.). These trees hold not only ecological significance but also cultural importance (Miller and Morris 2004; Attorre and Van Damme 2020). However, despite their value, these endemic species are currently facing severe threats, with the primary concern being a lack of natural regeneration associated with overgrazing (Maděra et al. 2019; Hamdiah et al. 2024).

The decline in regeneration in Socotra is driven by anthropogenic pressures, particularly overgrazing by goats, which have intensified due to the abandonment of traditional grazing practices. Overgrazing remains a significant threat to vegetation and soil health across various arid environments globally (Hempson et al. 2015; Dlamini et al. 2016). For example, in the Xinjiang Uygur Autonomous Region (China), long-term overgrazing has significantly reduced vegetation cover, negatively impacting ecosystem services like carbon sequestration and water regulation (Tai et al. 2021). In Iran, studies have demonstrated that overgrazing leads to a decline in species richness and an increase in the dominance of unpalatable species, underscoring the need for effective management and monitoring programs to mitigate overgrazing impacts (Rahmanian et al. 2020). Similar challenges have been observed in Socotra, where unsustainable grazing practices have contributed to the decline of several tree species, including *Boswellia* spp. and the endemic dragon's blood tree (*D. cinnabari*), highlighting the critical need for sustainable land management strategies that involve local communities (Habrová and Pavliš 2017; Maděra et al. 2019; Maděra et al. 2024; Hamdiah et al. 2024).

This shift may be linked to human population growth and an increase in livestock numbers, leading to widespread overgrazing and degradation of the island's unique habitats. The already scarce tree stands in Socotra may therefore decline further in the future, following human population expansion and development (Riccardi et al. 2020).

The impacts of overgrazing are compounded by extreme climatic events, such as prolonged droughts and cyclones. For example, two cyclones, Chapala and Megh, caused severe damage in 2015 to patches of the endemic *Boswellia elongata* Balf.f. forests in the Homhil area (Lvončík et al. 2020) and *Dracaena cinnabari* forest in the Firmihin area in Socotra (Vahalík et al. 2023). Similar effects of climate change on the survival of some endemic trees, specifically species of the genus *Commiphora*, have been modelled by La Montagna et al. (2023), forecasting that an increase in extreme events could trigger the extinction of *Commiphora socotrana* (Balf.f.) Engl. and *C. planifrons* (Balf.f.) Engl. The combined effects of these natural and anthropogenic pressures are impeding the natural reproductive cycles and growth of these trees, leading to a decline in natural tree populations.

The pressing need to conserve these endangered tree species in arid regions like Socotra necessitates innovative and sustainable solutions. Traditional conservation efforts have

primarily focused on reducing anthropogenic pressures, such as implementing grazing controls or creating enclosed and fenced areas (Xu et al. 2023; Hamdiah et al. 2024). However, while these methods can be effective locally, they may not be sufficient to reverse the overall decline in tree populations. Given the varied landscapes of Socotra, such measures need to be complemented by nature-based solutions that leverage ecological interactions to promote tree regeneration across broader areas.

One promising approach is the use of nurse plants—shrubs that can create microhabitats favourable for the growth and survival of tree seedlings. Despite anecdotal evidence suggesting the presence of facilitative interactions between shrubs and tree seedlings on Socotra (Miller and Morris 2004; Brown and Mies 2012), systematic research on the specific nurse species that could support tree regeneration on the island is lacking. The only studied facilitative effect on the island concerns *Dracaena cinnabari*, which has been shown to positively influence plant communities beneath its canopy (Rejžek et al. 2016). Nevertheless, many studies have used this approach for ecological restoration and conservation of non-endemic species in other arid regions (Aerts et al. 2006; Gómez-Aparicio 2009; Noumi 2020). Therefore, understanding plant–plant interactions is essential for developing effective conservation strategies in arid ecosystems, in this case tailored to Socotra's unique ecological context.

Our study aims to fill the knowledge gap by systematically assessing the role of six locally common shrub species on Socotra Island as key examples of potential facilitators of plant community composition and functional diversity in these arid environments. These species were selected based on a synthesis of existing literature and first-hand observations, focusing on their potential to create favourable microhabitats through morphological characteristics such as canopy structure and traits related to resistance to herbivory. Furthermore, there is a high chance of finding positive interactions among woody shrub species classified as nurse plants (Filazzola and Lortie 2014).

We hypothesise that these shrubs, by ameliorating environmental conditions, significantly influence species composition, functional traits, and trait-environment relationships. By comparing under-canopy and open-area plots across a variety of Socotran habitats, we aim to quantify the extent and nature of these facilitative effects, particularly their role in shaping biodiversity and plant functional traits.

The outcomes of this research are expected to provide critical insights into the ecological interactions underlying plant–plant facilitation, with a focus on tree species, contributing to sustainable conservation strategies in overgrazed arid ecosystems. The findings could also lay the groundwork for restoration projects in Socotra in particular, but also for broader applications across insular and arid ecosystems facing similar challenges, thereby enhancing ecological resilience and promoting sustainable management practices and enhancing biodiversity resilience of threatened habitats and their key plant species.

2 | Materials and Methods

2.1 | Study Area and Study Species

The Socotra Archipelago, located in the western Indian Ocean, 380 km south of Yemen and 100 km from the Horn of Africa, is recognised as a global biodiversity hotspot and centre of plant diversity (Maděra and Van Damme 2022). Separated from southern Arabia in the Oligo-Miocene period, the archipelago's altitudes range from sea level to 1550 m (Haggeher Mountains), with landscapes dominated by limestone plateaus and igneous rock (Beydoun and Bichan 1970; Cheung and DeVantier 2006; Culek 2013).

The climate is tropical (semi)arid, shaped by seasonally reversing monsoons. The NE monsoon from November to March brings most of the rainfall, while the SW monsoon is drier and stormier (Scholte and De Geest 2010). The island has an average temperature of 28.9°C, and rainfall varies, with coastal areas receiving as little as 125 mm annually, while mountainous areas can receive up to 1000 mm, largely from fog (Scholte and De Geest 2010) and horizontal precipitation, which is critical for vegetation (Kalivodová et al. 2020).

In the present study, we selected six shrub species distributed all over the island, occupying various altitudinal belts and vegetation types, to examine the variability of interactions between the plant communities under shrub canopies and the surrounding ones. These species are *Buxus hildebrandtii* Baill. (Buxaceae), *Cebatha balfourii* (Schweinf. ex Balf.f.) Kuntze (Menispermaceae), *Cissus hamaderohensis* Radcl.-Sm. and *C. subaphylla* (Balf.f.) Planch. (Vitaceae), *Lycium sokotranum* R.Wagner & Vierh. (Solanaceae), and *Pulicaria stephanocarpa* Balf.f. (Asteraceae). Except for *B. hildebrandtii* and *C. balfourii*, all these species are endemic to the Socotra Archipelago (Figure S1).

These shrubs vary in canopy structure. *B. hildebrandtii* has a dense and rounded canopy, providing ample shade, while *C. balfourii* forms a looser, sprawling, and spiny canopy with moderate shelter. Similarly, *C. hamaderohensis* and *C. subaphylla* have a loosely structured canopy. *L. sokotranum* features a sparse, spiny canopy offering limited shade, and *P. stephanocarpa* forms a low, diffuse canopy that allows significant sunlight penetration (Miller and Morris 2004).

On the coastal plains and limestone plateaus, up to 800 m a.s.l., it is possible to find *C. subaphylla*, *L. sokotranum* and *P. stephanocarpa*, the latter being more common in the western part of the island. *C. hamaderohensis* replaces *C. subaphylla* above 300 m a.s.l. on the limestone plateaus and escarpments, but it is absent from the granite of the Haggeher mountains.

The shrubs more confined to the mountains are *B. hildebrandtii* and *C. balfourii*. The former grows on both limestone and granite above 500 m, reaching 1050 m in elevation. The latter is restricted to granite substrates of the Haggeher mountains between 700 m and 1100 m a.s.l. (Miller and Morris 2004).

2.2 | Data Collection

We surveyed the vegetation composition of randomly selected individuals of each of the six shrub species and paired control plots in open areas from October to February 2023, the peak period for vegetative growth in plant communities. During the field campaign, we measured the height and perpendicular major and minor axes of the shrubs, assuming the areas to be ellipse-shaped. To investigate the plant communities, we employed a paired survey approach to compare species assemblages under shrub canopies and in open areas (Schöb et al. 2014). The size of the control plots was determined based on the area covered by each surveyed shrub to ensure consistency. Plots within the shrubs were selected at a distance equivalent to 20% of the shrub radius (calculated from the semi-major and semi-minor axes of the elliptical canopy) inward from the edge to minimise edge effects. Control plots in open areas were situated at least 1 m away from the shrubs (Chen et al. 2019; Ram and Chawla 2024).

We surveyed a total of 144 plots: 72 under shrub canopies and 72 in open areas, covering the geographical distribution of the six shrub species as comprehensively as possible (Figure 1). The survey focused on vascular plant species, including ferns. The total vegetation cover (expressed as the proportion of ground covered by vegetation) and percentage abundance of each species were visually estimated. For each recorded species, we selected a comprehensive set of functional traits based on existing literature (Miller and Morris 2004; Weigelt et al. 2020). In cases where information was unavailable, we inferred traits from collected plants and herbarium specimens (Herbarium code: E). The details of these traits and their ecological relevance are presented in Table 1. The identification of the species was carried out using Miller and Morris (2004) and the nomenclature was updated using POWO (2024).

Environmental variables, including mean annual temperature (bio01), annual temperature range (bio07), annual precipitation (bio12), mean relative humidity (Humidity), moisture index, and mean wind speed (Wind), were obtained from the CHELSA database (Karger et al. 2017; Table 2). These variables were downscaled to a 50 m resolution using bicubic interpolation, neighbour embedding in Google Earth Engine (Gorelick et al. 2017), with topographic variables at a 50 m resolution (elevation, slope, aspect) used as covariates to guide the interpolation. This method ensures spatial consistency while capturing fine-scale climatic gradients by explicitly incorporating the relationship between climate and topography.

The paired sampling method may overestimate facilitation due to microhabitat heterogeneity (Steinbauer et al. 2016). However, this heterogeneity may result from long-term feedback between vegetation and the abiotic environment, where nurses themselves create better microhabitats over time (Bera et al. 2021; Michalet et al. 2024).

2.3 | Statistical Analysis

All the statistical analysis used in this work were conducted in R Studio software (R Core Team 2024). Before starting the analysis, the environmental variables were checked for collinearity using correlation plots with the Pearson correlation measure. Moisture index and annual range of temperature variables were excluded because of the high correlation values ($r > 0.7$). Then, community data were transformed with the "Hellinger" method (Legendre and Gallagher 2001) to account for differences in species composition and the prevalence of zeros in biodiversity data, and categorical functional traits were converted into dummy variables through the "fastDummies" package (Kaplan 2020), to ensure they could be properly used in the subsequent analyses.

To explore the relationships between species, traits, and environmental variables, we used RLQ analysis with the R package "ade4" a robust method for identifying ecological strategies along environmental gradients (Bernhardt-Römermann et al. 2008). To further examine the associations between individual traits and environmental variables, we employed the fourth-corner model (Dray and Legendre 2008). This combined approach of RLQ and fourth-corner analyses helped

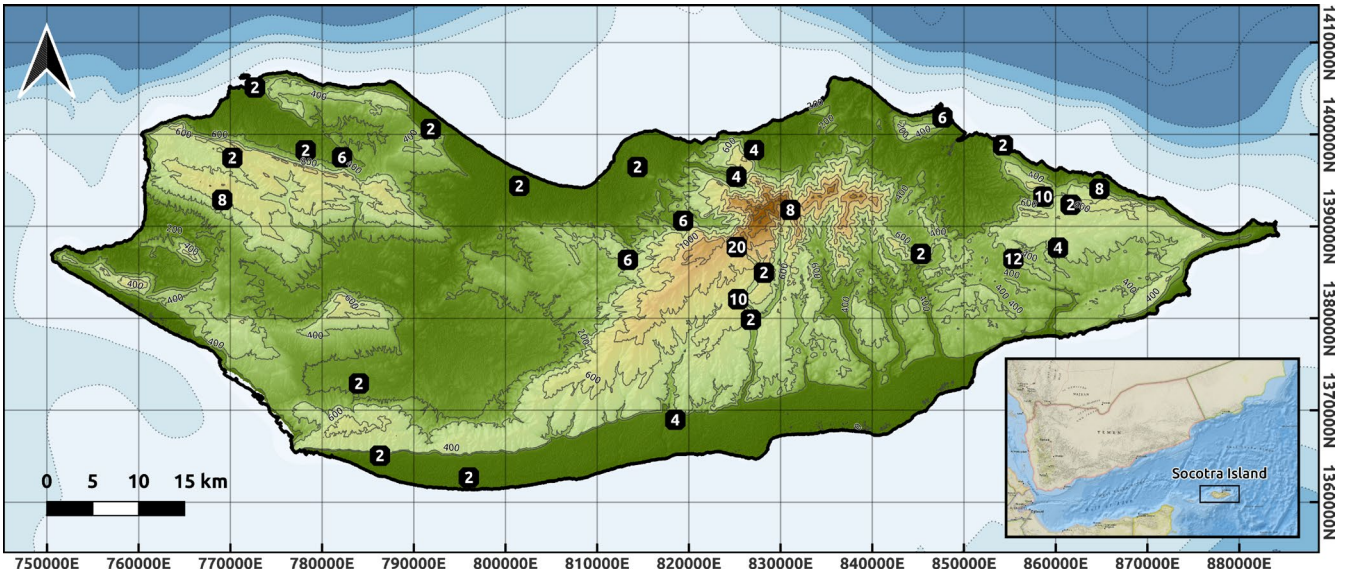


FIGURE 1 | Study area (Socotra Island, Yemen) with number of relevés.

TABLE 1 | Functional traits selected for the analysis. In the table the data type, definition, ecological relevance and source for each trait are shown.

Functional Trait	Type of trait		Definition	Ecological relevance	Source
Average maximum height		Continuous	Shortest distance between the upper boundary of the main photosynthetic tissues on a plant and the ground level	Competitive vigour, reproductive size, whole-plant fecundity, potential lifespan, tree potentiality	Miller and Morris (2004)
Legume		Binary	The presence of legume as fruit	"nutrient economy", i.e., the capture and use of nitrogen	GIFT Database (Weigelt et al. 2020)
Spinescence		Binary	The presence of spine and thorns	Anti-herbivore defence, especially against vertebrate herbivores	GIFT Database (Weigelt et al. 2020)
Climber	Categorical	Facultative Obligatory Self-supporting	Plant that roots in the soil but relies, at least initially, on external support for its upward growth and leaf positioning.	Potential contribution to microhabitat formation and structural shelter	GIFT Database (Weigelt et al. 2020)
Growth Form	Categorical	Graminoid Herb Shrub Tree	Relation of the plant's perennating tissue to the ground surface.	Perennating tissue is what enables the plant to survive harsh, unfavourable (cold or dry) seasons	GIFT Database (Weigelt et al. 2020)
Life Cycle	Categorical	Annual Annual-Perennial Perennial	Defined as the time period from establishment until no live part remains of the respective individual.	Indicator of population persistence and is therefore strongly related to land use and climate change	GIFT Database (Weigelt et al. 2020)
Plant habit	Categorical	Ascending Cushion Erect Pendant Prostrate Rambling Scandent Tussock	Structural growth pattern, which describes the way a plant spreads, climbs, or arranges its stems and branches.	Resource competition, adaptation to stress, and interactions with pollinators and herbivores.	Miller and Morris (2004)

TABLE 2 | Environmental variables employed in the analysis with description, measure unit, and source.

Environmental variables	Description	Unit	Source
Vegetation cover	Percentage of ground area covered by vegetation	%	Collected in the field
Plot area	Measurement of plot size	m^2	Collected in the field
Plot position	Specific shrub species or area outside	—	Collected in the field
Annual mean temperature (Bio01)	Mean annual daily mean temperatures averaged over 1 year	°C	Chelsa database (Karger et al. 2017)
Annual range of temperature (Bio07)	Difference between maximum temperature of warmest month and minimum temperature of coldest month	°C	Chelsa database (Karger et al. 2017)
Annual precipitation (Bio12)	Accumulated precipitation amount over 1 year	mm	Chelsa database (Karger et al. 2017)
Slope	Steepness of a surface	%	Collected in the field
Wind	Mean monthly near-surface wind speed	ms^{-1}	Chelsa database (Karger et al. 2017)
Humidity	Mean monthly near-surface relative humidity	%	Chelsa database (Karger et al. 2017)
Moisture index	Mean monthly climate moisture index	$kg\,m^{-2}\,month^{-1}$	Chelsa database (Karger et al. 2017)

identify patterns in species-environment interactions, providing insights into the ecological processes through both descriptive and inferential statistical techniques (specifications on these analyses can be found in Supporting Information). This analysis allowed us to identify the most ecologically influential environmental variables and functional traits on plant communities, which were then used for the mixed linear models. Between-Class Analysis (BCA) was performed on the RLQ results to evaluate how trait-environment relationships differed between plots categorised by nurse species and overall outside plots.

Species significantly associated with under-canopy and open area communities were identified using the Indicator Species Analysis (ISA, De Cáceres et al. 2010). We employed the "multipatt" function of the "vegan" package (Oksanen et al. 2017) with 4999 permutations to identify indicator species for the paired plots (under-canopy vs. open areas) and per each shrub species.

We analysed functional traits based on species abundances using the community-weighted mean (CWM, Lavorel et al. 2008), focusing on traits significant after the fourth-corner analysis. CWMs were calculated for each pair of plots (under the canopy and in open areas) to examine functional traits within different microsites and to reflect their relative prevalence. Binary traits calculated into CWMs represent the proportion of the community dominated by species with a given trait.

To further investigate the effects of environmental factors and nurse species on functional traits, we used Linear Mixed Models (LMMs) with the lme4 package (Bates et al. 2014). These models evaluated the overall influence of environmental variables and position (under-canopy vs. open areas) on various functional traits. CWM values were used as dependent variables to characterise the effects of all the nurse species on traits, and significant environmental variables from the RLQ analysis were used as predictors (fixed effects). To avoid spatial autocorrelation, we calculated nearest neighbour distances and compared the observed mean to the expected mean for a completely spatially random distribution, calculating the Clark–Evans test, which revealed a clustered pattern in our survey. K-means clustering was then applied, with the optimal number of clusters determined using the elbow method and identifying the "elbow" point at $k = 3$. Spatial groups, as determined by the clustering, and paired plots were treated as a random effect to account for non-independence. Initial models excluded statistical interactions; if multiple predictors were significant, a second model included interaction effects. In the comparisons of models with and without interaction terms, the Akaike Information Criterion (AIC) and Bayesian Information Criterion (BIC) were used to evaluate and select the model that provided the best fit to the data. Then, marginal and conditional R^2 values were estimated to indicate the model fit for fixed and random effects, respectively.

We further explored the interaction between under-canopy and open-area plant communities using species accumulation curves and the Relative Interaction Intensity index (RII; Armas et al. 2004). The RII, ranging from −1 to 1, detects competition or facilitation effects on vegetation assemblages.

$$\mathrm{RII} = \frac{\left(X_{\mathrm{inside}} - X_{\mathrm{outside}}\right)}{\left(X_{\mathrm{inside}} + X_{\mathrm{outside}}\right)}$$

Typically, RII is calculated using biomass or abundance/richness. We applied RII to these metrics and, due to the low values

of these factors in arid environments, we further adapted RII to functional traits by calculating CWMs for those traits statistically significant from the RLQ analysis to reflect the relative prevalence of traits in plant communities. RII values close to 1 indicate a higher relative dominance of the trait under shrubs compared to open areas, while values close to −1 indicate higher dominance in open areas. In this case, the position variable is intrinsic to the RII value, enabling us to discern differences between individual shrub species. This approach also allows us to evaluate relative shifts in the prevalence of functional traits. T-tests were conducted to determine if the accumulation curves are significantly different and if RII values significantly differed from zero for each nurse species.

3 | Results

3.1 | Phytosociological Relevés and Vegetation Measurements

The studied shrub species covered a range of sizes, with larger species such as *B. hildebrandtii*, *C. subaphylla*, and *C. balfourii*; medium-sized species like *C. hamaderohensis* and *L. sokotranum*; and the smaller *P. stephanocarpa* (Table S1).

When looking at species richness, several differences are noticeable between the interior of individual shrubs and the external plots. Specifically, mean species counts (± standard deviation), under the shrub canopy compared to the open areas, were as follows: *B. hildebrandtii* (45 ± 2 vs. 57 ± 3), *C. balfourii* (48 ± 6 vs. 38 ± 2), *C. hamaderohensis* (56 ± 4 vs. 45 ± 2), *C. subaphylla* (47 ± 3 vs. 40 ± 3), *L. sokotranum* (60 ± 4 vs. 60 ± 3), and *P. stephanocarpa* (39 ± 3 vs. 38 ± 2). Accumulation curves show that the number of species found within the shrubs is variable compared to the open areas, but the curves do not significantly differ in statistical terms. Despite this, a trend can be observed where *B. hildebrandtii* hosts fewer species under its canopy when compared to open areas. On the other hand, the two *Cissus* species and *C. balfourii* host a few more species compared to the outside plots (Figure S2).

3.2 | Species-Environment Relationships

BCA analysis separates the nurse species from the outside plots (Figure 2) whilst the PCA analyses separate some of the under-canopy plots and all the outside ones along the first axis, while the second axis distinguishes plots with higher wind speed and precipitation from those with higher mean temperatures (Figure S3). Trait loadings show a complex pattern, but it is possible to distinguish two main groups, or trait syndromes, along the second axis. Species typical of grasslands, such as graminoid species with a tussock habit and some annual species, are associated with positive loadings. Conversely, tree and shrub species (with higher Average Maximum Height—AMH) dominate the negative loadings, along with climber and rambling species typical of shrublands and woodlands (Figure S3).

The RLQ analysis shows significant results, confirmed by Monte Carlo permutation tests on Model 2 and Model 4 types, with $p < 0.001$ in both cases. Both RLQ axes contribute to the total co-inertia, with Axis 1 accounting for 47.77% and Axis 2 for 30.09%. Different environmental variables (e.g., annual mean temperature, annual precipitation, wind) and traits (e.g., AMH, graminoid growth form, perennial life cycle) are significantly related to these axes (Figure S3). Therefore, the RLQ axes can be defined as gradients of different trait-environment interactions or synthetic trait syndromes (Raevel et al. 2012).

Testing the relationships between environmental variables and functional traits using the fourth-corner analysis provides further insight into patterns that help characterise species-environment relationships. There are positive relationships between species with higher AMH and tree growth form with *C. subaphylla* ($p < 0.05$ and < 0.01, respectively). Conversely, these traits are negatively associated with the outside plots (both $p < 0.01$). In contrast,

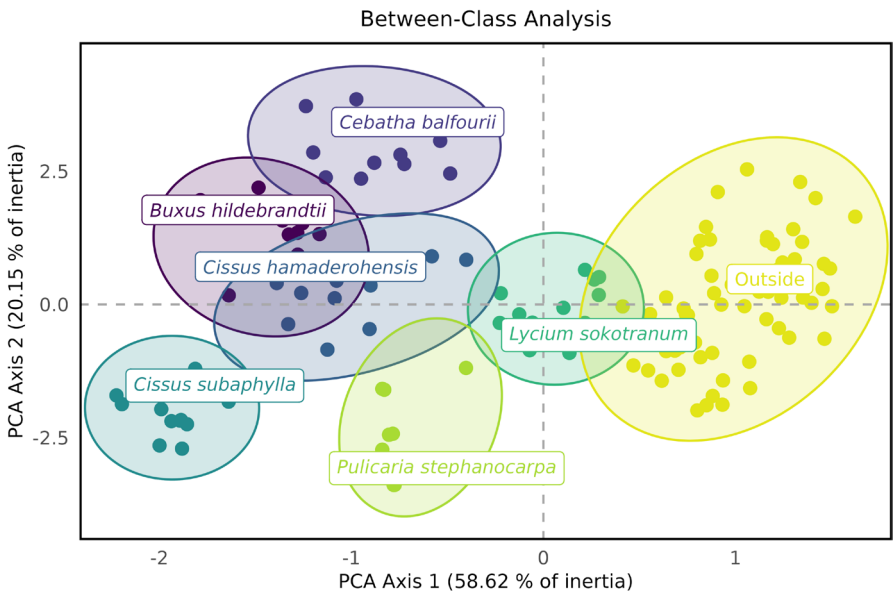


FIGURE 2 | Between-Class Analysis (BCA) plot showing species groupings based on the first two principal components (PCA Axis 1: 58.62%, PCA Axis 2: 20.15%). Each point represents an individual sample, with ellipses highlighting the variance within species groups.

the outside plots are significantly positively associated with traits such as the tussock habit and graminoid growth form ($p < 0.01$) which dominate open grassland habitats. Additionally, graminoids show a positive correlation with overall vegetation cover ($p < 0.01$). Finally, species with legume trait grouping exhibit a negative relationship with areas subjected to higher annual mean wind speeds ($p < 0.05$) and a positive correlation with areas characterised by higher mean annual temperatures ($p < 0.05$) (Figure S4).

Looking at the correlation between environmental variables and species traits with the two RLQ axes, different shrub species and outside plots are positively and negatively correlated with the two axes, respectively ($p < 0.05$), as shown in Figure S5. Vegetation cover is the only variable positively correlated with Axis 1 ($p < 0.05$). On Axis 2, annual mean temperature and annual precipitation amount are positively correlated ($p < 0.05$), whereas mean wind speed is negatively correlated ($p < 0.05$). The traits perennial, AMH, and Tree growth form are negatively correlated with Axis 1 ($p < 0.01$), while tussock and graminoid traits are positively correlated with Axis 1 ($p < 0.01$). The only two traits correlated with Axis 2 are legume, positively ($p < 0.01$), and shrub, negatively ($p < 0.05$).

The results of the ISA indicate characteristic plant assemblages for the outside plots and those under individual shrubs. Notably, there are 10 characteristic species found outside, most of which are grasses, along with some Leguminosae and tussock species. Furthermore, the results for the characteristic species of the individual shrubs demonstrate a clear characterisation of the communities within them, ranging from a minimum of two characteristic species in *P. stephanocarpa* to a maximum of 15 in *C. balfourii*. Specific details of these assemblages can be found in the Table S2.

Models fitting the CWM per each trait as dependent on the different environmental variables chosen showed different but comparable results (Table 3). The linear mixed models revealed that environmental variables play a crucial role in shaping CWMs calculated per each trait, with some effects being particularly pronounced. For example, the Average Maximum Height of plants is significantly influenced by the position of the plot ($p < 0.001$), so there is an effect of the under-canopy on taller plants. Similarly, legume functional type is significantly affected by climatic variables, such as annual mean temperature ($p < 0.05$) and plot position ($p < 0.05$), suggesting a complex interaction between climate and under-canopy vs. open areas. The interaction between annual mean temperature and position is also significant ($p < 0.05$), highlighting the subtle interplay between environmental conditions and plant traits (Figure 3).

For perennial plants, there was a significant reduction in Trait Community Weighted Means with changes in both position ($p < 0.01$) and cover ($p < 0.05$), pointing to the importance of spatial factors and vegetation density in determining the abundance of these plants. Tussocks, on the other hand, were significantly influenced by wind exposure ($p < 0.05$) and position ($p < 0.01$) (Figure 4).

Shrubs demonstrated sensitivity to both positional and climatic interactions, with significant effects observed for position ($p < 0.01$) and the interaction of annual mean temperature with position ($p < 0.05$). This suggests that shrubs are highly responsive to both spatial location and climatic variations, which may affect their growth and survival. Finally, for tree growth form, there is a significant effect of position ($p < 0.001$).

The random effects associated with "site" varied among traits, with some, like legume traits, showing high variability, indicating substantial differences between sites. This variability suggests that while fixed effects capture significant portions of the overall variability, site-specific factors also play an essential role in shaping plant traits.

The models explained a small to moderate proportion of the variability in Trait Community Weighted Means, with marginal R^2 values ranging from 0.14 to 0.52 and conditional R^2 values ranging from 0.2 to 0.56, highlighting both the variability captured by fixed effects and the additional contribution of random effects. The conditional R^2 values ranged from 0.2 (perennial) to 0.56 (Average Maximum Height), highlighting that both fixed and random effects account for significant portions of variability. The marginal R^2 values ranged from 0.14 to 0.52, indicating that fixed effects alone also provide a good fit for the data, particularly for traits such as graminoid ($R^2m = 0.52$).

The analysis of the Relative Interaction Index (RII) revealed significant effects of various shrub species on species richness, species abundance, and functional traits on Socotra Island. For species richness, *C. balfourii* showed positive RII values, indicating a significant positive effect ($p < 0.01$), whilst *B. hildebrandtii* showed negative values ($p < 0.05$). The other shrubs do not show significant effects on species richness ($p > 0.05$). Regarding species abundance, *B. hildebrandtii* exhibited a significant negative RII value ($p < 0.05$) (Figure 5).

In terms of functional traits, significant statistical interactions were observed with specific traits. For example, *B. hildebrandtii* and *C. subaphylla* had significant negative effects on legume traits ($p < 0.001$), indicating a higher frequency of occurrence of leguminous species outside. Looking at tree growth form, all the shrubs except for *B. hildebrandtii* show a higher prevalence of this trait ($p < 0.001$) (Figure 6).

4 | Discussion

4.1 | Shrubs Facilitation and Patterns of Species Richness

Our results showed clear differences in species composition and some differences in species richness between under-canopy areas of shrubs in comparison to the open plots. Accumulation curves highlighted non-significant differences in the number of species; not all shrub species hosted a higher number of species under their canopy. In most cases, species richness under or outside the shrubs was similar, with no significant differences. For one species, the open-area plots contained even more species, with *B. hildebrandtii* hosting fewer species than the surrounding plots. This finding was supported by the RII analyses, which indicated higher species richness, abundance, and composition in the open areas, suggesting that this shrub contributes less to fostering more diverse communities.

TABLE 3 | Summary of the linear mixed model to test the effects of environmental variables on the CWMs calculated per each trait. Marginal R^2 (R^2_m) represents the fit of the fixed terms; Conditional R^2 (R^2_c) represents the fit of the fixed terms plus the random effect.

	Random effect	Site	Spatial groups	Residual	Fixed effect	Intercept	Cover	Annual mean temperature	Annual precipitation	Wind	Position	Annual mean temperature: Position	Cover: Position	Annual precipitation: Position		
Average Maximum Height	Var ± SD	0.14 ± 0.38	/	0.19 ± 0.44	Estimate ± SD	5.70 ± 2.04	0.002 ± 0.002	−0.03 ± 0.06	−0.01 ± 0.01	0.01 ± 0.04	−0.68 ± 0.08	—	—	—	R^2_m	0.24
					t value	2.78	1.14	−0.46	−0.80	0.06	−8.39	—	—	—	R^2_c	0.57
					p	**< 0.01****	0.26	0.65	0.43	0.95	**< 0.001*****	—	—	—	R^2	0.37
Legume trait	Var ± SD	82.46 ± 9.1	1.67 ± 1.3	226.04 ± 15.1	Estimate ± SD	−108.9 ± 63.1	−0.13 ± 0.1	4.71 ± 2.1	0.09 ± 0.05	−2.22 ± 1.18	−99.8 ± 48.4	4.6 ± 1.9	—	—	R^2_m	0.35
					t value	−1.72	−1.61	2.18	1.63	−1.90	−2.06	2.33	—	—	R^2_c	0.53
					p	0.09	0.10	**< 0.05***	0.10	0.06	**< 0.05***	**< 0.05***	—	—	R^2	0.39
Perennial	Var ± SD	15.49 ± 3.9	10.1 ± 3.1	406.7 ± 20.1	Estimate ± SD	181.5 ± 62.3	−0.2 ± 0.09	−2.63 ± 2.06	−0.05 ± 0.06	−2.20 ± 1.3	−8.8 ± 3.6	—	−0.14 ± 0.1	—	R^2_m	0.15
					t value	2.90	−2.20	−1.27	−0.91	−1.75	−2.43	—	−0.91	—	R^2_c	0.2
					p	**< 0.01****	**< 0.05***	0.20	0.36	0.08	**< 0.01****	—	0.37	—	R^2	0.16
Tussock	Var ± SD	8.65 ± 2.9	0.02 ± 0.1	352.5 ± 18.7	Estimate ± SD	105.3 ± 57.9	0.21 ± 0.1	−2.85 ± 1.9	−0.16 ± 0.1	−0.16 ± 1.16	49.7 ± 18.3	—	—	−0.12 ± 0.07	R^2_m	0.36
					t value	1.82	1.89	−1.51	−0.14	−2.56	2.71	—	—	−1.64	R^2_c	0.37
					p	0.07	0.06	0.14	0.89	**< 0.05***	**< 0.01****	—	—	0.11	R^2	0.37
Graminoid	Var ± SD	10.8 ± 3.3	2.03 ± 1.4	416.2 ± 20.4	Estimate ± SD	66.6 ± 62.4	0.19 ± 0.13	−2.01 ± 2.1	−0.1 ± 0.05	1.71 ± 1.2	11.8 ± 7.7	—	0.41 ± 0.1	—	R^2_m	0.52
					t value	1.07	−1.48	−0.97	1.77	1.36	1.53	—	2.67	—	R^2_c	0.54
					p	0.29	0.14	0.33	0.08	0.18	0.13	—	**< 0.01****	—	R^2	0.53
Shrub	Var ± SD	8.6 ± 2.9	/	244.8 ± 15.6	Estimate ± SD	164.1 ± 54.2	−0.08 ± 0.07	−5.9 ± 1.9	−0.003 ± 0.04	0.54 ± 0.1	−135.3 ± 50.3	4.9 ± 2.3	—	—	R^2_m	0.25
					t value	3.02	−0.06	−1.09	0.56	−3.14	−2.69	2.41	—	—	R^2_c	0.28
					p	**< 0.01****	0.95	0.28	0.58	**< 0.01****	**< 0.01****	**< 0.05***	—	—	R^2	0.26
Tree	Var ± SD	78.7 ± 8.8	/	388.1 ± 19.7	Estimate ± SD	127.3 ± 69.1	−0.17 ± 0.1	−3.2 ± 2.3	−0.01 ± 0.06	0.14 ± 1.4	−32.3 ± 3.5	—	—	—	R^2_m	0.4
					t value	1.84	−1.73	−1.41	−0.29	0.10	−9.07	—	—	—	R^2_c	0.5
					p	0.07	0.09	0.16	0.77	0.92	**< 0.001*****	—	—	—	R^2	0.42

Note: The relative ranking of the "Position" variable for each trait was determined from the linear mixed model results, with Inside>Outside for "Average Maximum Height", "Perennial", "Shrub" and "Tree". Significance of bold values added with the mean of asterisks.

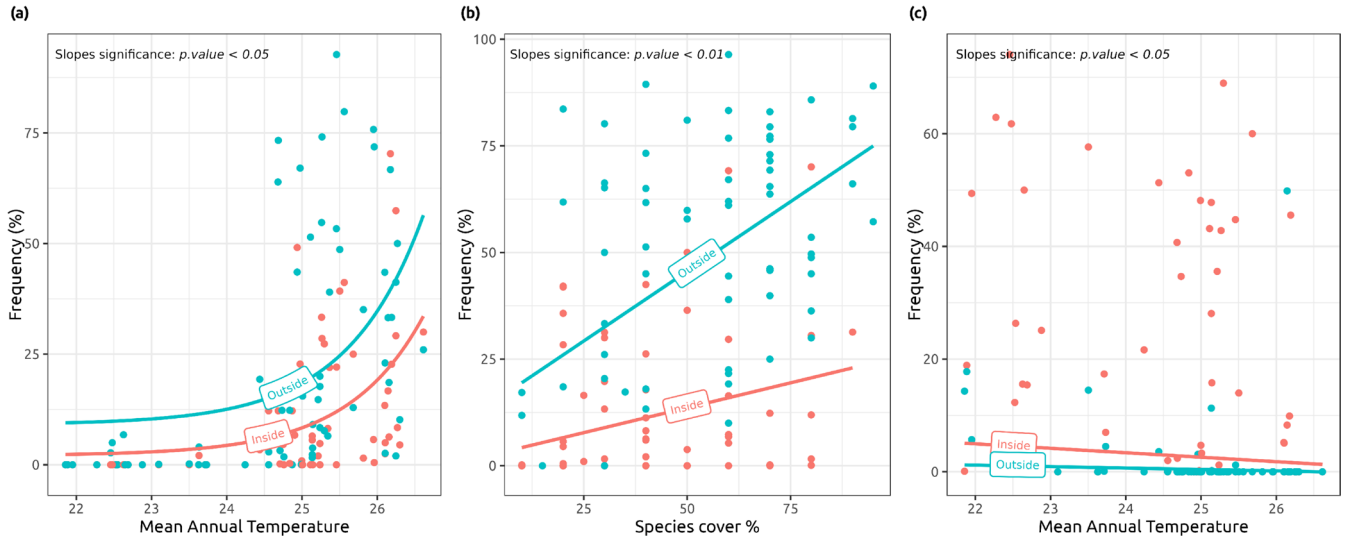


FIGURE 3 | Functional trait group percentage frequencies modelled against environmental variables. (a) Legumes vs. mean annual temperature, (b) Graminoids vs. species cover, and (c) Shrubs vs. mean annual temperature, comparing areas inside (pink) and outside (blue) the nurse species.

In contrast, *C. balfourii*, *C. hamaderohensis*, and *C. subaphylla* showed a higher number of species within their canopies, likely due to their loose canopy structure that allows more light to penetrate. However, only *C. balfourii* showed higher species richness, albeit with lower abundance. These results suggest that certain species are more frequently found under the canopy of specific shrubs, potentially due to protection from herbivory or other processes, such as microclimatic conditions created by the canopy or non-random seed dispersal.

4.2 | Plant Assemblages Are Influenced by Functional Traits and Environmental Gradients

The RLQ analysis further strengthened the distinction between under-canopy and open-area communities. Plant assemblages were arranged according to well-defined patterns based on environmental variables and functional traits. The second axis of the RLQ analysis described a clear gradient of altitude, defined by an increase in average wind speed and a decrease in annual mean temperature, which are negatively correlated. This was exemplified by the distribution of shrubs like *C. subaphylla* and *P. stephanocarpa*, predominantly found at altitudinal ranges between sea level and 600 m, while *C. balfourii* was the only shrub species that reached elevations of 1100 m, thriving in the mountainous areas of the island.

On the other hand, the first axis of the RLQ analysis was not strictly defined by environmental variables but rather by plot location and specific functional traits. The plots were divided into those under the canopy and those outside, with *L. sokotranum* showing no strong preference, likely because it does not act as a facilitator, as seen by the minimal differences in species richness and functional traits between under-canopy and open areas. Functionally, shrubs tended to have a greater prevalence of trees within their canopies, while graminoids were more common in open areas, indicating a differentiation of communities between the two habitats. This was further supported by the indicator species analysis, which identified characteristic species of open plots, particularly grasses.

Key functional traits help distinguish the plant communities within and outside shrub canopies, defining two distinct environments. For instance, the presence of plants with low average height, tussock grasses, graminoids, and legumes characterise grasslands, specifically pastures (Shankarnarayan 1977; Kurtz et al. 2018), like those on Socotra, which have been shaped by the effects of overgrazing for several centuries (Van Damme and Banfield 2011). One evident impact of grazing is the increase in tussock grasses and graminoids, as many species (e.g., *Heteropogon contortus*, *Aristida adscensionis*) are unpalatable, and some only become unpalatable after the early growing season (Miller and Morris 2004; Yaqoob and Javed 2008). Hempson et al. (2022) define many plant species as 'avoiders' and 'tufted attractors', including some that also occur on Socotra that we encountered in the open-area plots; these grow in moderately disturbed, regularly grazed areas. In the case of extreme grazing, tussocks would entirely disappear, with annual species dominating instead (Noy-Meir et al. 1989; Díaz et al. 2007). The presence of legumes, which are more frequent in disturbed environments, indicates significant disruption caused by grazing and livestock trampling (Al-Rowaily et al. 2015). Legumes are typically early colonisers that restore disturbed soils, facilitating conditions for future plant succession (Grime 2001; Menge and Chazdon 2016; Wang et al. 2021). On Socotra, however, free-roaming livestock keep maintaining these grazed areas in a perpetual pioneer stage.

4.3 | Nurse Shrubs Serve as Shelters for Tree Regeneration and Species Conservation

Within the shrub canopies, a different set of species with distinct functional traits dominates. Species with shrub-like and tree-like growth forms, capable of achieving greater height,

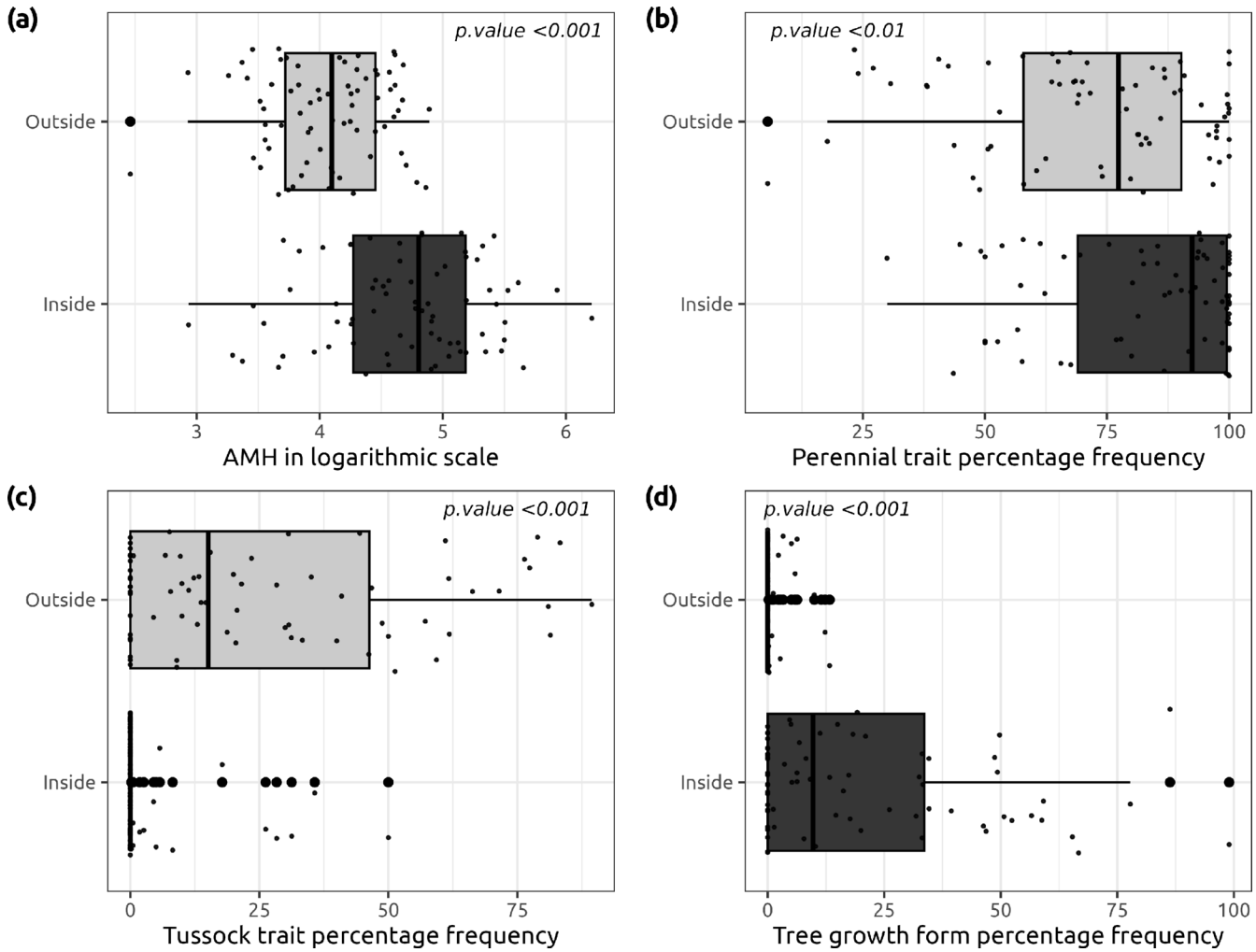


FIGURE 4 | Boxplots from linear mixed models without statistical interactions. (a) Average Maximum Height (log scale), (b) Perennial, (c) Tussock, and (d) Tree growth form trait frequencies, comparing inside and outside the nurse species.

are more common here. This is evidenced by the elevated average maximum height (AMH) within shrubs, which supports the idea that these, or at least some of them, may facilitate the presence of trees by offering shelter, creating more favourable conditions (e.g., increase moisture) and protection from overgrazing. Although it cannot be definitively stated that these shrubs function as "nurse species," trees like *Boswellia* spp. and *Commiphora* spp. do germinate outside of them, albeit with a reduced chance of survival in grazed areas versus exclosures, as demonstrated by Hamdiah et al. (2024). Thus, the role of shrubs as protective microhabitats for plant communities remains clear, offering refuge from grazing and improving survival rates for different species. Certain shrub species play a crucial role in supporting the survival of several endemic and/or threatened trees on Socotra. For example, *Boswellia elongata*, *Commiphora planifrons*, *Maerua angolensis* subsp. *socotrana*, *Dendrosycios socotranus*, *Barleria popovii*, and *Cephalocrotonopsis socotranus* are frequently associated with the protected environment of shrub canopies. The wide distribution of these shrubs across various altitudinal zones helps to protect endangered species, increasing their potential for use in future conservation efforts.

Examining individual shrub performance offers valuable insights into selecting the best species for restoration ecology projects. Species such as *C. hamaderohensis* and *C. balfourii* demonstrate strong potential due to their ability to facilitate the regeneration of trees and shrubs. Both species have loose canopies that allow sunlight to penetrate, enabling photosynthesis in the plants beneath them. Moreover, their intricate structures and unpalatability form a physical barrier, preventing livestock from accessing the plants beneath. It is also fascinating to note the ethnobotanical practice among locals, who often plant trees in the centre of shrubs, particularly under *C. hamaderohensis* (Miller and Morris 2004), as a way to promote growth.

The facilitative role of shrubs like *C. balfourii* and *C. hamaderohensis* is significant in the context of Socotra, where overgrazing has severely impacted endemic tree species. These shrubs mitigate the effects of overgrazing by providing protective microenvironments, reducing herbivory, and enhancing seedling establishment. This supports the findings by Hamdiah et al. (2024), who observed that seedling survival drastically decreases in unfenced areas, reinforcing the importance of natural shelters like nurse shrubs in such environments. Moreover, the unpalatability of the shrub species studied here aligns with the "repellent plant hypothesis", where grazing-intolerant plants are sheltered by surrounding plants more tolerant to grazing effect (Milchunas and Noy-Meir 2002).

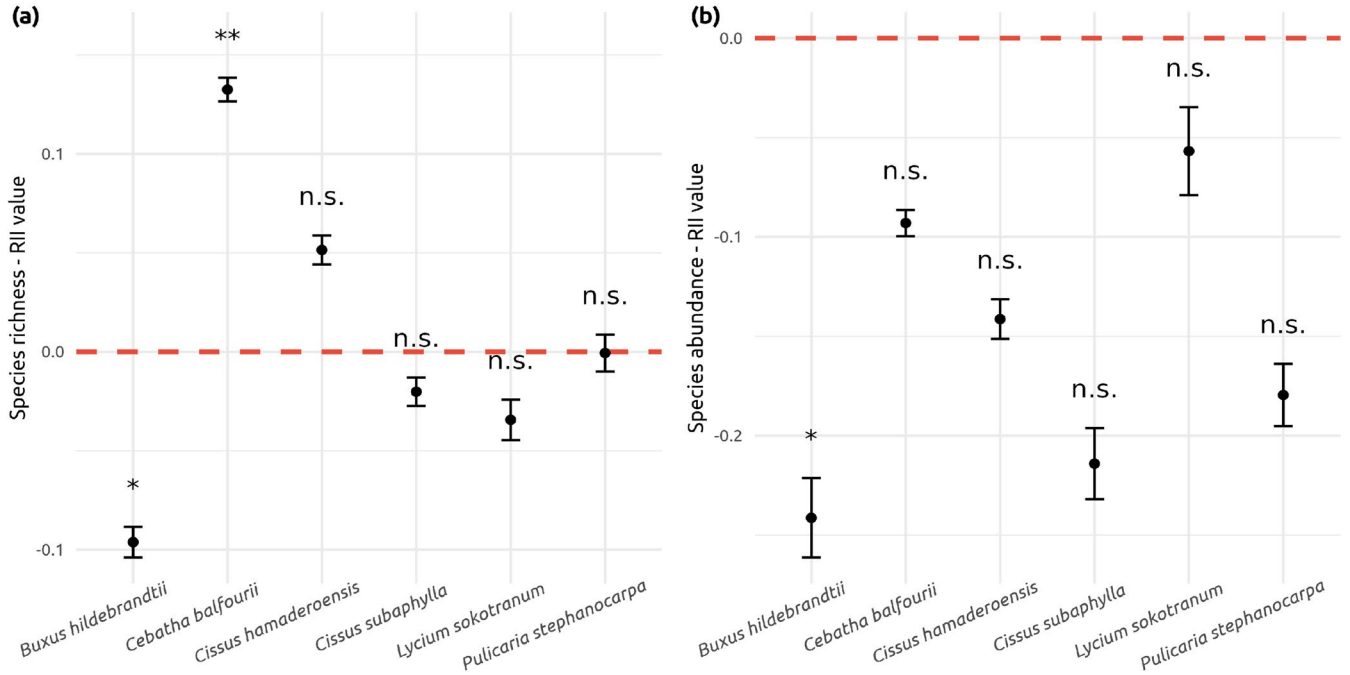


FIGURE 5 | Relative Interaction Intensity (RII) index for different nurse species about species richness (a) and species abundance (b). Error bars indicate Standard Error (SE). Significant positive or negative effects are indicated, with 'n.s.' denoting non-significant results whilst asterisks indicate significance levels (*$p < 0.05$, **$p < 0.01$).

On Socotra Island, it is not possible to find natural areas unaffected by grazing, since livestock freely graze across all areas. Consequently, stratifying the study into grazed and ungrazed areas was not feasible. In arid environments such as Socotra, facilitation by shrubs often occurs due to their ability to retain soil moisture, improve soil fertility, increase soil organic matter, and create favourable microclimatic conditions, thereby mitigating the effects of aridity (Ellis and Swift 1988; Soliveres et al. 2011; Habrová and Pavliš 2017). However, in heavily grazed landscapes, alleviating grazing pressure can also play an important role in facilitation, highlighting the complex interplay between mitigating resource limitations and reducing environmental stresses (Soliveres et al. 2012). In our study, both aridity and grazing pressure are assumed to be limiting factors. The results suggest that the studied shrubs can facilitate species assemblages by mitigating the effects of these stresses through a combination of resource enhancement and stress reduction.

4.4 | Promoting Shrub Facilitation for Long-Term Conservation on Socotra Island

Our results align with previous studies on the role of nurse plants in arid environments. Indeed, shrubs often provide shelters that mitigate environmental stress and promote seedling establishment. For instance, Padilla and Pugnaire (2006) documented similar facilitative effects in Mediterranean environments, where nurse shrubs enhanced diversity and vegetation cover in degraded areas. Similarly, studies in arid China have shown that shrubs like *Caragana korshinskii* improve seedling survival by moderating temperature extremes and improving soil moisture (Tian and Wang 2015).

Additionally, the positive relationship between shrubs and tree growth forms, as revealed here by RLQ and fourth-corner analyses, suggests that these shrubs not only protect seedlings but potentially support their development into mature trees. This has critical implications for conservation strategies, as using nurse shrubs in restoration projects could strengthen Socotra's flora against both biotic and abiotic stressors.

The study also highlights key interactions between environmental variables and plant functional traits. Shrubs like *C. balfourii* and *C. hamaderohensis* are more prevalent at higher altitudes, where they face stronger winds and lower temperatures. Their morphological characteristics probably allow them to buffer these harsh conditions, facilitating the survival of tree seedlings. This is consistent with findings from other arid regions, such as Noumi (2020), who observed that the effectiveness of nurse plants varies significantly along environmental gradients like altitude and temperature.

Identifying these trait-environment interactions is essential for understanding plant community dynamics on Socotra and predicting how these communities may respond to future environmental changes. For instance, the negative relationship between graminoid traits and shrub canopies suggests that shrubs suppress grasses, potentially reducing competition for tree seedlings, which is particularly important in grass-dominated areas where grasses might otherwise outcompete tree seedlings.

While *C. balfourii* and *C. hamaderohensis* facilitated higher species richness within their canopies, *B. hildebrandtii* was associated with lower species richness, possibly due to allelopathic effects. Although there are no specific studies on the allelopathic properties of *Buxus* species, their production of the alkaloid buxine—common in the Buxaceae family—suggests potential

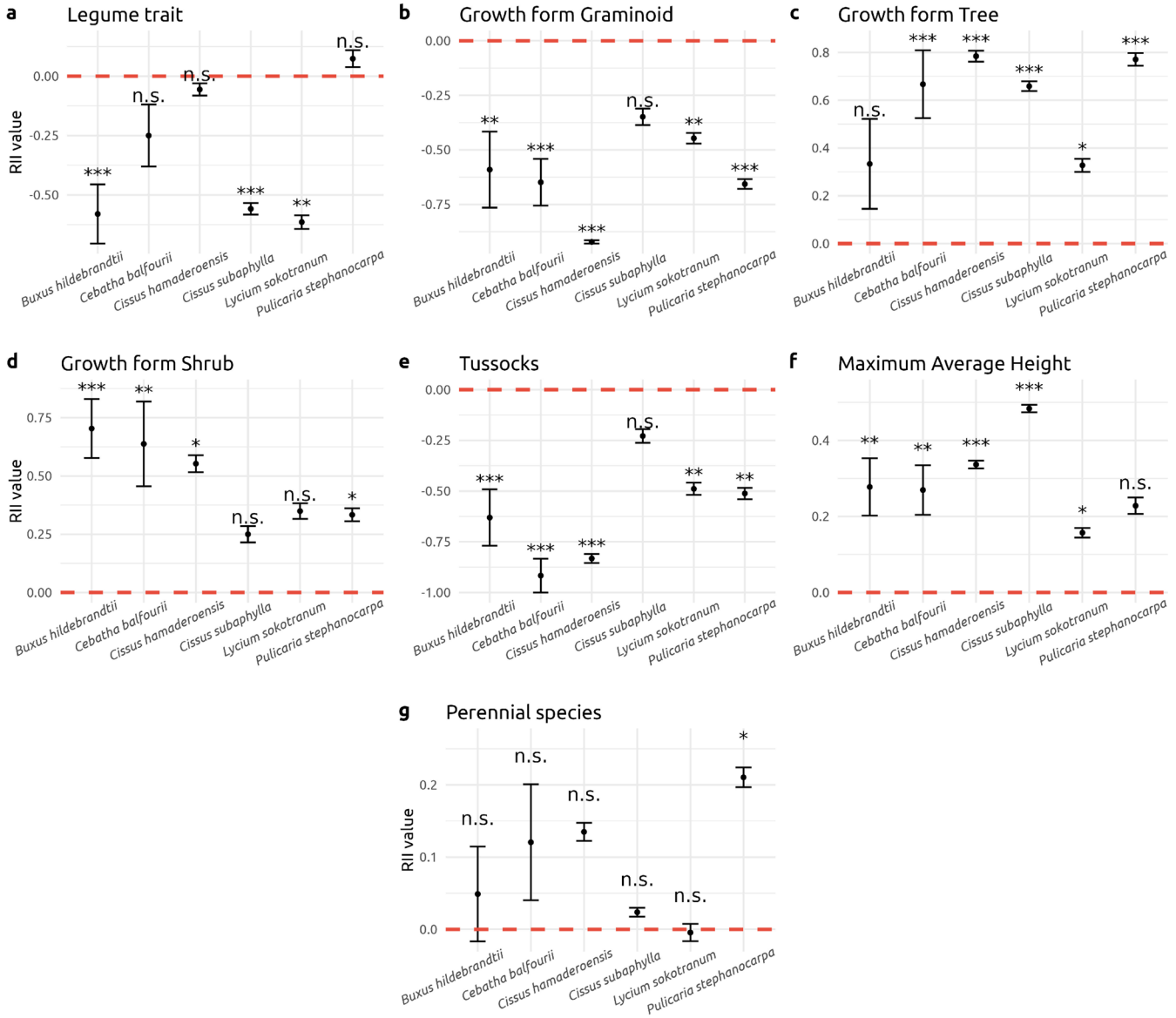


FIGURE 6 | Relative Interaction Intensity (RII) index calculated from traits CWMs for different nurse species. (a) Legume trait, (b) Graminoid growth form, (c) Tree growth form, (d) Shrub growth form, (e) Tussocks, (f) Maximum average height, and (g) Perennial species. Significant positive (RII > 0) or negative (RII < 0) effects are indicated, with 'n.s.' denoting non-significant results. Asterisks indicate significance levels (*$p < 0.05$, **$p < 0.01$, ***$p < 0.001$).

for growth inhibition in other plant species under its canopy (Friedman 2017; Latif et al. 2017). Further research is needed to determine the exact allelopathic potential of this compound.

The findings from this study offer practical recommendations for conservation and restoration efforts on Socotra Island and in other arid ecosystems with similar impacts and stressors. Effective nurse species like *C. balfourii* and *C. hamaderohensis* should be prioritised in reforestation projects aimed at regenerating endangered tree species. These species may protect seedlings from herbivores and potentially create favourable conditions that support their growth. It must be stressed that *C. balfourii* is not an endemic species of Socotra; its geographic distribution spans over the southern part of the Arabian Peninsula, where other plant species are threatened due to climate changes and overgrazing (Ghazanfar 2024).

While our study provides valuable insights, it is important to note that these findings represent a snapshot in time. Future studies should focus on long-term monitoring to assess the persistence of the facilitative effects observed here. Additionally, more research is needed on the allelopathic properties of *B. hildebrandtii* and other shrub species to refine species selection for restoration projects.

Expanding this research to other arid ecosystems could also provide a broader understanding of how these facilitative interactions operate under different environmental conditions and inform restoration efforts in similar degraded landscapes. In conclusion, our study underscores the importance of nurse shrubs in promoting species diversity and facilitating woody species on Socotra Island, offering valuable insights for future conservation and restoration initiatives.

5 | Conclusion

Our study confirms the vital role of nurse shrubs in promoting species diversity and enhancing tree regeneration on Socotra Island, as a case study for arid environments. The results demonstrate that shrub canopies create beneficial microhabitats that protect plant species from harsh environmental conditions and herbivory, distinct plant communities compared to open areas, with a higher percentage of woody species under the canopies. These findings have broader implications for ecological restoration, suggesting that using nurse plants could be an effective strategy, particularly in arid ecosystems like those on Socotra, which face challenges such as overgrazing and climate stress. This nature-based approach offers a sustainable solution to enhance biodiversity, improve ecosystem resilience, and support long-term environmental management in arid and degraded landscapes.

Future research should focus on testing direct interventions with species from the direct surroundings (in order not to mix populations), such as seed planting or transplanting within nurse shrubs, to evaluate their effectiveness in promoting regeneration. Long-term monitoring of these interventions will be crucial, along with further exploration of other facilitation strategies and potential nurse species to maximise the benefits of nurse-plant facilitation in similar ecosystems.

Acknowledgements

With particular thanks to the local team (Amar M., Keybani S., Shanayeghen M., and Keybani M.), we would like to express our sincere gratitude to the Socotran people for their important knowledge and assistance throughout the expeditions. The study was possible because of the support of the Franklinia Foundation within the project "Conservation of the endangered endemic *Boswellia* trees on Socotra Island (Yemen)" Phase I (Grant No. 2020-03) and Phase II (Grant No. 2023-03). All field surveys were carried out with permission and collaboration of the local communities in Socotra, the Environmental Protection Authority of Yemen (EPA, Socotra Branch), and under the official auspices of the Socotra Archipelago Governor's Administration (Socotra Governorate, namely Eng. Raafat Ali Al-Thaqali), to whom we are very grateful. D. L. M. is grateful that this PhD project's study was made possible by the Ministry of Academia and Research (Programma Operativo Nazionale). Finally, a special thanks to the three anonymous reviewers and the editor who helped us in improving the manuscript. Open access publishing facilitated by Universita degli Studi di Roma La Sapienza, as part of the Wiley - CRUI-CARE agreement.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

All the data sets used in this article are available from the Zenodo repository and can be accessed at https://zenodo.org/records/14499718.

References

Aerts, R., W. Maes, E. November, A. Negussie, M. Hermy, and B. Muys. 2006. "Restoring Dry Afromontane Forest Using Bird and Nurse Plant Effects: Direct Sowing of *Olea europaea ssp. cuspidata* Seeds." *Forest Ecology and Management* 230, no. 1–3: 23–31. https://doi.org/10.1016/j.foreco.2006.04.001.

Al-Rowaily, S. L., M. I. El-Bana, D. A. Al-Bakre, A. M. Assaeed, A. K. Hegazy, and M. B. Ali. 2015. "Effects of Open Grazing and Livestock Exclusion on Floristic Composition and Diversity in Natural Ecosystem of Western Saudi Arabia." *Saudi Journal of Biological Sciences* 22, no. 4: 430–437. https://doi.org/10.1016/j.sjbs.2015.04.012.

Armas, C., R. Ordiales, and F. I. Pugnaire. 2004. "Measuring Plant Interactions: A New Comparative Index." *Ecology* 85, no. 10: 2682–2686. https://doi.org/10.1890/03-0650.

Attorre, F., and K. Van Damme. 2020. "Twenty Years of Biodiversity Research and Nature Conservation in the Socotra Archipelago (Yemen)." *Rendiconti Lincei. Scienze Fisiche e Naturali* 31: 563–569. https://doi.org/10.1007/s12210-020-00941-7.

Badano, E. I., O. R. Samour-Nieva, J. Flores, J. L. Flores-Flores, J. A. Flores-Cano, and J. P. Rodas-Ortíz. 2016. "Facilitation by Nurse Plants Contributes to Vegetation Recovery in Human-Disturbed Desert Ecosystems." *Journal of Plant Ecology* 9, no. 5: 485–497. https://doi.org/10.1093/jpe/rtw002.

Bates, D., M. Mächler, B. Bolker, and S. Walker. 2014. "Fitting Linear Mixed-Effects Models Using lme4." *arXiv* Preprint arXiv, 1406.5823. https://doi.org/10.48550/arXiv.1406.5823.

Bera, B. K., O. Tzuk, J. J. R. Bennett, and E. Meron. 2021. "Linking Spatial Self-Organization to Community Assembly and Biodiversity." *eLife* 10: e73819. https://doi.org/10.7554/eLife.73819.

Bernhardt-Römermann, M., C. Römermann, R. Nuske, et al. 2008. "On the Identification of the Most Suitable Traits for Plant Functional Trait Analyses." *Oikos* 117, no. 10: 1533–1541. https://doi.org/10.1111/j.0030-1299.2008.16776.x.

Beydoun, Z. R., and H. R. Bichan. 1970. "The Geology of Socotra Island, Gulf of Aden." *Quarterly Journal of the Geological Society of London* 125: 413–446.

Brown, G., and B. Mies. 2012. *Vegetation Ecology of Socotra*. Vol. 7. Springer Science & Business Media.

Bruno, J. F., J. J. Stachowicz, and M. D. Bertness. 2003. "Inclusion of Facilitation Into Ecological Theory." *Trends in Ecology & Evolution* 18: 119–125. https://doi.org/10.1016/S0169-5347(02)00045-9.

Butterfield, B. J., J. L. Betancourt, R. M. Turner, and J. M. Briggs. 2010. "Facilitation Drives 65 Years of Vegetation Change in the Sonoran Desert." *Ecology* 91, no. 4: 1132–1139. https://doi.org/10.1890/09-0145.1.

Callaway, R. M., ed. 2007. *Positive Interactions and Interdependence in Plant Communities*. Springer.

Chen, J. G., X. F. He, S. W. Wang, Y. Yang, and H. Sun. 2019. "Cushion and Shrub Ecosystem Engineers Contribute Differently to Diversity and Functions in Alpine Ecosystems." *Journal of Vegetation Science* 30: 362–374. https://doi.org/10.1111/jvs.12725.

Cheung, C., and L. DeVantier. 2006. *Socotra–A Natural History of the Islands and Their People*, edited by K. van Damme. Odyssey Books and Guides, Airphoto International Ltd., Hong Kong.

Culek, M. 2013. "Geological and Morphological Evolution of the Socotra Archipelago (Yemen) From the Biogeographical View." *Journal of Landscape Ecology* 6, no. 3: 84–108. https://doi.org/10.2478/jlecol-2014-0005.

De Cáceres, M., P. Legendre, and M. Moretti. 2010. "Improving Indicator Species Analysis by Combining Groups of Sites." *Oikos* 119, no. 10: 1674–1684. https://doi.org/10.1111/j.1600-0706.2010.18334.x.

Díaz, S., S. Lavorel, S. U. E. McIntyre, et al. 2007. "Plant Trait Responses to Grazing–a Global Synthesis." *Global Change Biology* 13, no. 2: 313–341. https://doi.org/10.1111/j.1365-2486.2006.01288.x.

Dlamini, P., P. Chivenge, and V. Chaplot. 2016. "Overgrazing Decreases Soil Organic Carbon Stocks the Most Under Dry Climates and Low Soil pH: A Meta-Analysis Shows." *Agriculture, Ecosystems & Environment* 221: 258–269. https://doi.org/10.1016/j.agee.2016.01.026.

Dray, S., and P. Legendre. 2008. "Testing the Species Traits–Environment Relationships: The Fourth-Corner Problem Revisited." *Ecology* 89, no. 12: 3400–3412. https://doi.org/10.1890/08-0349.1.

Ellis, J. E., and D. M. Swift. 1988. "Stability of African Pastoral Ecosystems: Alternate Paradigms and Implications for Development." *Journal of Range Management Archives* 41, no. 6: 450–459.

Filazzola, A., and C. J. Lortie. 2014. "A Systematic Review and Conceptual Framework for the Mechanistic Pathways of Nurse Plants." *Global Ecology and Biogeography* 23, no. 12: 1335–1345. https://doi.org/10.1111/geb.12202.

Friedman, J. 2017. "Allelopathy, Autotoxicity, and Germination." In *Seed Development and Germination*, edited by J. Kigel, 629–644. Routledge.

Ghazanfar, S. A. 2024. "Biogeography and Conservation in the Arabian Peninsula: A Present Perspective." *Plants* 13, no. 15: 2091. https://doi.org/10.3390/plants13152091.

Gómez-Aparicio, L. 2009. "The Role of Plant Interactions in the Restoration of Degraded Ecosystems: A Meta-Analysis Across Life-Forms and Ecosystems." *Journal of Ecology* 97, no. 6: 1202–1214. https://doi.org/10.1111/j.1365-2745.2009.01573.x.

Gorelick, N., M. Hancher, M. Dixon, S. Ilyushchenko, D. Thau, and R. Moore. 2017. "Google Earth Engine: Planetary-Scale Geospatial Analysis for Everyone." *Remote Sensing of Environment* 202: 18–27. https://doi.org/10.1016/j.rse.2017.06.031.

Grime, J. P. 2001. *Plant Strategies, Vegetation Processes, and Ecosystem Properties*. 2nd ed. John Wiley & Sons.

Habrová, H., and J. Pavliš. 2017. "Dynamic Response of Woody Vegetation on Fencing Protection in Semi-Arid Areas; Case Study: Pilot Exclosure on the Firmihin Plateau, Socotra Island." *Saudi Journal of Biological Sciences* 24: 338–346. https://doi.org/10.1016/j.sjbs.2015.09.030.

Hamdiah, S., K. Eler, K. Van Damme, et al. 2024. "Overgrazing Strongly Impedes the Natural Regeneration of the Endemic Boswellia Species on Socotra Island." *Journal of Forest Science* 70, no. 5: 249–263. https://doi.org/10.17221/3/2024-JFS.

Hempson, G. P., S. Archibald, W. J. Bond, et al. 2015. "Ecology of Grazing Lawns in Africa." *Biological Reviews* 90, no. 3: 979–994. https://doi.org/10.1111/brv.12145.

Hempson, G. P., C. L. Parr, C. E. R. Lehmann, and S. Archibald. 2022. "Grazing Lawns and Overgrazing in Frequently Grazed Grass Communities." *Ecology and Evolution* 12: e9268. https://doi.org/10.1002/ece3.9268.

Kalivodová, H., M. Culek, M. Čermák, P. Maděra, and H. Habrová. 2020. "Potential Importance of Socotra dragon's Blood Tree Cloud Forests and Woodlands for Capturing Horizontal Precipitation." *Rendiconti Lincei. Scienze Fisiche e Naturali* 31, no. 3: 607–621. https://doi.org/10.1007/s12210-020-00933-7.

Kaplan, J. 2020. "fastDummies: Fast Creation of Dummy (Binary) Columns and Rows From Categorical Variables." R Package Version, 1(3).

Karger, D. N., O. Conrad, J. Böhner, et al. 2017. "Climatologies at High Resolution for the Earth Land Surface Areas." *Scientific Data* 4: 170122. https://doi.org/10.1038/sdata.2017.122.

Kurtz, D. B., M. Giese, F. Asch, S. H. Windisch, and M. C. Goldfarb. 2018. "Effects of High Impact Grazing on Species Diversity and Plant Functional Groups in Grasslands of Northern Argentina." *Sustainability* 10, no. 9: 3153. https://doi.org/10.3390/su10093153.

La Montagna, D., F. Attorre, S. Hamdiah, et al. 2023. "Climate Change Effects on the Potential Distribution of the Endemic Commiphora Species (Burseraceae) on the Island of Socotra." *Frontiers in Forests and Global Change* 6: 1183858. https://doi.org/10.3389/ffgc.2023.1183858.

Latif, S., G. Chiapusio, and L. A. Weston. 2017. "Allelopathy and the Role of Allelochemicals in Plant Defence." *Advances in Botanical Research* 82: 19–54.

Lavorel, S., K. Grigulis, S. McIntyre, et al. 2008. "Assessing Functional Diversity in the Field - Methodology Matters!" *Functional Ecology* 22, no. 1: 134–147. https://doi.org/10.1111/j.1365-2435.2007.01339.x.

Legendre, P., and E. D. Gallagher. 2001. "Ecologically Meaningful Transformations for Ordination of Species Data." *Oecologia* 129, no. 2: 271–280. https://doi.org/10.1007/s004420100716.

Lvončík, S., P. Vahalík, F. Bongers, et al. 2020. "Development of a Population of Boswellia Elongata Balf. F. In Homhil Nature Sanctuary, Socotra Island (Yemen)." *Rendiconti Lincei. Scienze Fisiche e Naturali* 31: 747–759. https://doi.org/10.1007/s12210-020-00936-4.

Maděra, P., H. Habrová, M. Šenfeldr, et al. 2019. "Growth Dynamics of Endemic *Dracaena cinnabari* of Socotra Island Suggest Essential Elements for a Conservation Strategy." *Biologia* 74, no. 4: 339–349. https://doi.org/10.2478/s11756-018-0152-0.

Maděra, P., P. Vahalík, S. Hamdiah, et al. 2024. "Distribution, Ecology, and Threats Assessment of 11 Endemic Frankincense Tree Taxa (Boswellia) in the Socotra Archipelago (Yemen)." *Plants, People, Planet* 1–20: 1552–1571. https://doi.org/10.1002/ppp3.10563.

Maděra, P., and K. Van Damme. 2022. "Socotra archipelago (Yemen)." In *Imperiled: The Encyclopedia of Conservation*, edited by D. A. DellaSala and M. I. Goldstein, 267–281. Elsevier. https://doi.org/10.1016/b978-0-12-821139-7.00009-x.

Maděra, P., D. Volařík, Z. Patočka, et al. 2019. "Sustainable Land Use Management Needed to Conserve the dragon's Blood Tree of Socotra Island, a Vulnerable Endemic Umbrella Species." *Sustainability* 11, no. 13: 3557. https://doi.org/10.3390/su11133557.

Menge, D. N., and R. L. Chazdon. 2016. "Higher Survival Drives the Success of Nitrogen-Fixing Trees Through Succession in Costa Rican Rainforests." *New Phytologist* 209: 965–977. https://doi.org/10.1111/nph.13734.

Michalet, R., G. Losapio, Z. Kikvidze, et al. 2024. "Assessing the Accuracy of Paired and Random Sampling for Quantifying Plant–Plant Interactions in Natural Communities." *Population Ecology* 66, no. 1: 39–52. https://doi.org/10.1002/1438-390X.12161.

Milchunas, D. G., and I. Noy-Meir. 2002. "Grazing Refuges, External Avoidance of Herbivory and Plant Diversity." *Oikos* 99, no. 1: 113–130. https://doi.org/10.1034/j.1600-0706.2002.990112.x.

Miller, A. G., and M. Morris. 2004. *Ethnoflora of the Soqotra Archipelago*, 759. Royal Botanic Garder Edinburgh.

Noumi, Z. 2020. "Can Native Shrubs Facilitate the Establishment of Trees Under Arid Bioclimate? A Case Study From Tunisia." *Flora* 263: 151517. https://doi.org/10.1016/j.flora.2019.151517.

Noy-Meir, I., M. Gutman, and Y. Kaplan. 1989. "Responses of Mediterranean Grassland Plants to Grazing and Protection." *Journal of Ecology* 77: 290–310.

Oksanen, J., F. G. Blanchet, M. Friendly, et al. 2017. "Vegan: Community Ecology Package. Version 2.6-8." https://cran.r-project.org/web/packages/vegan/index.html.

Padilla, F. M., and F. I. Pugnaire. 2006. "The Role of Nurse Plants in the Restoration of Degraded Environments." *Frontiers in Ecology and the Environment* 4: 196–202. https://doi.org/10.1890/1540-9295(2006)004[0196:TRONPI]2.0.CO;2.

POWO. 2024. "Plants of the World Online. Facilitated by the Royal Botanic Gardens." Kew. Accessed 5 July 2024. https://powo.science.kew.org/.

R Core Team. 2024. "R: A Language and Environment for Statistical Computing." https://www.r-project.org/.

Raevel, V., C. Violle, and F. Munoz. 2012. "Mechanisms of Ecological Succession: Insights From Plant Functional Strategies." *Oikos* 121, no. 11: 1761–1770. https://doi.org/10.1111/j.1600-0706.2012.20261.x.

Rahmanian, S., M. Hejda, H. Ejtehadi, M. Farzam, P. Pyšek, and F. Memariani. 2020. "Effects of Livestock Grazing on Plant Species Diversity Vary Along a Climatic Gradient in Northeastern Iran." *Applied Vegetation Science* 23: 551–561. https://doi.org/10.1111/avsc.12512.

Ram, B., and A. Chawla. 2024. "Shrubs Exhibit Competitive Interactions With Herbaceous Plants and Shape Community Assemblage and Functional Composition in the Alpine Western Himalaya." *Journal of Vegetation Science* 35: e13269. https://doi.org/10.1111/jvs.13269.

Rejžek, M., M. Svátek, J. Šebesta, R. Adolt, P. Maděra, and R. Matula. 2016. "Loss of a Single Tree Species Will Lead to an Overall Decline in Plant Diversity: Effect of *Dracaena cinnabari* Balf. f. on the Vegetation of Socotra Island." *Biological Conservation* 196: 165–172. https://doi.org/10.1016/j.biocon.2016.02.016.

Riccardi, T., L. Malatesta, K. Van Damme, et al. 2020. "Environmental Factors and Human Activity as Drivers of Tree Cover and Density on the Island of Socotra, Yemen." *Rendiconti Lincei. Scienze Fisiche e Naturali* 31, no. 3: 703–718. https://doi.org/10.1007/s12210-020-00923-9.

Schöb, C., R. M. Callaway, F. Anthelme, et al. 2014. "The Context Dependence of Beneficiary Feedback Effects on Benefactors in Plant Facilitation." *New Phytologist* 204: 386–396. https://doi.org/10.1111/nph.12908.

Scholte, P., and P. De Geest. 2010. "The Climate of Socotra Island (Yemen): A First-Time Assessment of the Timing of the Monsoon Wind Reversal and Its Influence on Precipitation and Vegetation Patterns." *Journal of Arid Environments* 74, no. 11: 1507–1515. https://doi.org/10.1016/j.jaridenv.2010.05.017.

Shankarnarayan, K. A. 1977. "Impact of Overgrazing on the Grasslands." *Annals of Arid Zone* 16, no. 3: 349–359.

Soliveres, S., D. J. Eldridge, F. Hemmings, and F. T. Maestre. 2012. "Nurse Plant Effects on Plant Species Richness in Drylands: The Role of Grazing, Rainfall and Species Specificity." *Perspectives in Plant Ecology, Evolution and Systematics* 14, no. 6: 402–410. https://doi.org/10.1016/j.ppees.2012.09.003.

Soliveres, S., D. J. Eldridge, F. T. Maestre, M. A. Bowker, M. Tighe, and A. Escudero. 2011. "Microhabitat Amelioration and Reduced Competition Among Understorey Plants as Drivers of Facilitation Across Environmental Gradients: Towards a Unifying Framework." *Perspectives in Plant Ecology, Evolution and Systematics* 13, no. 4: 247–258. https://doi.org/10.1016/j.ppees.2011.06.001.

Steinbauer, M. J., C. Beierkuhnlein, M. A. S. Arfin Khan, et al. 2016. "How to Differentiate Facilitation and Environmentally Driven Co-Existence." *Journal of Vegetation Science* 27, no. 5: 1071–1079. https://doi.org/10.1111/jvs.12441.

Tai, X., H. E. Epstein, and B. Li. 2021. "Effects of Grazing Exclusion on Spring and Autumn Pastures in Arid Regions of China: Insights From Field Surveys and Landsat Images." *Agriculture, Ecosystems & Environment* 310: 107302. https://doi.org/10.1016/j.agee.2021.107302.

Tian, L., and X. Wang. 2015. "Role of Nurse Shrubs for Restoration Planting of Two Conifers in Southeast of Mu us Sandland, China." *Journal of Environmental Biology* 36, no. 1: 331–336.

Vahalík, P., K. Van Damme, R. Nétek, et al. 2023. "UAV Inventory of the Last Remaining Dragon Tree Forest on Earth." *Forests* 14: 766. https://doi.org/10.3390/f14040766.

Van Damme, K., and L. Banfield. 2011. "Past and Present Human Impacts on the Biodiversity of Socotra Island (Yemen): Implications for Future Conservation." *Zoology in the Middle East* 54: 31–88. https://doi.org/10.1080/09397140.2011.10648899.

Wang, J., Q. He, Y. Wu, et al. 2021. "Effects of Pioneer N2-Fixing Plants on the Resource Status and Establishment of Neighboring Non-N2-Fixing Plants in a Newly Formed Glacier Floodplain, Eastern Tibetan Plateau." *Plant and Soil* 458: 261–276. https://doi.org/10.1007/s11104-020-04462-y.

Weigelt, P., C. König, and H. Kreft. 2020. "GIFT–A Global Inventory of Floras and Traits for Macroecology and Biogeography." *Journal of Biogeography* 47, no. 1: 16–43. https://doi.org/10.1111/jbi.13623.

Xu, C., B. R. Silliman, J. Chen, et al. 2023. "Herbivory Limits Success of Vegetation Restoration Globally." *Science* 382, no. 6670: 589–594. https://doi.org/10.1126/science.add2814.

Yaqoob, M., and I. Javed. 2008. "Mineral Composition, Palatability and Digestibility of Free Rangeland Grasses of Northern Grasslands of Pakistan." *Pakistan Journal of Botany* 40, no. 5: 2059–2070.

Supporting Information

Additional supporting information can be found online in the Supporting Information section.