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The Role of Nurse Trees in the Plant Community of Park Grassland: A Case Study in Southern Brazil

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ABSTRACT

Aims: Understanding the mechanisms that act in the assembly of the grassy-woody plant community in park grassland is important to define conservation, management, and restoration strategies. We investigated the facilitation of three nurse tree species typical of park grassland (*Prosopis affinis*, *Prosopis nigra*, and *Aspidosperma quebracho-blanco*) on the composition and structure of the plant community and the mechanisms through which these species facilitate the establishment of other species under their canopies.

Location: Park grasslands of Rio Grande do Sul, Brazil.

Methods: We carried out a paired vegetation survey in 30 circular plots (under trees and in open areas) in park grassland isolated from grazing, located in the Espinilho State Park, Rio Grande do Sul, southern Brazil. We evaluated attributes related to the composition and structure, dimensions of each tree, and environmental variables, aiming to understand the mechanisms of plant community assembly.

Results: Nurse trees play an important role in the assembly of the plant community, promoting changes in abiotic (provide shade, increased litter, decreased exposed soil) and biotic (decreased herbaceous abundance) conditions. Consequently, they provide microhabitat for herbaceous and woody plants. These tree species are decisive in the assembly of the plant community in park grassland, and their conservation is fundamental for the maintenance of associated species. However, they can act as nuclei for woody plants typical of forests and possibly contribute to forest expansion in the long term.

Conclusions: Given the nursing role they play, these tree species demonstrate potential for application in ecological restoration, as well as promoting the conservation of local biodiversity in park grasslands.

1 | Introduction

Non-forest ecosystems, such as grasslands and savannas, are among the global ecosystems that suffer most from degradation and conversion (Dudley et al. 2020). They present enormous challenges for biodiversity conservation and ecological restoration (Overbeck et al. 2015). In the Brazilian Pampa, the natural landscapes are highly altered by the conversion of areas to agriculture and forestry (De Oliveira et al. 2017). The losses recorded were 3.4 Mha of native vegetation in the last 37 years

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(1985–2022), including grassland and forests (MapBiomas 2022). Among the mosaic of grassland, shrubland, and forest that make up the Brazilian Pampa vegetation are the park grasslands (Bencke et al. 2016). This plant typology is characterized by the presence of thorny trees, scattered within a dense herbaceous layer composed mainly of grasses (Inofuentes and Säumel 2022; Hasenack et al. 2023). Its unique vegetation is composed of a set of xerophytic woody plants, mainly legumes, as well as herbs, grasses, and cacti adapted to conditions of high soil salinity and short dry periods during the summer (Marchiori and Alves 2010; Marchiori et al. 2014).

Park grassland consists of an extension of predominant vegetation in the northeast of Argentina that extends across the alluvial plain of the Uruguay River, being restricted in Brazilian territory to the extreme southwest of Rio Grande do Sul (Marchiori et al. 2013, 2014; Bencke et al. 2016). This formation originally occupied an area of 13,909.69 km^2, corresponding to 4.95% of the territory of Rio Grande do Sul (Hasenack et al. 2023). However, its original coverage suffered intense reductions due to the conversion of native vegetation to pastures and grain cultivation, such as rice and soybeans (Watzlawick et al. 2010).

The last park grassland preserved remnants are found in the Espinilho State Park (Marchiori et al. 2014), the only conservation unit protecting this vegetation in Brazilian territory (State Decree no. 41,440/2002, Rio Grande do Sul 2002). Despite its reduced coverage and unique biodiversity, park grassland is still little studied in Brazil (Redin et al. 2011). Recent studies have quantitatively investigated ecological aspects, growth, and dynamics of tree vegetation, and the effect of grazing on these formations (Watzlawick et al. 2010; Redin et al. 2011, 2017), showing that grazing influences the structure and composition of tree species. Nonetheless, there are still gaps to be filled in the understanding of biotic and abiotic interactions related to natural vegetation patterns (Inofuentes and Säumel 2022), mainly the relationship between woody and herbaceous plants and other life forms.

Positive interactions, such as facilitation, have been recognized as an important structuring force in natural plant communities, particularly in harsh and highly disturbed environments (Bertness and Callaway 1994; Brooker et al. 2008). Facilitation occurs when one species, usually a nurse plant, makes the local environment more favorable to another, either directly, by modifying abiotic and/or biotic conditions (Bertness and Callaway 1994), or indirectly, when beneficial effects are promoted from negative effects, such as interspecific competition (Mcintire and Fajardo 2014). Nurse plants act throughout the life cycle of the species that is benefited, through various mechanisms, such as improving substrate and microclimate conditions, capturing seeds, protecting against herbivores, and reducing interspecific competition under their influence area (Filazolla and Lortie 2014; Gavini et al. 2019).

Although most evidence of plant–plant facilitation has been recorded in harsh environments, mainly in arid and semiarid ecosystems (e.g., deserts, arctic or alpine tundra) (Brooker et al. 2008; Filazolla and Lortie 2014), facilitation also plays an important role in benign environments (Holmgren and Scheffer 2010; Anthelme et al. 2014). In humid ecosystems, for example, organisms tend to be more sensitive to stress due to adaptation to mild local conditions increasing the importance of facilitation (Holmgren and Scheffer 2010). Studies have reported the occurrence of facilitation in subtropical and tropical ecosystems where environmental conditions are less stressful, such as in cloud forests in Ecuador (Anthelme et al. 2014), park grassland in Uruguay (Inofuentes and Säumel 2022), and in regions with high precipitation along the South American Chaco (Velasco et al. 2024). In Brazil, studies have identified the facilitation effects of nurse plants (trees and shrub) mainly in grasslands (Korndörfer et al. 2015; Marcilio-Silva et al. 2015) and savannas (Abreu et al. 2021), where they promoted the nucleation of woody plants (Yarranton and Morrison 1974) by improving microhabitat conditions and by the perch effect, contributing to forest expansion. Perch and nurse effects function in a synergistic way, with bird dispersal bringing fleshy-fruited species' seeds to the safe germination sites under canopies of the nurse trees (Inofuentes and Säumel 2022). The nucleation process with subsequent aggregation of nuclei is one of the mechanisms by which forest expansion over grasslands occurs (Schinestsck et al. 2019). To date, there are no studies addressing facilitation effects in park grassland in Brazil. Therefore, understanding these positive interactions is essential to support management, conservation, and restoration strategies of this ecosystem.

Herein, we investigated the facilitation of three tree species typical of park grassland (*Prosopis affinis*, *Prosopis nigra,* and *Aspidosperma quebracho-blanco*) on the composition and structure of the plant community and attempted to understand the mechanisms through which these species facilitate the establishment of woody and herbaceous plants under their canopies. We seek to answer the following questions: (I) Are trees promoting conditions more favorable to the establishment of other species under their canopies in park grassland? (II) Is the microhabitat under the canopy more favorable to the establishment of herbaceous or woody plants? (III) Are trees favoring the establishment of woody regenerants nuclei for further expansion? Based on these questions, our findings can contribute to the definition of conservation, management, and restoration strategies for this vegetation type, which is among the most threatened and poorly studied environments in the Brazilian Pampa.

2 | Material and Methods

2.1 | Study Area

The study was carried out in Espinilho State Park (ESP), located in the extreme southwest of the state of Rio Grande do Sul, southern Brazil (Figure 1a). The region's climate, according to the Köppen classification, is *Cfa*, humid mesothermal with hot summers, and an average annual temperature of 18.5°C and annual rainfall of 1468 mm (Alvares et al. 2013). The region's relief is flat, with an average altitude of 60 m. The predominant soil in the study area is Solonetz, with high fertility, high sodium content, and imperfect drainage (IUSS 2022).

The ESP vegetation is predominantly composed of grassy-woody vegetation, called “park grassland,” in association with riparian forests (Marchiori et al. 2014; Hasenack et al. 2023). Our study area comprises 93.7 ha (Figure 1a) of park grassland, with the significant

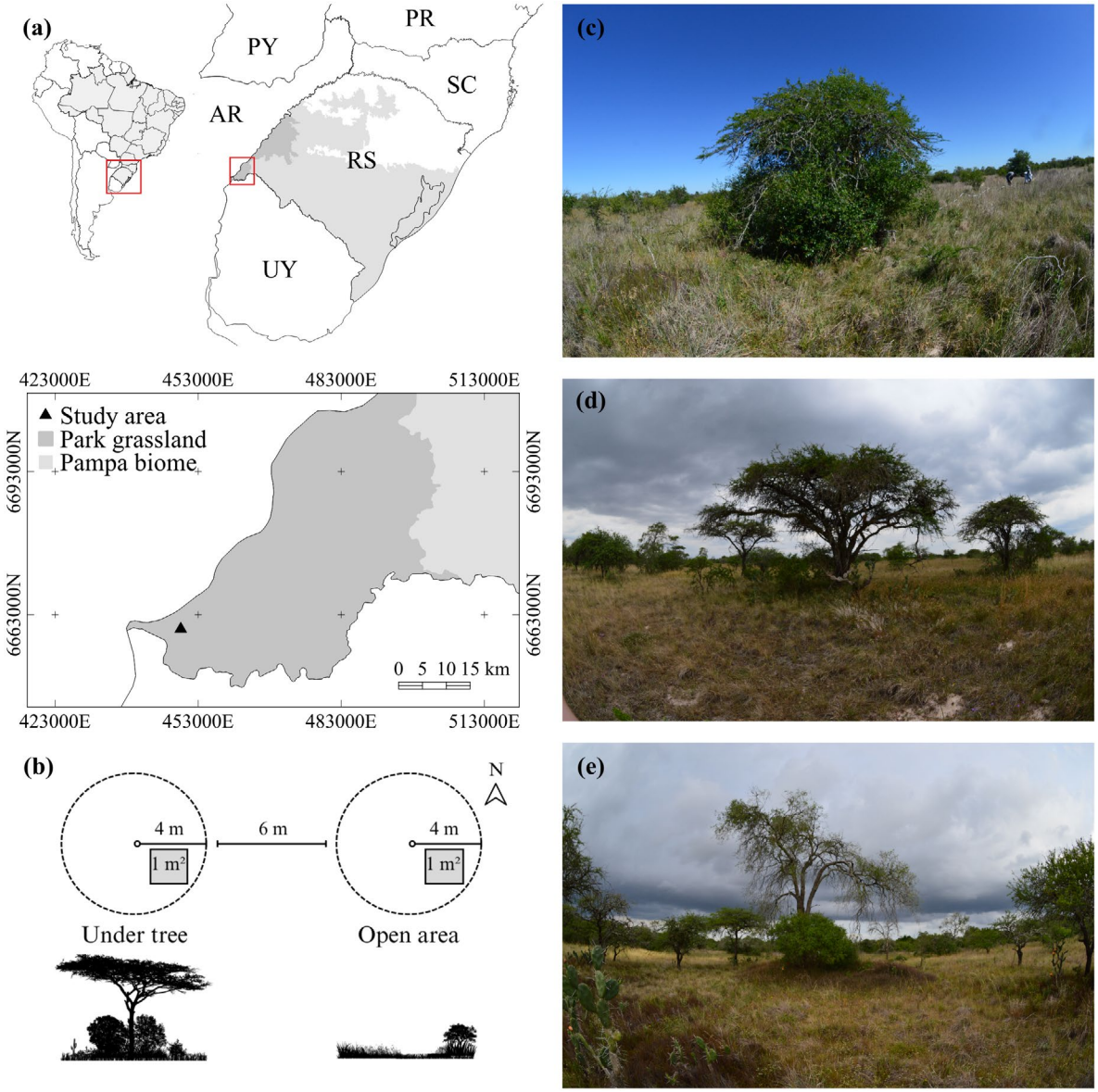


FIGURE 1 | Description of the study area: (a) location of the study area in Espinilho State Park, Barra do Quaraí, Rio Grande do Sul, Southern Brazil; (b) sample design of the survey of woody (circular plot) and herbaceous (quadrant) plants under the tree canopy and in an open area; (c–e) characterization of the park grassland, marked by scattered trees, including *Prosopis affinis*, *Prosopis nigra*, and *Aspidosperma quebracho-blanco*, respectively.

presence of *Prosopis nigra*, in association with *Aspidosperma quebracho-blanco*, *Prosopis affinis* and *Vachellia caven*, as well as other woody species in lower density. The herbaceous layer is sparse, composed mainly of Poaceae and Cyperaceae, in addition to numerous halophyte species that inhabit patches of bare soil with a high sodium content, called "*blanqueales*" (Marchiori et al. 2013, 2014). The area was isolated of livestock for at least 15 years and without receiving management since then.

2.2 | Species Description

We selected three tree species typical of the park grassland: *Prosopis nigra*, *Prosopis affinis*, and *Aspidosperma quebracho-blanco* (Figure 1c–e). The choice of these three species took into consideration their importance for the structure and composition of this plant typology (Watzlawick et al. 2010; Marchiori et al. 2014), their nursing potential (Inofuentes and Säumel 2022), and their presence on the list of endangered species in the Rio Grande do Sul state (State Decree no. 52,109/2014, Rio Grande do Sul 2014).

Prosopis affinis (Fabaceae) has a flattened, umbrella-shaped crown with rigid, thorny branches. Its leaves are bipinnately compound, with short petioles and nearly imbricated leaflets. It can reach up to 10 m in height and 60 cm in diameter. *Prosopis nigra* (Fabaceae) has a more globose crown, also umbrella-shaped, with hanging, slightly thorny branches. Its leaves are bipinnately compound, with long petioles and separate leaflets. It can easily exceed 10 m in height and 60 cm in diameter (Fagúndez-Pachón 2015). *Aspidosperma quebracho-blanco* (Apocynaceae) has a rigid, sclerophyte crown architecture, with generally hanging branches.

Its leaves are thick, hard, and subsessile, arranged in triple whorls, elliptical in shape and with an acute apex. It can reach up to 30 m in height (Barchuck and Valiente-Banuet 2006).

In the study area, both species occur quite sparsely, expressing a characteristic that is more open to vegetation. The populations of species such as *P. nigra* and *A. quebracho-blanco* are associated with halomorphic soils, popularly known as "*blanqueales*" (Marchiori et al. 2014). *Prosopis nigra* is the predominant species, with individuals not exceeding 7 m in height, while *Prosopis affinis* occurs in a smaller proportion, with individuals not exceeding 6 m in height. Both species form the general vegetation stratum. *Aspidosperma quebracho-blanco* also occurs in high abundance, although more sparsely, reaching up to 9 m in height (Marchiori and Galvão 1985).

2.3 | Sampling

We carried out a paired vegetation survey, evaluating attributes related to composition and structure (species richness, abundance of woody and herbaceous plants, canopy cover, soil cover, leaf area index (LAI), and litter depth) under the trees and in a paired open area (adapted from Abreu et al. 2021).

In total, 15 trees were sampled, five of each species. Trees were selected when they met pre-established criteria, defined according to the requirements proposed by Abreu et al. (2021). We also consider the characteristics of the plant typology observed in the field in this process. Thus, the criteria used were: (a) diameter at breast height (DBH) greater than or equal to 15 cm and crown diameter of at least 4 m; (b) distance of at least 50 m from watercourses and forest fragments; (c) minimum distance of 30 m from any other evaluated nurse tree.

To sample the vegetation under the canopy, we used circular plots measuring 4 m in diameter (12.57 m^2), centered on the trunk of each tree (Figure 1b). The plots in open areas were allocated approximately two times the crown distance from the nurse tree. Thus, the study comprised 30 plots (15 under the trees and 15 in the open areas).

2.4 | Data Collection

In each plot, all woody regenerating individuals greater than 30 cm in height were collected and identified. We also sampled herbaceous vegetation using the surface sampling method, with a 1 m^{-2} quadrant (Andrade et al. 2019), arranged at half the diameter of the circular plots (2 m) (Figure 1b). In these quadrants, we counted the abundance of individuals for each herbaceous species and performed a visual estimate of soil cover by native species, exotic species, and exposed soil and litter, using the modified Braun-Blanquet cover abundance scale (Mueller-Dombois and Ellenberg 1974), counting the percentage of each class (0%–100%). All data were collected in November 2022 (spring season in the Southern Hemisphere).

We measured litter depth at four points within each circular plot under the tree canopies and in the open areas (Abreu et al. 2021). We obtained the canopy coverage and leaf area index (LAI) indirectly from hemispherical photographs (Nikon D3200 digital camera and Fisheye-Nikon AF DX 10.5 mm f/2.8 G ED converter). The images were taken under the trees and in the paired open areas. The camera was positioned and leveled in the center of each plot at a height of 1.30 m above the ground, and photographs were taken at each cardinal point. Images were processed using Gap Light Analyzer software (GLA v2 Inc.) (Frazer et al. 1999). LAI is a dimensionless measure of the amount of leaf area (m^2) in a canopy per unit of soil area (m^2) (Asner et al. 2003), used here as an indication of shading by the nurse trees canopies.

We also measured dendrometric variables of the trees to identify possible relationships with the structure and composition of woody regeneration under their canopies. For each tree, the diameter at breast height (DBH) at 1.30 m above ground, total height, stem height (from the ground to the lowest branch), crown diameter, crown area, and canopy cover were obtained. Heights were measured with a digital hypsometer, and diameters were found with a measuring tape.

2.5 | Data Analysis

2.5.1 | Effect of Nurse Trees on the Environment

To evaluate the effect of nurse trees on the environment, we also compared the following variables between microhabitats (under trees and open areas): native herbaceous cover (%), exposed soil (%), exotic herbaceous cover (%), litter cover (%), litter depth (cm), and LAI. Data were tested for normality and homoscedasticity by the Shapiro–Wilk test and Bartlett test, respectively. We used the Mann–Whitney test to compare non-parametric data.

2.5.2 | Effect of Nurse Trees on Plant Abundance

The effect of nurse trees on plant community was analyzed with generalized linear mixed models (GLMMs) using the negative binomial distribution and log-link function (Zuur et al. 2009). We compared the abundance of woody and herbaceous plants between the microhabitats (under tree and open area). We used the abundance as a response variable, microhabitats as fixed terms and paired plots as random effects. We also assessed the effect of each nurse tree species on woody and herbaceous plant abundance, using only data for canopy plots (i.e., 15 plots). In this model, we considered the species of nurse tree as fixed terms and plots as random effects. In case of significant interactions detected, we performed contrast analysis using the *emmeans* package (Lenth et al. 2024).

2.5.3 | Effect of Nurse Trees on Floristic Composition

We identify all the species by consulting regional bibliography, experts, and herbarium (SMDB Herbarium—Federal University of Santa Maria). The taxonomic nomenclature followed APG IV (Angiosperm Phylogeny Group 2016) and Flora and Fungi of Brazil (Reflora 2023). We evaluated the effect of nurse trees on the floristic composition of the plant community by non-metric multidimensional scaling (NMDS), using an abundance matrix

of woody and herbaceous species based on Bray–Curtis dissimilarity, with the *vegan* package (Oksanen et al. 2022). The suitability of the ordering was assessed by the stress value. To verify the differences in floristic composition between microhabitats, we used permutational multivariate analysis of variance (PERMANOVA). We compared woody and herbaceous plant richness between the microhabitats and among nurse tree species. For this, we used the same GLMM described for abundance (see Section 2.5.2). We also assessed species diversity (Shannon index) between microhabitats and among nurse tree species (only plots under trees), using the Hutcheson *t*-test (Salinas and Ramirez-Delgado 2021).

2.5.4 | Functional Aspects of the Plant Community

We calculated the Relative Interaction Index (RII) for each of the species: $RII = (Ut — Oa)/(Ut + Oa)$, where *Ut* and *Oa* are the abundances of each species growing under the canopy and in the open area, respectively (Armas et al. 2004). RII values range from −1 for non-facilitated species (open area) to +1 for facilitated species (under tree), while values close to zero indicate species that grow equally in both microhabitats. RII was used to classify species according to the type of facilitation, as proposed by Gavini et al. (2019). Thereby, the species were classified as non-facilitated ($RII < -0.2$, competitive exclusion category), facilitated ($RII > +0.2$, facilitation category) and neutral ($-0.2 < RII > +0.2$, neutral category). We calculated the abundance of plants by type of facilitation and compared them using the Kruskal–Wallis test ($p < 0.05$).

To understand whether trees promote nucleation by woody regenerants, we classified woody plants according to habitat preference (typical of forest or park grassland) and dispersal syndrome (zoochoric and non-zoochoric) based on a specific review of regional literature (for more information, see Appendix S2). We calculated the abundance of woody regenerants by habitat preference and type of dispersal syndrome, comparing them between microhabitats (under trees and open areas), using the same GLMM described for abundance (see Section 2.5.2), followed by contrast analysis, with the *emmeans* package (Lenth et al. 2024).

2.5.5 | Factors That Explain Nucleation by Woody Species Under the Canopy

To assess whether nurse trees act as nuclei for the regeneration of woody plants, we used the same GLMM described for abundance (see Section 2.5.2). The predictor variables explored were native herbaceous cover, exotic herbaceous cover, litter cover, exposed soil, crown diameter, total height, stem height, litter depth, and LAI. Here, we considered the abundance of woody regenerants as the response variable and paired plots as a random variable. We selected these variables based on a minimum multicollinearity criterion using the variance inflation factor (VIF < 10), through the *metan* package (Olivoto and Dal'Col Lúcio 2020). For analyses involving tree characteristics (crown diameter, total height, and stem height), we only considered the plots under trees. All analyses were performed using R software, version 4.1.1 (R Core Team 2021).

3 | Results

3.1 | Effect of Nurse Trees on the Environment

The nurse trees had a significant effect on some of the variables analyzed (Table 1). The percentage of exposed soil under the trees was 79% lower. Litter cover was 46% higher and litter depth was 1.7 times greater to than the open areas. LAI was 196 times greater under tree canopies than the open areas.

3.2 | Effect of Nurse Trees on Plant Abundance

The abundance of woody regenerants was almost 20 times higher under trees (26.0 ± 15.2 ind) than the open areas (1.30 ± 1.50 ind) ($Z = 12.923$, $p < 0.0001$, Figure 2a), while the abundance of herbaceous plants was twice as high in the open areas (100.4 ± 32.3 ind) ($Z = -5.232$, $p < 0.0001$, Figure 2b). When we compared the abundance only under the tree canopies, we did not identify significant differences for the abundance of woody regenerants among tree species ($p > 0.05$, Figure 2c). The abundance of herbaceous plants differed significantly only under the canopies of *Aspidosperma quebracho-blanco* and *Prosopis nigra* ($p = 0.038$, Figure 2d), being almost twice as high for the first species. In contrast, the abundance of herbaceous plants under the canopies of *Prosopis affinis* did not differ significantly when compared to *Prosopis nigra* and *Aspidosperma quebracho-blanco* ($p > 0.05$, Figure 2d).

3.3 | Effect of Nurse Trees on Floristic Composition

We recorded 132 woody and herbaceous species, belonging to 40 botanical families (Appendices S1 and S2). Of these, 27 are woody regenerants and 105 are herbaceous, with three of the latter being exotic species (*Eragrostis plana*, *Senecio madagascariensis,* and *Nuttalanthus texanus*). The families with the greatest

TABLE 1 | Environmental variables under trees and in paired open areas (mean ± standard deviation) in park grassland, Southern Brazil.

Variables	Under tree	Open area	*p*
Native herbaceous cover (%)	49.90 ± 18.60	44.10 ± 21.00	0.6027
Exposed soil (%)	5.20 ± 10.20	24.50 ± 18.80	**0.0009**
Exotic herbaceous cover (%)	3.20 ± 7.30	4.60 ± 10.20	0.1470
Litter cover (%)	41.70 ± 18.70	22.70 ± 15.60	**0.0416**
Litter depth (cm)	1.59 ± 0.88	0.92 ± 0.62	**0.0023**
Leaf area index (LAI)	1.83 ± 0.68	0.009 ± 0.04	**< 0.0001**

Note: Values in bold indicate a significant statistical difference between microhabitats using the Mann–Whitney test ($p < 0.05$).

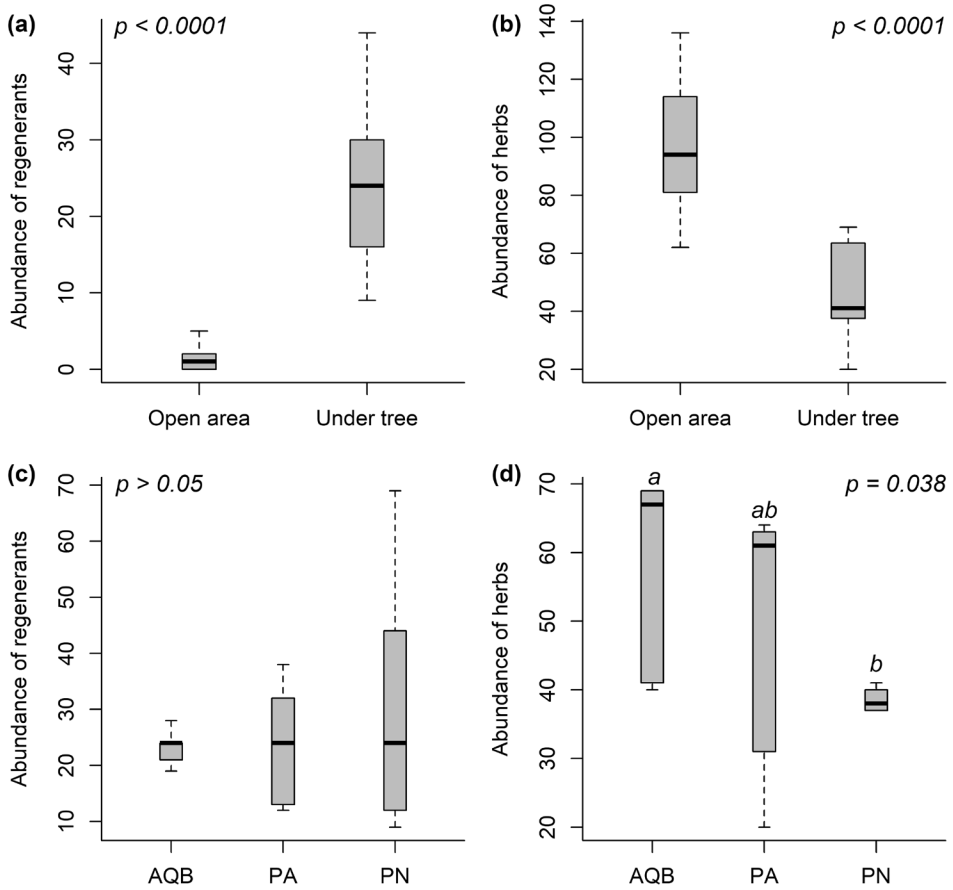


FIGURE 2 | Abundance of woody regenerants (a) and herbaceous plants (b) in the microhabitats (under trees and open areas). Abundance of woody regenerants (c) and herbaceous plants (d) under the canopy of each tree species. Significant differences among trees were identified by contrast analysis. AQB = *Aspidosperma quebracho-blanco*, PA = *Prosopis affinis*, PN = *Prosopis nigra*.

richness of woody species were Asteraceae (six species) and Myrtaceae (three). In the herbaceous component, the families with the greatest richness were Poaceae (26), Asteraceae (14), and Cyperaceae (12).

We recorded 92 species under trees and 87 species in the open areas (46 in common). *Blepharocalyx salicifolius* and *Dyckia pampeana* occurred exclusively under the tree canopies, presenting the highest abundances. In the open areas, the most abundant species were *Evolvulus sericeus* and *Sisyrinchium* sp. (morphospecies 1) (non-exclusive) and *Bulbostylis communis* and *Rhynchospora praecincta* (exclusive) (Appendices S1 and S2).

Of the 27 woody species, 15 (55.5%) occurred exclusively under trees (e.g., *Blepharocalyx salicifolius, Chrysophyllum marginatum*, *Allophylus guaraniticus*, *Schinus longifolia*, and *Eugenia uniflora*). Some cacti also occurred exclusively in this microhabitat (e.g., *Frailea schilinzkyana, Lepismium lumbricoides*, and *Cereus hildmannianus*) (Appendices S1 and S2). Exotic species were present in both microhabitats (under trees and open areas), except for *N. texanus*, which was found only under the canopy of trees.

The NMDS presented a stress value of 10.72%, indicating the adequacy of the ordering. The species composition differed between microhabitats by PERMANOVA ($F = 6.97$; $R^2 = 0.19$; $p = 0.001$; Figure 3), with the formation of two distinct floristic–structural groups, one composed of trees and vegetation under the tree canopies and another for the vegetation of paired open areas.

The richness of woody species (4.93 ± 2.81) was almost six times higher under trees compared to paired open areas ($Z = 5.760$, $p < 0.0001$, Figure 4a), while the richness of herbaceous (16.46 ± 4.69) plants was approximately 1.5 times higher in the open areas ($Z = -3.887$, $p < 0.0001$, Figure 4b). We did not identify significant differences for woody and herbaceous species richness among tree species ($p > 0.05$, Figure 4c,d), when comparing only the plots under trees. Species diversity also does not differ significantly between microhabitats ($p = 0.59$; Figure 4e) or among tree species ($p > 0.05$; Figure 4f), when comparing only the plots under trees.

3.4 | Functional Aspects of the Plant Community

Woody regenerants with zoochoric dispersion showed 43 times greater abundance (22.8 ± 15.5 ind) under the tree canopies than the open areas (0.53 ± 0.74 ind) ($Z = 7.746$, $p < 0.0001$, Figure 5a). The abundance of woody regenerants with non-zoochoric dispersion did not differ significantly between microhabitats ($p = 0.18$). Under trees, zoochoric dispersal syndrome presented greater abundance, while in the open areas, there were no significant differences between the abundance of plants with zoochoric and non-zoochoric dispersal syndromes ($p = 0.98$).

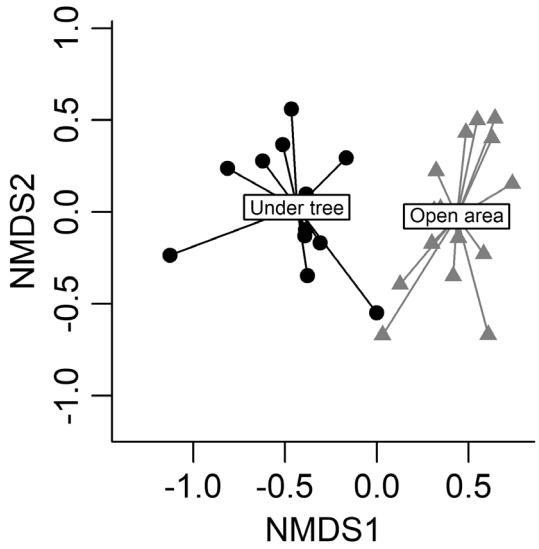


FIGURE 3 | Non-metric multidimensional scaling (NMDS) of the floristic-structural composition of the plant community under tree canopies and in paired open areas based on the abundance of individuals per species (distance matrix of Bray–Curtis). Significant differences in floristic composition between microhabitats by PERMANOVA ($p = 0.001$).

There was a significant interaction between the microhabitat and the habitat preference of woody species ($Z = 5.659$; $p < 0.0001$; Figure 5b), indicating that woody species typical of forest and park grassland are favored by nurse trees. Typical forest woody species showed greater abundance (21.33 ± 14.8 ind) ($p < 0.0001$; Figure 5b) under trees than the open areas (0.06 ± 0.26 ind), also being higher than the abundance of woody species typical of park grassland under trees (4.93 ± 3.22 ind) ($p < 0.0001$; Figure 5b). The abundance of woody species typical of park grassland was also higher under trees than in the open areas (1.26 ± 1.39 ind) ($Z = 4.418$, $p < 0.0001$; Figure 5b). The nurse trees increased the abundance of woody species typical of forest by 99.7% and the abundance of woody species typical of park grassland by 74% under their canopies.

The species facilitated by nurse trees represent 49.6% of all recorded species (62 species) of which 20 are woody and 42 are herbaceous species. Non-facilitated species represent 45.5% of the total (60 species), mainly comprising herb and grass species (54 species). Neutral species represent only 7.5% of the total (10 species), including herbaceous and two woody species (*Aspidosperma quabracho-blanco* and *Vachellia caven*) (Appendices S1 and S2). Abundance did not show a significant difference between the types of facilitation ($p = 0.18$; Figure 5c).

3.5 | Factors Explaining Nucleation by Woody Species

Tree characteristics, including total height ($Z = -0.621$, $p = 0.534$), stem height ($Z = 1.355$, $p = 0.175$), and crown diameter ($Z = 0.159$, $p = 0.874$), did not have a significant effect on the abundance of woody regenerants (Figure 6a–c). Among the other variables analyzed, LAI showed a significant positive effect ($Z = 11.67$; $p = 0.0001$; Figure 6d) on the abundance of woody regenerants, being higher under trees (Table 1). Litter cover ($Z = 2.446$; $p = 0.014$; Figure 6g) also showed a positive effect, and exposed soil showed a negative effect ($Z = -2.843$; $p = 0.004$; Figure 6i), while the litter depth had no significant effect ($Z = 1.871$; $p = 0.065$, Figure 6h). Although native herbaceous cover ($Z = -0.495$; $p = 0.621$; Figure 6e) and exotic herbaceous cover ($Z = -0.686$; $p = 0.483$; Figure 6f) did not affect the abundance of woody regenerants, the abundance of herbaceous plants negatively affected this variable ($Z = -3.600$; $p = 0.0003$; Figure 6j).

4 | Discussion

Our results confirm the nursing role of *Prosopis affinis, Prosopis nigra*, and *Aspidosperma quebracho-blanco* and highlight their importance in the assembly of the plant community of park grassland. We found a relevant effect of nurse trees on the recruitment of woody plants typical of forests and with zoochoric dispersion under their canopies, indicating a process of nucleation by woody plants over grassland vegetation. They promote changes in abiotic (shade provision, increased litter deposition and decreased exposed soil) and biotic (decreased herbaceous abundance) conditions, forming microhabitats favorable under their canopies, for woody and herbaceous species. Although several abiotic variables such as soil fertility, soil moisture, and daily temperature range were not measured here and are known to be relevant during facilitation (Korndörfer et al. 2015; Whitford and Duval 2020; Abreu et al. 2021), these variables are possibly mediated by shade provision, increased litter deposition, and decreased exposed soil, as observed in our study.

The increase in litter coverage and depth observed under the trees contributed to the decrease in the percentage of exposed soil, a common characteristic in the studied environment, associated with the presence of "*blanqueales*." The litter layer formed under the canopy of nurse trees can contribute to improving soil fertility (Navarro-Cano et al. 2019) and creating roughness, allowing the retention of organic matter, water, sediments, nutrients, and seeds in the microhabitat formed (Aumond and Maçaneiro 2014). Therefore, the litter could contribute to the establishment of natural regeneration of woody species, providing adequate substrate and protection for seed germination within grassland vegetation.

When we analyzed plant abundance and species richness between microhabitats, it is clear that nurse trees favor the regeneration of woody species. This facilitation occurred possibly due to the changes caused by nurse trees in the environment, since the characteristics of the trees (total height, stem height, and crown diameter) had no effects on the abundance of woody regenerants. The changes in abiotic and biotic variables observed under trees probably favored the increase in the abundance of woody regenerants. In grazed park grassland in Uruguay, increased shade and reduced competition with grasses were the main mechanisms by which nurse trees promoted the recruitment of woody species, increasing the density of woody species under the canopies when compared to the open areas (Inofuentes and Säumel 2022). The species *Blepharocalyx salicifolius* was the most abundant woody species under the canopy of nurse trees. Traits such as shade tolerance and dispersal by

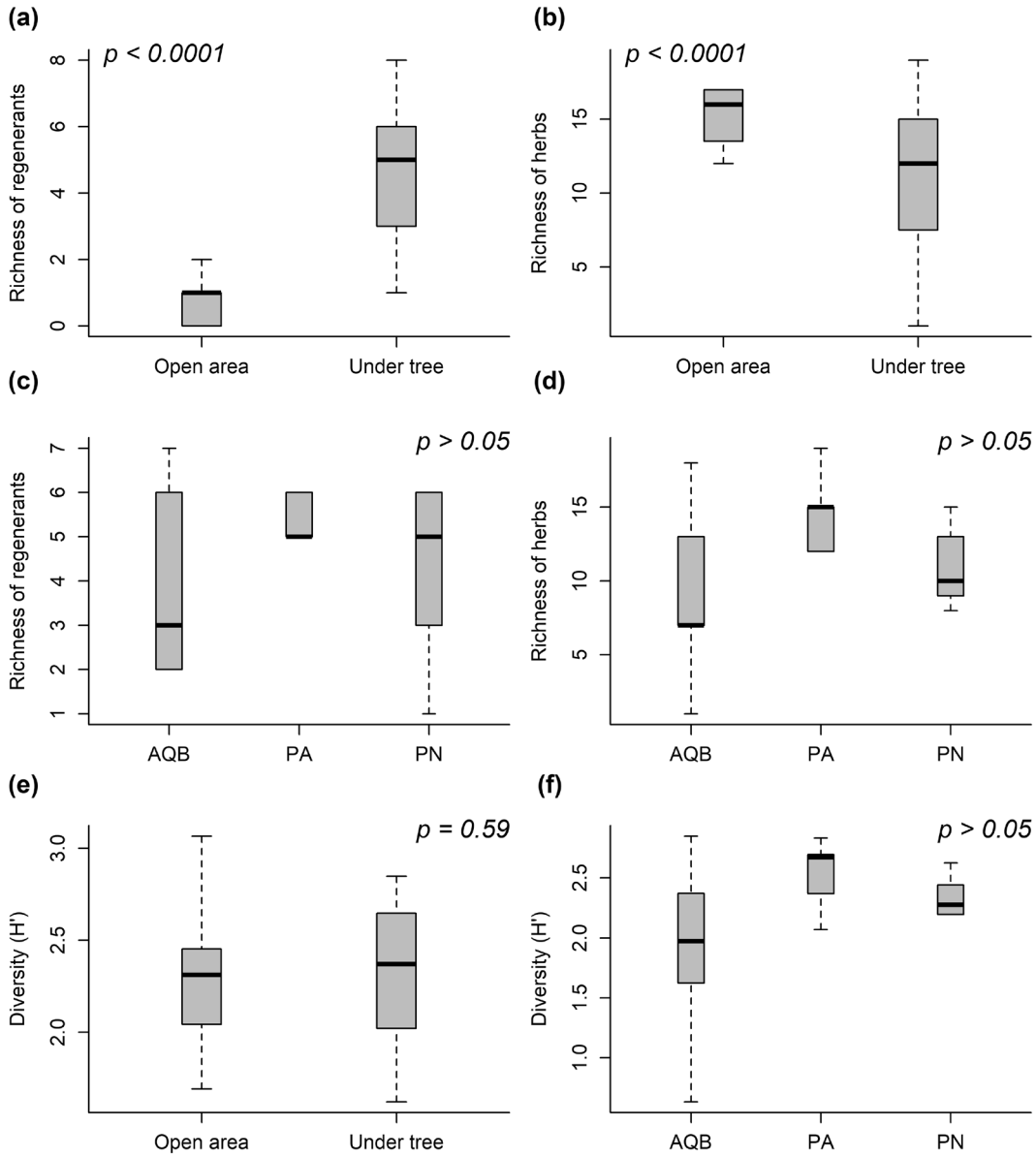


FIGURE 4 | Richness of woody regenerants (a) and herbaceous species (b) in the microhabitats (under trees and open areas). Richness of woody regenerants (c) and herbaceous species (d) under the canopy of each tree species and species diversity in microhabitats (under trees and open areas) (e) and under the canopy of each tree species (f). AQB = *Aspidosperma quebracho-blanco*, PA = *Prosopis affinis*, PN = *Prosopis nigra*. Differences for diversity (H′) were tested using Hutcheson's *t*-test.

avifauna contributed to the establishment of this species in high abundance under the canopies of nurse trees and in areas excluded from grazing in Uruguay (Etchebarne and Brazeiro 2016; Inofuentes and Säumel 2022). Woody species such as *Sapium haematospermum* and *Celtis iguanaea* that benefit from nurse trees also have their participation increased in park grasslands excluded from grazing (Redin et al. 2017) probably benefited from the nucleation process in the absence of this disturbance factor.

Despite favoring the regeneration of woody plants, nurse trees benefit numerous herbaceous species typical of the park grassland. Poaceae, Asteraceae, Cactaceae, and Solanaceae are the families with the largest number of facilitated species, among them: *Nassela neesiana, Pffafia gnaphalioides*, *Frailea schilinzkyana*, and *Bouchetia anomala*. The sparsely foliated canopy of these tree species favors the development of the herbaceous layer, with the presence of grasses such as *Paspalum notatum*, species of the genus *Nassela*, as well as specimens from the Oxalidaceae, Verbenaeae, and Asteraceae families (Marchiori 2004). Thus, even though in lower abundance under canopies, the herbaceous plants also benefited. The presence of beneficiary species that deviate from their physiological optimum and that are related to nurse plants, as is the case of herbaceous plants in this study, increases the importance of nurse plants as mediators of greater diversity at the ecosystem level (O'Brien et al. 2019).

Even though most exotic species are not facilitated by the tree canopies, they remain a threat that cannot be ignored in this ecosystem. *Eragrostis plana* and *Senecio madagascariensis*, which are more abundant in open areas, are among the

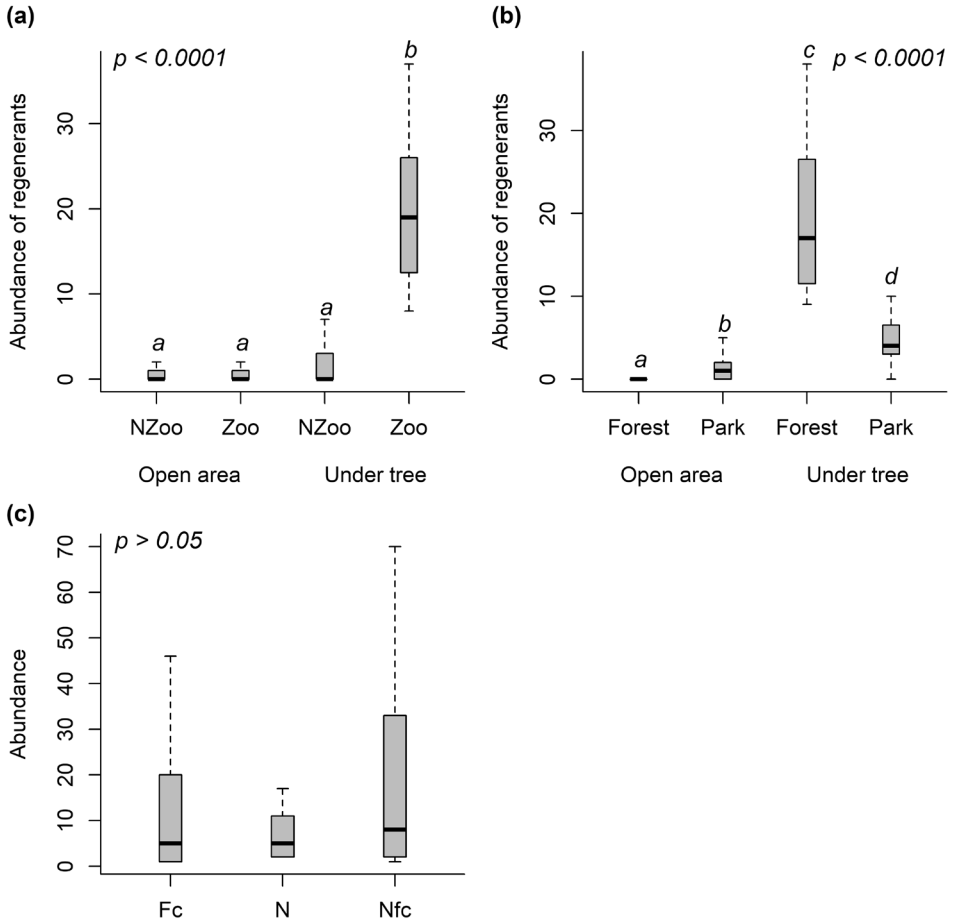


FIGURE 5 | Abundance of plants by functional aspect. (a) Dispersal syndrome of woody species by microhabitats (under trees and open areas): zoochoric (Zoo) and non-zoochoric (NZoo); (b) habitat preference of woody species by microhabitats (under trees and open areas): typical of forest (Forest) or park grassland (Park) and (c) type of facilitation of woody regenerants and herbaceous species: facilitated (Fc), not-facilitated (Nfc), and neutral (N). Significant differences (lowercase letters) between microhabitats were identified by contrast analysis.

four most invasive species in the pastures of southern Brazil (Guido et al. 2016). *Eragrostis plana* has a high reproductive and propagation capacity, with seeds easily dispersed by human activity, grazing, water, and wind (Nabinger and Dall'Agnol 2020; Zabala-Pardo and Lamego 2024). *Senecio madagascariensis* produces large quantities of highly viable seeds, mainly dispersed by wind and animals (Nabinger and Dall'Agnol 2020), but little is known about its invasion mechanisms in the grasslands of southern Brazil (Guido et al. 2016). Regarding *Nuttallanthus texanus*, this species is facilitated by the tree canopies but does not pose a major threat to this ecosystem due to its low abundance. No information was found regarding its invasive behavior.

Another interesting result is that although there was no variation in the abundance of woody regenerants among nurse tree species, herbaceous abundance showed a difference between the canopies of *Aspidosperma quebracho-blanco* and *Prosopis nigra*, probably indicating an effect of tree canopy growth architecture. Even though this relationship was not tested in the current study, we believe that the greater total height and greater insertion height of the branches of *Aspidosperma quebracho-blanco* contribute to a greater incidence of light, allowing greater development of the herbaceous component. Taller trees with greater crown height favored herbaceous cover when compared to smaller trees in semi-arid grasslands in Ethiopia, indicating that herbaceous cover responds differently to tree species (Beley and Moe 2015).

When we evaluated the habitat preference of woody species and the dispersal syndrome, we found that woody species typical of forests and with zoochoric dispersal are more favored by nurse trees. They also create favorable environments for the establishment of woody species typical of park grassland, such as *Schinus longifolia* and *Chromolaena* cf. *ivifolia*. This result indicates that isolated trees within grassland vegetation facilitate the nucleation process by woody species under their canopies. This behavior has already been observed in other studies, for isolated trees of *Araucaria angustifolia* and other woody species in highland grassland in southern Brazil (Duarte et al. 2006; Korndörfer et al. 2015; Marcilio-Silva et al. 2015), for native forest species isolated in the Cerrado biome (Abreu et al. 2021) and for trees typical of park grassland in Uruguay (Inofuentes and Säumel 2022), which are also the targets of this study.

The nucleation process is favored by the perch effect performed by nurse trees that facilitates the establishment of zoochoric woody species under tree canopies (Inofuentes and Säumel 2022). It also can explain the association of cacti (e.g., *Cereus hildmannianus* and *Opuntia elata*) with the nurse tree

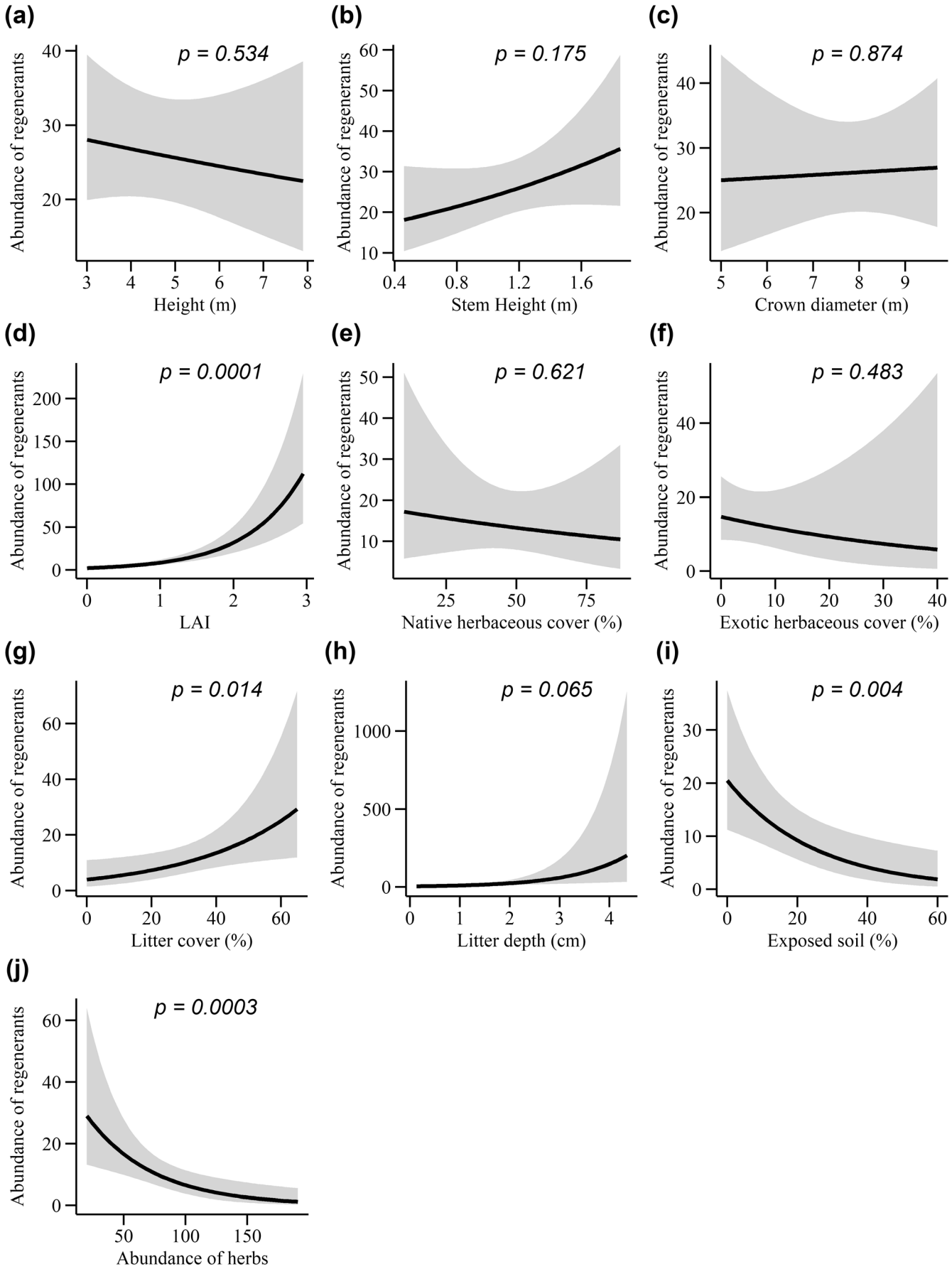


FIGURE 6 | Legend on next page.

FIGURE 6 | Effect of dendrometric variables (a–c) and environmental variables (d–i) and herbaceous abundance (j) on the woody regenerant abundance, based on a generalized linear mixed model (GLMM). Average effects are represented with the solid line. The shaded region corresponds to the 95% confidence intervals.

canopies. The establishment of Cactaceae species under shrubby nurse plants in desert environments has been related to the dispersal of fleshy fruits by fauna, which deposits the seeds under the canopies, allowing germination and growth in less severe environmental conditions (Badano et al. 2016). The same authors also found that the association of Asteraceae species with nurse plants occurs due to the trap effect, where seeds dispersed by the wind are captured in vegetation nuclei, which can justify the regeneration of non-zoochoric species, verified under the trees in the current study.

Although there are no differences in species diversity between the microhabitats (under trees and open areas), we found that their floristic-structural composition is different, indicating a high replacement of the herbaceous component by woody plants under the canopies of nurse trees. The predominance of woody species typical of the forest under the canopy of nurse trees is indicative of the nucleation process and the change in the typical composition and structure of the plant community (Abreu et al. 2021). However, some aspects observed in our study area and listed below allow us to infer that the nucleation process is slow. First, this area has been isolated from disturbances (e.g., cattle grazing and fire) for more than a decade, which implies the absence of one of the main factors that limit forest expansion. Second, forest regeneration is limited below the tree canopy, in a few situations expanding beyond it or exceeding its height. Third, regenerants of tree species typical of park grassland (*Prosopis* spp., *Vachellia caven*, and *Aspidosperma quebracho-blanco*) are neutral or non-facilitated and are found in greater abundance than woody species typical of forest in open areas.

In any case, we must consider that forest expansion by nuclei in originally grassland areas depends on an overlap of processes (e.g., distance from forest areas, propagule pressure, resource availability) that occur at different times, providing the transition of vegetation state progressively over time (Schinestsck et al. 2019). Furthermore, the facilitating processes act simultaneously with environmental heterogeneity in the assembly of plant communities (Villegas et al. 2023); they can change over time for competitive effects in more advanced stages of the successional trajectory (Liu et al. 2020).

We recognize that this study has limitations, especially considering the absence of variables related to soil fertility and microclimatic variables (e.g., air temperature and moisture, soil temperature and moisture). The supply of nutrients to the soil and the improvement in the local microclimate are mechanisms through which nurse trees facilitate the establishment of other plant species under their canopies (Duarte et al. 2006; Korndörfer et al. 2015; Abreu et al. 2021). Therefore, these variables should be included in future studies to better understand the interactions between facilitators and beneficiaries in this vegetation type. Likewise, the patterns identified here can be tested experimentally in future studies, since this study is correlative. We also recognize the sampling limitations of our study, mainly due to the restricted area of the ecosystem investigated. The park grasslands occupy a small portion of the territory of Rio Grande do Sul and have been intensely converted by agriculture in recent decades, with only remnants remaining preserved in the Espinilho State Park (Watzlawick et al. 2010; Marchiori et al. 2014). This scenario imposes a spatial restriction on suitable locations for data collection, reducing the possibility of representative samples and compromising the statistical replication necessary for analyses that are more robust. However, we highlight that the effort made in this study is essential to the scientific knowledge of this ecosystem.

The results obtained in this study have direct implications for the conservation, restoration, and management of park grassland. *Aspidosperma quebracho-blanco*, *Prosopis affinis*, and *Prosopis nigra* benefit numerous woody and herbaceous species, including rare and endangered species, such as *Dyckia pampeana* (Büneker et al. 2018), *Frailea schilinzkyana* (Carneiro et al. 2016), *Bouchetia anomala*, *Pfaffia gnaphaloides* (Rio Grande do Sul 2014), which highlights the need to conserve them due to the countless exclusive interactions they have. These species also present great potential for use in ecological restoration, due to their role as nurse plants, reducing environmental stress. They can be used in the restoration of park grassland under grazing systems, combined with temporary grazing exclusions to promote natural regeneration under their canopies (Inofuentes and Säumel 2022). The adoption of management actions to control woody nuclei in the study area (e.g., mowing and controlled grazing) can be considered in the long term. Currently, the process of nucleation by woody plants appears to be slow, not posing a problem. Therefore, we recommend that any management actions should be analyzed with caution for a better understanding of the possible effects on the composition, structure, and ecological processes of the plant community. We emphasize that the study area is susceptible to biological invasion by *Eragrostis plana* and *Senecio madagascariensis*, a condition that could be worsened by inadequate vegetation management.

5 | Conclusions

Both nurse tree species studied promote more favorable conditions under their canopies for woody and herbaceous species, mainly by changing the biotic (decreased herbaceous abundance) and abiotic (provide shade, increased litter and decreased exposed soil) conditions. Despite benefiting many herbaceous species, the microhabitat formed under the canopies is more favorable to the establishment of woody plants, which occur in greater abundance. Thus, woody nucleation is facilitated in park grassland, which may culminate in forest expansion in the long term. These three tree species play an important role in the conservation of the biodiversity associated with them in park grassland and can be used in ecological restoration projects of this threatened ecosystem.

Author Contributions

G.D.F. and A.P.M.R. conceived the idea and designed the methodology; G.D.F., B.C., D.P., and E.T.P.A. collected the data; P.J.S.S.F. assisted in the identification of the species; G.D.F. and R.B.S. analyzed the data; G.D.F. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data supporting the findings of this study are available at https://doi.org/10.6084/m9.figshare.25648761.

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Supporting Information

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