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Nurse species facilitate persistence of dry forests in agricultural landscapes in Uruguay

Paola Pozo Inofuentes[1] | Ina Säumel[2]

[1]Thuenen Institute of Forestry, Hamburg-Bergedorf, Germany

[2]Integrative Research Institute THESys Transformation of Human-Environment-Systems Humboldt-Universität zu Berlin, Berlin, Germany

Correspondence
Ina Säumel, Humboldt Universität zu Berlin, IRITHSys, Unter den Linden 6, 10099 Berlin, Germany
Email: ina.saeumel@hu-berlin.de

Paola Pozo Inofuentes, Thünen Institute of Forestry, Leuschnerstraße 9, 21031 Hamburg-Bergedorf, Germany
E-mail: paola.pozo@thuenen.de

Abstract

Questions: Park forests are shaped by extensive cattle ranching in the transition between natural riverine forests and open grasslands. The underlying mechanisms driving tree regeneration have not been studied, however, they determine biodiversity, sustainability and multifunctionality of these ecosystems. We explored patterns of tree regeneration by analyzing nurse–beneficiary interactions and tree community composition.

Location: Park forests within the departments of Rio Negro, Paysandú, Artigas and Tacuarembó, República Oriental del Uruguay, South America.

Methods: We established 205 (1 × 1 m²) paired plots in open microhabitat and under the tree canopy to evaluate the patterns of tree regeneration. To assess tree community composition and diversity we carried out forest inventories within one-hectare plots of ten park forests.

Results: Scattered trees in park forests had a positive effect on tree regeneration density, whereas, dense grass coverage had a negative effect. Regeneration density increased and grass cover reduced under the canopy of nurse trees. Regeneration beneficiaries were mainly bird dispersed species with different life strategies. Tree communities varied between forest types and spatially closer forests were more similar.

Conclusions: Our study outlines the importance of park forest trees to the promotion of forest regeneration and recovery in grazed forests. Our results found a positive interaction effect between nurse trees and saplings, based on our results we suggested possible facilitation mechanisms including the provision of shade, reduction of grass competition and the attraction of seed dispersers.

KEYWORDS
composition, dispersal, grazing, land use change, nurse tree, park forest, regeneration, silvopastoral systems

1 | INTRODUCTION

Shifting the scientific gaze from merely natural ecosystems to human-modified landscapes regarding biodiversity conservation is an important goal to meet the challenges of the Anthropocene (Seddon et al., 2016; Johnson et al., 2017). Within the South American grassland biome, the heavily used Campos region of Uruguay is subject to expanding land use changes to establish monocultures for the globalized market (Céspedes-Payret et al., 2012). Native forests are scattered within a landscape matrix dominated by grasslands, timber and crop plantations, forming biological corridors for avian and mammalian biodiversity (Nores et al., 2005; Haretche et al., 2012). Among them, the so-called park forests ('monte parque') are composed of native xerophilous trees growing in a dense herbaceous stratum shaped by cattle ranching. Quantitative studies in park forests are scarce (but see Bernardi et al., 2016; Pozo & Säumel, 2018). Some qualitative studies have reported on the geographical variation in species composition denoting a high affinity with the Flora Paranaense and the seasonal dry forests of the Chaco and Espinal of central South America (Grela, 2004; Brussa & Grela, 2007).

Together with the worldwide loss of dry forests (Miles et al., 2006; Hansen et al., 2013), park forests have been greatly threatened by agricultural expansion (e.g. Tiscornia et al., 2014). The western part of Uruguay, in particular, has experienced the highest loss of natural habitats due to soybean farming and afforestation (Brazeiro et al., 2008, 2020). The survival of park forests depends on forest regeneration, which is determined by a balance of complex biotic and abiotic interactions.

In general, several biotic factors negatively affect forest regeneration (Catterall, 2016; Martinez-Ramos et al., 2016). Wild and domestic herbivores can deter regeneration (Macdougall et al., 2010), annual herbs out-compete tree seedlings when colonizing fields or large forest gaps (Cuesta et al., 2010) or exotic species suppress the native species (Catterall, 2016): *Ligustrum lucidum* and *Gleditsia triacanthos* inhibit the regeneration of native species (Costa & Delgado, 2001; Plaza Behr et al., 2016).

In contrast, positive interactions have been recognized as a major driving force for species coexistence in plant communities, particularly in harsh environments (Bertness & Callaway, 1994). Nurse plants facilitate regeneration and maintain plant species richness under grazing across a range of ecosystems and productivity levels (Smit et al., 2007; Manning et al., 2009; Catterall, 2016). The nurse plant mitigates the abiotic stresses and/or disturbances that plants experience outside the nurse canopy (Gómez-Aparicio, 2009), such as high temperatures, lack of water and nutrients, low soil moisture and fertility, thus providing suitable microsites for seedling establishment (Padilla & Pugnaire, 2006). In addition, indirect interactions occur via diverse pathways (Sotomayor & Lortie, 2015) especially indirect facilitation (e.g. Pages & Michalet, 2003; Saccone et al., 2010; Schöb et al., 2013; Michalet et al., 2015). For example, neighbouring plants can also influence seedling establishment by acting as a physical barrier (e.g. thorns, spines), through chemical compounds or by concealment of seedlings (Baraza et al., 2006; Guignabert

et al., 2020). Nurse species can also indirectly facilitate other species by reducing the negative effect of strong competitors (Pages & Michalet, 2003; Saccone et al., 2010).

Direct and indirect facilitation under high abiotic stress has been examined across many species and a wide range of environmental conditions especially in semi-arid and arid ecosystems and at high elevations (e.g. Abdallah & Chaieb, 2012; Soliveres et al., 2012; Andivia et al., 2017; Anthelme et al., 2017). However, few studies have addressed facilitation in temperate forests or productive grasslands (Oesterheld & Oyarzábal, 2004; Duarte et al., 2006; Fidelis et al., 2009), such as Uruguayan temperate grasslands or forests. Specifically, no studies exist on patterns of tree regeneration in Uruguayan park forests, but such knowledge is critical to their conservation and sustainable management.

We explored the role of scattered trees in regeneration by analyzing the natural occurrence of nurse–beneficiary interactions. Additionally, to contribute to the knowledge of parks forests and their nurse tree species, we also characterized the tree community composition. We hypothesized that scattered trees facilitate tree regeneration under their canopies by three different mechanisms: (i) by providing shade for light sensitive or shade-tolerant species; (ii) by reducing grass competition within the dense grass matrix; and (iii) by promoting forest regeneration linked to the attraction of seed dispersers. Assessing these hypotheses contributes to the development of strategies to design multifunctional landscapes in agri-and silvicultural landscapes in Uruguay and provide valuable information for the management of one of the most threatened and poorly studied forests of Uruguay.

2 | MATERIALS AND METHODS

2.1 | Study area

Uruguay is located in the temperate zone of South America and covers an area of about 176,215 km^2. Mean annual temperature ranges from 16°C in the south to 20°C in the north and the annual rainfall average is approximately 1,500 mm in the north to 1,000 mm in the south (Redo et al., 2012). Our study sites are located in the western sedimentary basin along the Uruguay River ('Cuenca sedimentaria del Oeste') and the Basaltic Region ('Cuesta Basaltica'). Livestock ranching on grasslands is one of the main economic activities. Livestock roams through nearby forests looking for shade, water, and forage, especially when grassland productivity is low (Etchebarne & Brazeiro, 2016), forming natural silvopastoral systems.

Native forests are classified visually according to their physiognomy and topographic location into gallery forests along rivers, park forests — a transition zone between riverine forest and grasslands — creek forest in the rocky parts of the mountains that surround water streams, and hill forests on hillsides (Brussa & Grela, 2007). Park forests are composed of scattered thorny tree species and an understorey of grasses. They vary from the typical, relict park forest known as 'algarrobal' composed mainly of *Prosopis affinis*

and *Prosopis nigra* to a successional and sometimes dominant form named 'espinillar' composed mainly of *Vachellia caven* (Haretche et al., 2012; Delgado & Nebel, 2014).

The study sites include 'blanqueales' associated with the alkaline floodplains of the Rio Uruguay in the surroundings of San Javier (Rio Negro department). They are exceptionally flooded, with park vegetation used for grazing covered by grasses and scattered woody species (*Prosopis nigra* and *Vachellia caven*) of variable density. Soils are alkaline (white areas), eutrophic Brunosols with a low fertility and imperfect drainage.

The 'algarrobales' of Artigas correspond to gently undulating interfluves, the exceptionally flooded litoral of the Rio Cuarem, with a vegetation used for grazing and covered by grasses and scattered trees dominated by *Prosopis affinis*. Soils are sub-nutric Brunosols with a sandy loam texture, medium fertility and moderately good drainage.

The 'algarrobales' of Paysandú are located in the plains of the Rio Queguay Grande and are flat and seasonally (for short times) flooded. The study sites present park vegetation used for grazing, associated with water courses and with a variable density of trees, dominated by *Prosopis affinis*. Soils are shallow eutrophic Planosols, dark brown to black in colour, with a high fertility and imperfect drainage.

The 'espinillares' of Tacuarembo are located in the plains of the Rio Tacuarembo adjacent to drainage routes; they are flat and seasonally (for short times) flooded areas. The vegetation is used for grazing, covered by grasses and disperse woody species of (mainly) *Vachellia caven*. Soils are dystric Planosols with sandy loam, deep variable colours and imperfect drainage.

2.2 | Nurse interactions

To assess the performance of regeneration of tree species we designed a series of paired 1 m × 1 m plots located in two types of microhabitat of regeneration sites, under the canopy of the trees and the other in the open area, approximately two times the crown distance from the nurse tree (Figure 1c). Each paired treatment was repeated 210 times: 60 in 'blanqueales' of Rio Negro, 45 in 'algarrobales' of Artigas, 60 in 'algarrobales' of Paysandú and 45 in 'espinillares' of Tacuarembo. We recorded grass cover as a fraction of the total plot from 0% to 100%. For each tree, we recorded species, total height, crown diameter, leaf area index (LAI) and diameter at breast height (DBH). Crown diameter was measured as the average length of the longest spread from edge to edge across the crown and the longest spread perpendicular to the first cross-section through the central mass of the crown (Pretzsch et al., 2015). LAI is a dimensionless measure defined as the amount of leaf area (m^2) in a canopy per unit ground area (m^2) (Asner et al., 2003) which was used as a proxy to estimate the effect of shading by nurse trees. LAI was measured with the LAI-2000 canopy analyzer (Li-Cor, Lincoln, NE, USA) as the average of three readings taken under the canopy and in the open area (Figure 1b).

2.3 | Field inventory design

Forest inventories were undertaken between October and December 2017. Our study sites are located where park forests are principally distributed including the north, west and the central part of Uruguay within the departments of Rio Negro, Paysandú, Artigas and Tacuarembo (Figure 1a). We used the FAO forest definition that forests have a canopy coverage with trees higher than 5 m of at least 10% and a stand area of more than 0.5 ha (FAO, 2016). A total of ten permanent plots, each of one hectare, were established in park forests where livestock ranching is the most extensive, traditional productive activity. The initial location of the plots was selected arbitrarily to avoid the selection of habitat formations outside the scope of the study. Tree inventories were undertaken in three 20 m × 10 m plots located in the corners and centre of the permanent plot (Figure 1b). Attributes such as species name, DBH and height were recorded for all individual or multistem adult living trees (DBH ≥ 2.5 cm at 1.3 m) and regenerating trees (DBH < 2.5 cm diameter and height < 1 m).

2.4 | Data analysis

The nurse effects of trees on plant regeneration were analyzed with generalized linear mixed-effects models (GLMMs) using the Poisson distribution. We used the regeneration density, calculated as the total number of saplings per area. We tested for multicollinearity among the variables by calculating variance inflation factors (VIF). A VIF greater than 10 is regarded as severe multicollinearity (Zuur et al., 2010). VIF analysis suggested that no input variables were problematically correlated.

We assessed how the regeneration density of tree species was affected by the microhabitat, LAI and relative grass cover. We used paired treatments and study sites as a random effect to account for unmeasured influences within paired plots and sites.

We carried out the same analysis with relative grass cover as response variable and habitat and LAI as predictor variables. We separately analyzed plots with scattered trees using the same mixed-effects model and using crown diameter, height and DBH as explanatory variables to identify differences in interactions across tree nurse variables.

We calculated the 'relative interaction index' (RII) to estimate the intensity of the interactions (Armas et al., 2004). RII indices were used to directly compare the performances of understorey regenerating trees among treatments:

$$RII = (P_{+N} - P_{-N})/(P_{+N} + P_{-N}),$$

where P_{+N} and P_{-N} denote the performances of regeneration in the presence and absence of the nurse tree, respectively. RII was calculated based on the regeneration density. RII results significantly above zero indicated facilitation, the intensity of which increases up to 1. RII significantly below zero revealed competitive
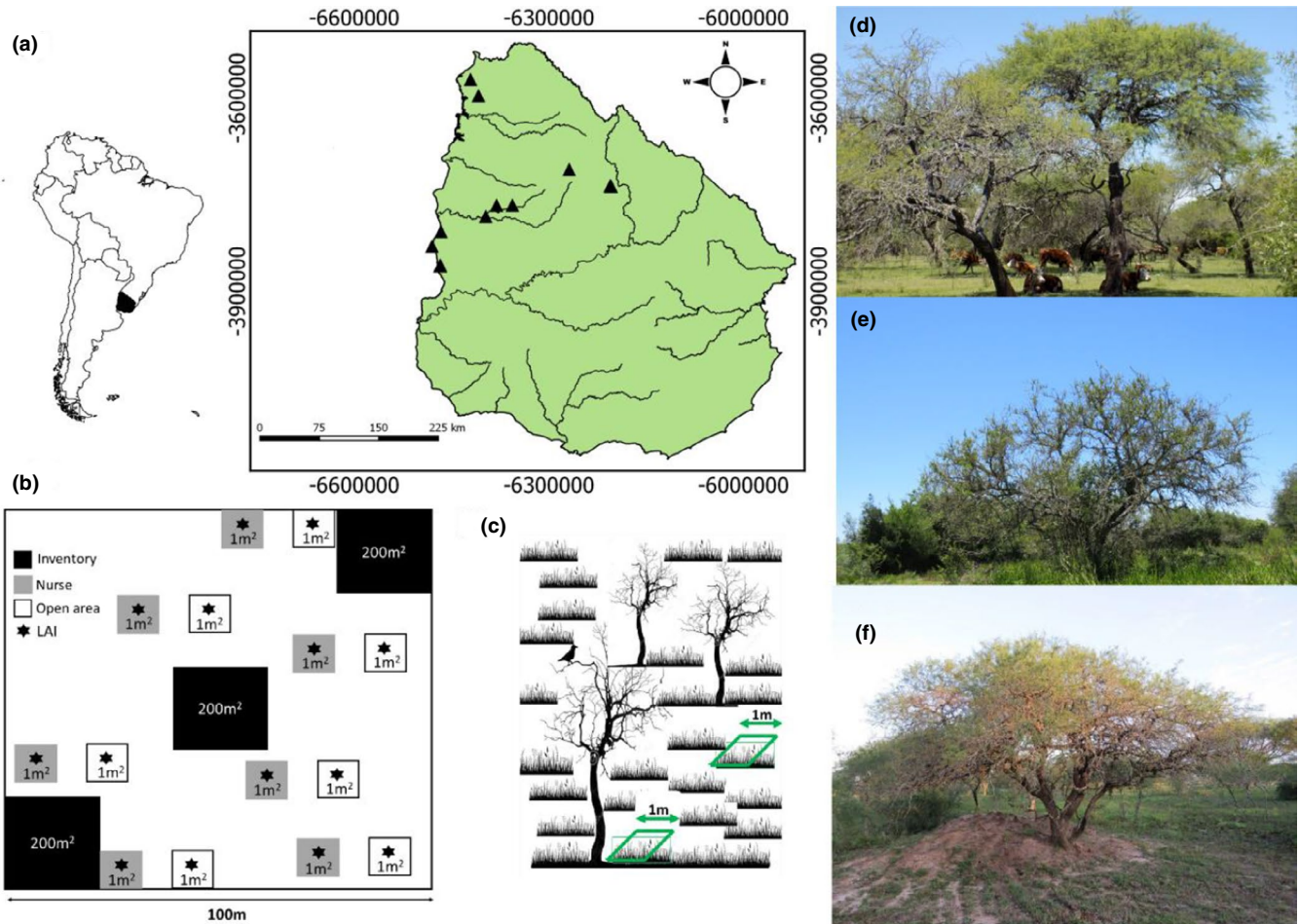
FIGURE 1 Description of the study area: (a) the study sites in Uruguay including the north, west and the central part of Uruguay within the departments of Rio Negro, Paysandú, Artigas and Tacuarembo, coordinate system UTM zone 21 S; (b) sampling design composed of permanent plots (100 m² × 100 m²), inventory plots (200 m²), treatment plots (1 m²), and measurement points of leaf area index (LAI); (c) nurse interaction design showing the "open microhabitat" and "nurse" treatments; (d–f) park forests characterized by dispersed trees of *Prosopis* spp. "algarrobal" (Department of Artigas), *Vachellia caven* "espinillar" (Department of Tacuarembo) and with alkaline soils "blanqueal" (Department of Rio Negro) respectively

interactions, the intensity of which increases up to –1 (Armas et al., 2004).

We reviewed existing literature on each species for three different traits: dispersal mode, life strategy and facilitation type (see Table 2). The dispersal mode was classified into anemochoric (wind-dispersed seeds or fruits), zoochoric (seed or fruits dispersed by animals) and autochoric species (seed or fruits dispersed by explosive mechanisms); see van der Pijl (1982). We classified tree species according to their life strategy as light-demanding shade-intolerant, intermediate shade-tolerant and shade-tolerant species (Anderson et al., 1969). Categories of 'shade-tolerant' and 'shade-intolerant' species refer to their ability to germinate and grow under various light regimes (Swaine & Whitmore, 1988; Whitmore, 1989).

Finally, facilitation type was classified into either facilitation obligates, facilitation beneficiaries (Butterfield, 2009) and non-facilitated species. We considered as facilitation obligates those tree species found only under the canopy of a given nurse tree but not in the open microhabitat, while facilitation beneficiaries were tree species with more individuals growing under the canopy of a nurse than in the open microhabitat. For specific information on the literature see Table 2. We then calculated the regeneration density of each trait (0 to 100) by dividing the density of a given trait by the total density of all the traits and multiplying by 100.

We compared the variation of: (i) strength and direction of RII between forest types; (ii) regeneration density, LAI and relative grass cover between open and closed microhabitats; (iii) regeneration density within dispersal modes, life strategies and facilitation types; and (iv) Shannon diversity index between forest types. The data were tested for normality using the Shapiro–Wilk test. We used one-way ANOVA to test for differences in species diversity between forest types and a post-hoc Tukey test after finding significantly different results. The Kruskal–Wallis H test followed by Dunn post-hoc tests were used with non-parametric data. Statistical analyses were undertaken with the open-source software package R version 3.3.2 (R Foundation for Statistical Computing, Vienna, Austria) using the packages *vegan* (Oksanen et al., 2017), *mass* (Ripley et al., 2016)

and *lme4* (Bates et al., 2015) with an adopted alpha of 0.05 or less considered as significant.

We also analyzed the park forest communities in our study sites by tree forest composition and diversity. We used non-metric multidimensional scaling (NMDS) on the Bray–Curtis dissimilarity matrix of tree species abundance, a robust unconstrained ordination method to visualize patterns of composition between forest sites (Clarke, 1993). The Bray–Curtis distance was chosen because it is based on quantitative data and has been shown to be one of the best for detecting gradients of species composition (Minchin, 1987). The significance of the compositional differences was tested with a permutational multivariate analysis of variance (PERMANOVA) using the 'Adonis' function in the *vegan* package (Anderson, 2001). To assess species diversity, we calculated the Shannon index (H') (Shannon & Weaver, 1949).

3 | RESULTS

3.1 | Nurse interactions

Park forest trees had a positive effect on tree regeneration density (Table 1, Figure 2a) indicated by the higher regeneration density under trees than in the open area ($H = 92.8$, $p < 0.001$) with an increase of around 1600%. In total, 16 tree species were recorded regenerating under the canopy of park forest trees (Table 2). *Schinus longifolia*, *Celtis ehrenbergiana* and *Blepharocalyx salicifolius* were the densest species, whereas *Erythrina crista-galli*, *Geoffroea decorticans* and *Populus alba* were not recorded under the nurse trees. High grass cover had a significant negative effect on tree regeneration density (Table 1, Figure 2b). Nurse-specific variables including variations in DBH, height and crown diameter did not influence tree regeneration density (Table 1, Figure 2d–f). There was a shift from significantly facilitative net interactions in 'espinillares' to non-significantly facilitative or neutral net interactions in 'algarrobales' ($H = 36.3$, $p < 0.001$; Figure 3a). LAI displayed 61% more shade under trees than in the open area ($H = 249.1$, $p < 0.001$; Figure 3b), while grass cover was significantly lower ($H = 53.8$; $p < 0.001$, Figure 3c) with a decrease of around 24% under the trees. Within all regenerating species, dispersal mode varied significantly ($H = 23.5$, $p < 0.001$; Figure 3d, Table 2), and density of zoochorous species (mainly mediated by birds) was significantly higher than that of anemochorous ($p < 0.001$) and autochorous species ($p < 0.001$). Life strategy traits had a similar density in the regenerating species ($F = 0.6$, $p > 0.05$; Figure 3e, Table 2). Post-hoc pairwise comparisons indicated a higher density of facilitative obligates ($p < 0.01$) and facilitative beneficiary trees ($p < 0.01$) in comparison with non-facilitated trees.

3.2 | Composition and diversity

In total, we identified 21 tree species (see Appendix S1) from 14 different families, 20 native species and the exotic *Populus alba*. The tree layer was composed of 14 species and the regeneration layer of 20 species. Of the recruits 75% belonged to *Vachellia caven*, *Prosopis nigra* and *Prosopis affinis*. Differences in the composition of plant communities were noted between park forest types ($F = 1.59$; $R^2 = 0.44$, $p < 0.01$), the 'espinillares' having the greatest distance to the 'blanqueales' and 'algarrobales' (Figure 4a). These differences were associated more to adult tree species composition ($F = 3.31$; $R^2 = 0.62$, $p < 0.01$) than regenerating species composition ($F = 1.35$; $R^2 = 0.40$, $p > 0.01$). Tree species diversity ($F = 4.39$, $p = 0.058$; Figure 4b) and regenerating species diversity ($F = 3.34$, $p = 0.097$; Figure 4c) did not vary between different park forest types.

Espinillares were dominated by *Vachellia caven* and species like *Blepharocalyx salicifolius*, and *Celtis ehrenbergiana*, with regeneration of *Allophyllus edulis*, *Maytenus ilicifolia* and *Vachellia caven*. Blanqueales were dominated by *Prosopis nigra* followed by *Vachellia caven* and *Aspidosperma quebracho-blanco*, regeneration was significant in species like *Schinus longifolia*, *Celtis ehrenbergiana* and *Xylosma tweediana*. Algarrobales were dominated by *Prosopis affinis* followed by *Vachellia caven* and *Celtis ehrenbergiana*, and the most abundant regenerating species were *Celtis ehrenbergiana*, *Vachellia caven*, *Schinus longifolia* and *Prosopis affini*s.

TABLE 1 Results of the generalized linearmixed models (GLMM). *Z* values for the fixed effects and SD that fitted the random effects (sites and treatments) are shown

Model	Fixed terms	*Z* value	*p* value	Random effects	SD
Regeneration (trees m^{-2}) Open and closed	Microhabitat	−7.3	<0.001***	Sites	0.84
	Grass cover	−4.5	<0.001***	Treatment	0.00
	LAI	1.6	<0.09 ns		
Grass cover (%) Open and closed	Microhabitat	13.4	<0.001***	Sites	0.27
	LAI	0.4	0.64 ns	Treatment	0.00
Regeneration (trees m^{-2}) Close	Grass cover	−3.4	<0.001***	Sites	0.92
	LAI	1.3	0.18 ns		
	Tree height	−0.5	0.60 ns		
	DBH	0.8	0.38 ns		
	Crown diameter	0.1	0.87 ns		

Abbreviations: DBH, diameter at breast height; LAI, Leaf area index; ns, not significant.

***$p < 0.001$, **$p < 0.01$; *$p < 0.05$.
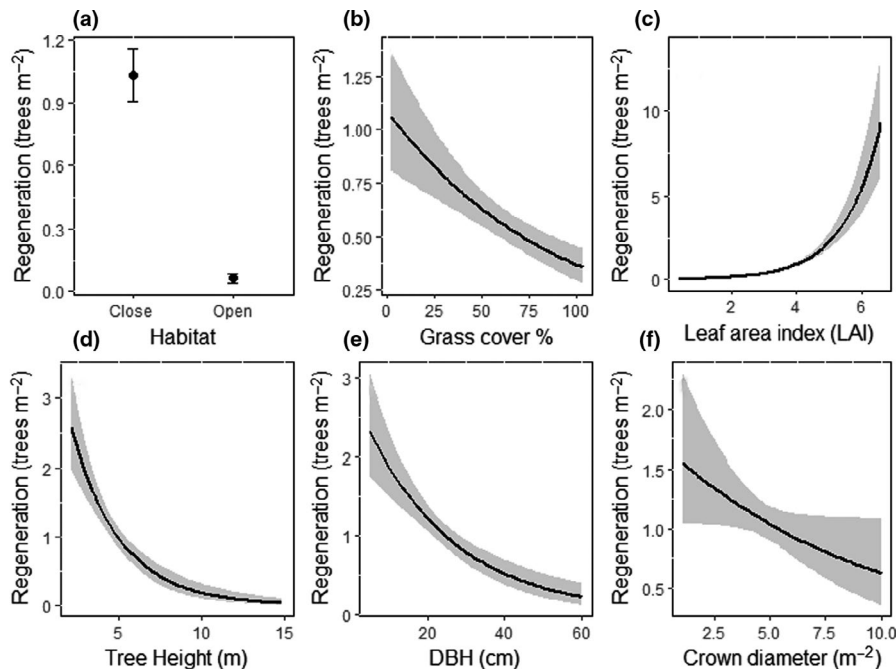
FIGURE 2 Effect graphs based on the generalized linear mixed-effects model (GLMM), testing the effects of microhabitat and tree parameters on tree regeneration. Mean partial effects on tree regeneration are shown (solid lines). Circles show arithmetic means, error bars represent standard errors. Shaded regions correspond to 95% confidence intervals for each section. For parameter definition see section 2. *Materials and Methods*, for results see Table 1

4 | DISCUSSION

4.1 | Trees facilitate regeneration in grazed park forests

Studies in Uruguay have been limited to assessment of the grazing effect on tree regeneration of hill forests (Etchebarne & Brazeiro, 2016), palm forests (Báez & Jaurena, 2000; Rivas, 2005) and a coastal forest (Rodríguez-Gallego, 2006). To our knowledge, no study has assessed the occurrence and importance of facilitation mechanisms in Uruguayan park forests.

Our study clearly confirmed a pattern of tree regeneration under nurse trees in park forests with 1600% more seedling density under the trees than in open areas (Figure 2a, Table 1). This indicates that adult trees facilitate the establishment of new individuals, a form of 'parental care' in plants as was found in an Araucaria Forest in South Brazil (Duarte et al., 2006), in a sclerophyllus forest and the forest–grassland ecotone in Chile (Fajardo & McIntire, 2011; Cavieres & Peñaloza, 2012; Root-Bernstein & Jaksic, 2013) and in seasonally dry forests in Argentina (Tálamo et al., 2015; Torres & Renison, 2015). However, the 'perch effect' is also an option for all fleshy-fruited species that are dispersed by birds (see Table 2; e.g. *Celtis ehrenbergiana* [Palacios et al., 2014] or *Schinus longifolia*]. Nurse and perch effects are not mutually exclusive, rather both effects function in a synergistic way: bird dispersal brings seeds to the safe germination sites of the nurse tree.

Our results agree with findings by Gómez-Aparicio et al. (2008) and Guignabert et al. (2020) where tree regeneration was facilitated by nurse plants in the presence of herivores. Specific nurse characteristics including fine variations of shape and size are suggested as major drivers of interactions (Anthelme et al., 2017). However, in our study we did not find an effect of variations of the stem diameter,

stem height and crown diameter of nurse trees on tree regeneration (Figure 2d-f, Table1).

In our study, trees significantly increase shade in the understorey (+61%) (Figure 3b). Open areas in park forests are subject to high solar radiation, and nurse trees can provide shade and reduce light intensity. Similar studies emphasize the provision of shade and reduction of light intensity by nurse trees (Abdallah & Chaieb, 2012), resulting in lower seedling mortality compared to open microhabitats (Manning et al., 2006). The nurse trees analyzed in this study, *Prosopis* spp., and *Vachellia caven*, are also able to improve soil conditions for regeneration as a result of their nitrogen fixation capacity (Root-Bernstein et al., 2017). Isolated trees of *Vachellia caven* improve soil fertility and herbaceous biomass in Uruguayan grasslands (Bernardi et al., 2016). The nurse effect of *Vachellia caven* was also recorded in a sclerophyllous forest of central Chile (Root-Bernstein et al., 2017). *Vachellia caven* display a lower height, multi-branched stems and the presence of spines that creates a structure that restricts cattle browsing, grazing and trampling. In fact, our data provide evidence for the greater effectiveness of *Vachellia caven* ('espinillares') in facilitating regeneration in comparison with *Prosopis* spp. ('algarrobales' and 'blanqueales') (Figure 3a). In contrast, despite the presence of spines *Prosopis* species have characteristics that limit their protective role, such as a growth architecture that leaves open spaces beneath them, allowing relatively easy access to herbivores.

We recorded 24% less grass cover under trees compared to the open habitat (Figure 3c). Shade provided by nurse plants is able to reduce the growth of competing herbs (Pages & Michalet, et al., 2003; Cuesta et al., 2010; Saccone et al., 2010; Prévosto et al., 2012). Such an indirect positive effect on tree seedlings plays an important role in systems where grass competition is an important limiting factor. Grasses have large negative effects on woody species due to their fibrous roots and a large root:shoot ratio, which allows them to

TABLE 2 Tree and regeneration species composition in park forests in Uruguay, with codes used in the NMDS analysis. Dispersal mode (DM): Zoo (Zoochorous), Ane (Anemochorous), Aut (Autochorous). Life strategy (LS): Shi (light-demanding shade-intolerant), Int (intermediate shade-tolerant), Sht (shade-tolerant species). Facilitation type (FT): Obl (facilitation obligates), Ben (facilitation beneficiaries), Nof (species non-facilitated). R: Species recorded in the facilitation experiments. For references see Appendix S2

Family	Species/Author/Code	DM	LS	FT	DE, References
Anacardiaceae	*Schinus longifolia* (Lindl.) Speg. (ScLo)	Zoo	Sht	Ben	1. Abraham de Noir et al. (2002)
Apocynaceae	*Aspidosperma quebracho-blanco* Schltdl. (AsQb)	Ane	Int	Ben	2. Assunção et al. (2014)
Berberidaceae	*Berberis laurina* Billb. (BeLa) [R]	Zoo	Shi	Obl	3. Barberis et al. (2002)
Bignoniaceae	*Tabebuia impetiginosa* (Mart. ex DC) Standl. (TaRor) [R]	Ane	Int	Obl	4. Barchuk & Díaz (2005) 5. Chaneton et al. (2013)
Celastraceae	*Maytenus ilicifolia* Mart. ex Reissek (MaIlr) [R]	Zoo	Int, Sht	Obl	6. Etchebarne and Brazeiro (2016) 7. Fontoura et al. (2006)
Euphorbiaceae	*Sebastiania brasiliensis* Spreng. (SeBr)	Aut	Shi, Int	Obl	8. González & Cadenazzi (2015)
Flacourtaceae	*Xylosma tweediana* (Clos) Eichler (XyTw) [R]	Zoo	Shi	Obl	9. Madeira et al. (2009)
Leguminosae	*Erythrina crista-galli* L. (ErCrr) [R]	Ane	Shi	Nof	10. Mielke & Schaffer (2010) 11. Plaza Behr et al. (2016)
Leguminosae	*Geoffroea decorticans* (Gillies ex Hook. & Arn.) Burkart (GeDe)	Zoo	Shi, Int	Nof	12. da Silva Possete et al. (2015) 13. Redin et al. (2017)
Leguminosae	*Prosopis affinis* Spreng. (PrAf) [R]	Zoo	Shi	Ben	14. Risio et al. (2014)
Leguminosae	*Prosopis nigra* (Griseb.) Hieron. (PrNi)	Zoo	Shi	Nof	15. Streit et al. (2014)
Leguminosae	*Vachellia caven* (Molina) Seigler & Ebinger (VaCa) [R]	Zoo	Shi	Ben	16. Zalba & Villamil (2002)
Myrtaceae	*Blepharocalyx salicifolius* (Kunth) O.Berg (BlSa) [R]	Zoo	Int, Sht	Obl	
Myrtaceae	*Eugenia uniflora* L. (EuUn) [R]	Zoo	Shi, Int	Obl	
Myrtaceae	*Myrcianthes cisplatensis* (Cambess.) O.Berg (MyCi)	Zoo	Shi	Obl	
Myrtaceae	*Myrrhinium atropurpureum* Schott (MyAt) [R]	Zoo	Int, Shi, Sht	Obl	
Rhamnaceae	*Scutia buxifolia* Reissek (ScBu) [R]	Zoo	Shi, Int	Obl	
Salicaceae	*Populus alba* L. (PoAl) [R]	Ane	Shi	Nof	
Sapindaceae	*Allophylus edulis* (A.St.-Hil., A.Juss. & Cambess.) Hieron. ex Niederl. (AlEd) [R]	Zoo	Shi	Obl	
Thymelaeaceae	*Daphnopsis racemosa* Griseb. (DaRar) [R]	Zoo	Shi, Int, Sht	Obl	
Ulmaceae	*Celtis ehrenbergiana* (Klotzsch) Liebm. (CeTa) [R]	Zoo	Int	Obl	

compete efficiently for soil and water resources (Gómez-Aparicio, 2009).

Recruited tree species in our study were predominantly zoochorous and dispersed mainly by birds (Table 2, Figure 3d). Scattered trees in landscapes used by livestock are known to act as habitat islands, providing connectivity across open habitats and attracting frugivorous birds that use trees for perching, which results in a seed rain beneath nurse trees (Manning et al., 2006). Regenerating species were predominately facilitative obligates and facilitative beneficiaries, whereas non-facilitated species were significantly less frequent (Figure 3f, Table 2). Some species like *Schinus longifolia*, *Celtis ehrenbergiana*, and *Blepharocalyx salicifolius* showed a notably higher regeneration density. This is consistent with the fact that these species are intermediately shade-tolerant species, whereas light-demanding species like *Erythrina crista-galli* and *Geoffroea decorticans* were only recorded in open areas (Table 2). In general, studies have shown that the nurse effect is more beneficial for stress-intolerant than for stress-tolerant species (Gómez-Aparicio et al., 2008). Shade-tolerant species were also benefitted when livestock was excluded from a hillside forest in Uruguay (Etchebarne & Brazeiro, 2016). Life strategy traits had similar densities in the regenerating species. In fact,

park forest trees were able to promote the regeneration of species with three different life strategies, highlighting their important role within the ecosystem (Figure 3e, Table 2).

4.2 | Community composition but not diversity varies across park forests

Quantitative studies on park forests are scarce and limited to some local studies. We characterized here, for the first time, a large number of park forests across Uruguay. The park forests analyzed are similar in species diversity (Figure 4b, c) and the values are comparable with results in another study that evaluated other park forests in northwestern Uruguay (Pozo & Säumel, 2018), but higher than those recorded in the 'espinillares' in Brazil (Watzlawick et al., 2010; Redin et al., 2011). Tree communities have a distinct species composition (Figure 4a). In general, *Vachellia caven*, *Prosopis affinis* and *Prosopis nigra* were the most characteristic and abundant species, comprising 75% of the total abundance, as has been recorded for other park forests of Uruguay and Brazil (Redin et al., 2011; Pozo & Säumel, 2018). Species like *Aspidosperma quebracho-blanco*, *Geoffroea decorticans*
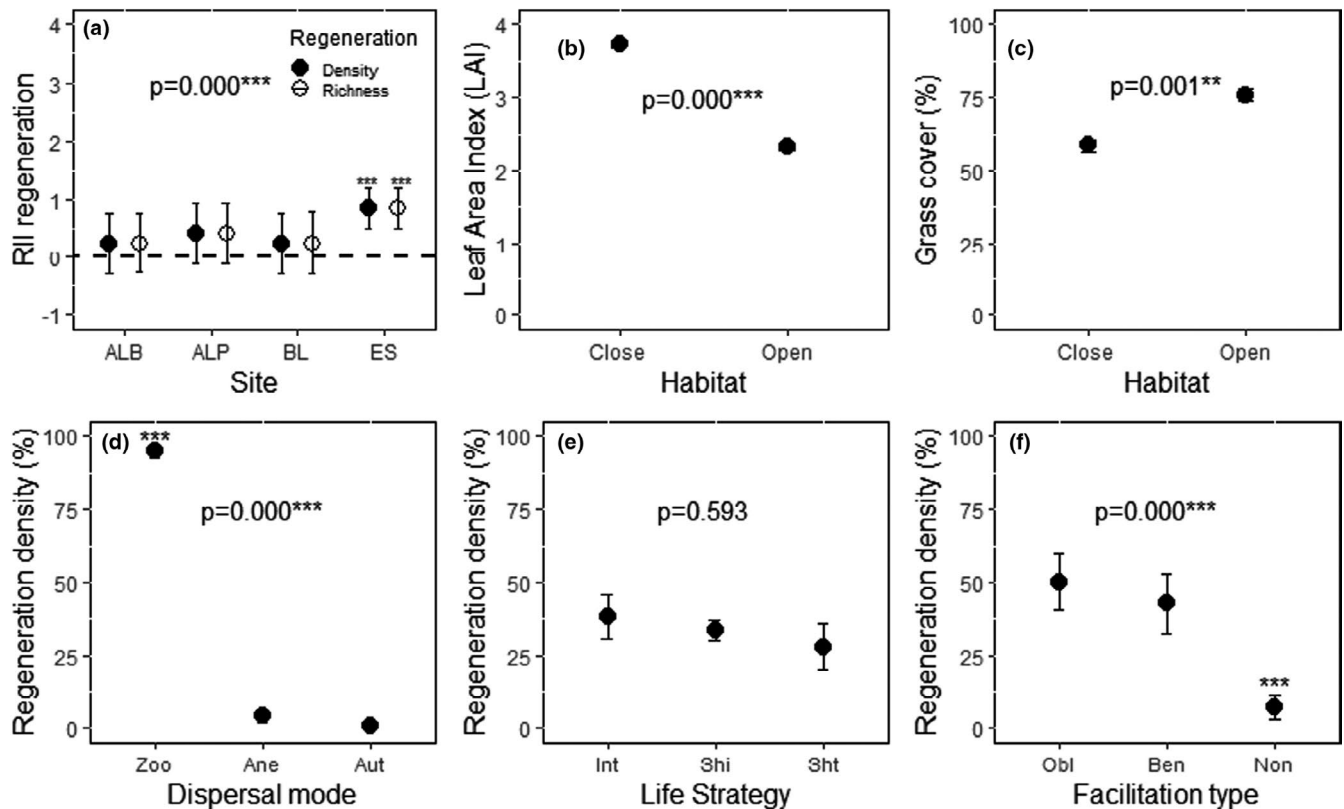
FIGURE 3 Variations of: (a) relative interaction index (RII) of trees on tree regeneration density and richness; (b) value of Leaf Area Index (LAI) between open and closed microhabitats; (c) grass cover between open and closed microhabitats; (d) regeneration density distributed across dispersal modes, (e) life strategy and (f) facilitation type. Abreviations: BL ('blanqueales', Rio Negro), ALB ('algarrobales', Artigas), ALP ('algarrobales', Paysandú), ES ('espinillares', Tacuarembo); Zoo (zoochorous), Ane (anemochorous), Aut (autochorous); Shi (light-demanding shade-intolerant), Int (intermediate shade-tolerant), Sht (shade-tolerant species); Obl (facilitation obligates), Ben (facilitation beneficiaries), Nof (species non-facilitated). Circles show aritmetic means, error bars represent standard errors. Values of *p* are given: ***, *p* < 0.001; **, *p* < 0.01; *, *p* < 0.05. For variable definition see section 2. *Materials and Methods*

and *Prosopis nigra* were more common in 'blanqueales' than in the other park forest types. This observation agrees with previous studies in Uruguay which highlight the presence of *Prosopis nigra* exclusively on halomorphic soils in 'blanqueales' (Fagúndez, 2015). The majority of native forest species found in our study have wide distributions in Uruguay and in South America (Brussa & Grela, 2007; González, 2013) and have been reported in other park forests of Uruguay (Costa & Delgado, 2001; Grela & Brussa, 2003). Affinity with the Chaco and Espinal flora was evident in the park forests from the presence of species like *Vachellia caven*, *Celtis ehrenbergiana*, *Prosopis affinis*, *Prosopis nigra*, *Schinus longifolia*, *Aspidosperma quebracho-blanco* and *Scutia buxifolia* (Haretche et al., 2012; Noy-Meir et al., 2012; Watzlawick et al., 2014; Cabido et al., 2018). We recorded the exotic species *Populus alba* regenerating in the 'algarrobales'. This species was originally introduced in Uruguay by silvicultural practices (Masciadri et al., 2010). Likewise, other studies recorded exotic species such as *Ligustrum lucidum*, *Gleditsia triacanthos*, and *Melia azedarach* invading park forests in Uruguay (Piaggio & Delfino, 2009; Traversa-Tejero & Alejano-Monge, 2013; Pozo & Säumel, 2018) and invading Espinal forests in Argentina (Lewis et al., 2009; Noy-Meir et al., 2012).

4.3 | Restoration of park forests

Our results have practical implications for the management of park forests: woody species such as *Prosopis affinis*, *Prosopis nigra* and *Vachellia caven* appeared as excellent candidates for use as nurses in the restoration of all system types and can be combined with temporal exclosures of grazing to foster regeneration and growth. Restoration approaches that promote revegetation and minimize cost and effort can be achieved using facilitation as a restoration tool, especially in developing countries that have few resources at their disposal and lack incentives to restore degraded forests (Gómez-Aparicio, 2009). In addition, our results suggest that preserving forest remnants will accelerate secondary succession in these areas (passive restoration) by acting as seed sources and providing a habitat for dispersers (Rey Benayas et al., 2008). As in the majority of dry forests worldwide (Miles et al., 2006; Hansen et al., 2013), park forests have been destroyed because of agricultural expansion, over-grazing and selective wood extraction for fuel or other products (especially *Prosopis* spp.). The same forest type in Argentina, the Espinal, has been almost completely destroyed due to agricultural intensification (Noy-Meir et al., 2012). In areas where
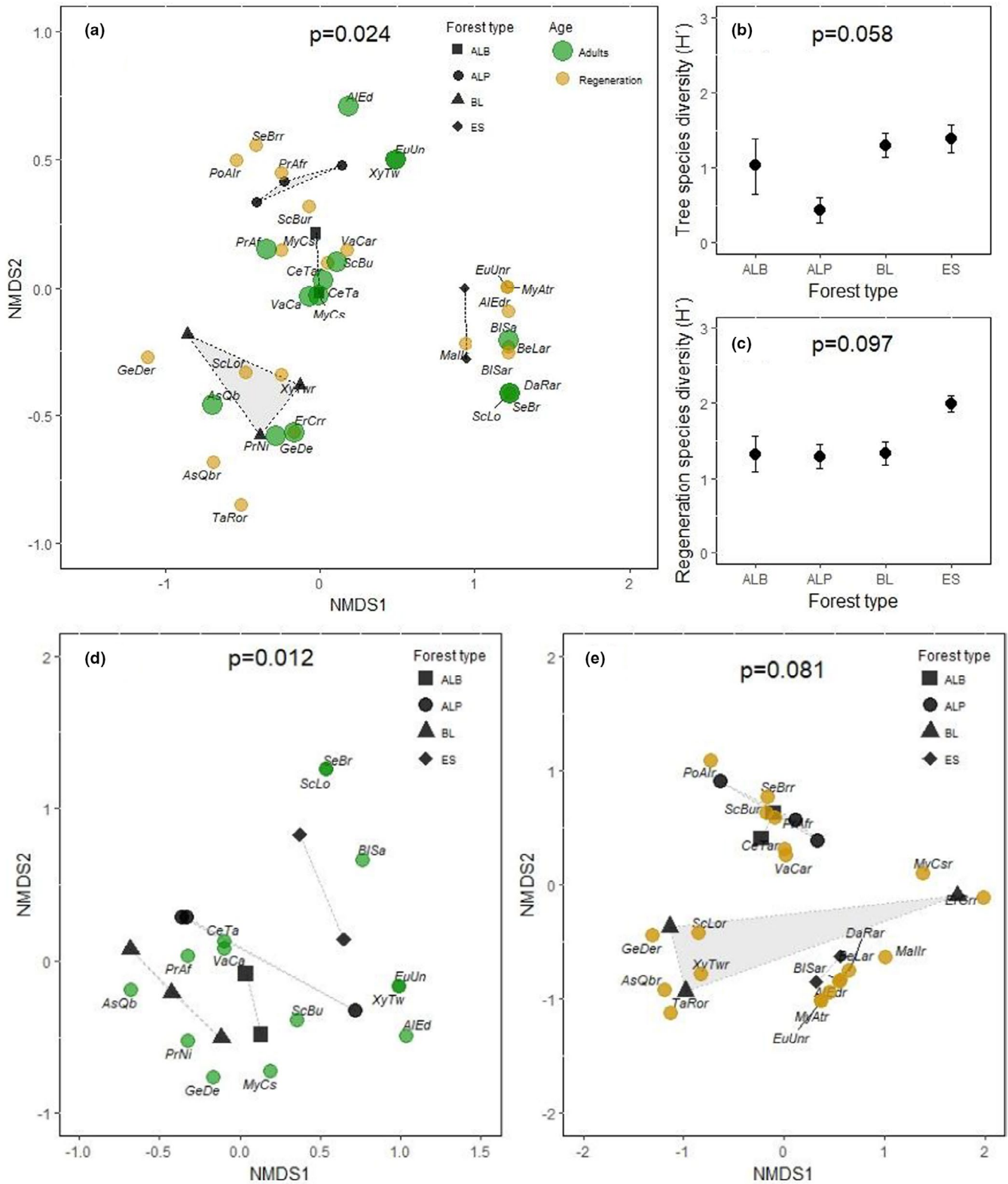
FIGURE 4 (a) Non-metric multidimensional scaling (NMDS) ordination of tree species from different park forests using the Bray–Curtis distance based on species abundance, showing distance between sites and tree species (adults and regeneration species). (b, c) Shannon diversity index (*H*) of tree species (b) and regeneration species (c); circles show aritmetic means, error bars represent standard errors. Abreviations: BL ('blanqueales', Rio Negro), ALB ('algarrobales', Artigas), ALP ('algarrobales', Paysandú), ES ('espinillares', Tacuarembo). (d) NMDS ordination showing distance between sites and adults. (e) NMDS ordination showing distance between sites and regeneration species. Species were abbreviated with the first four letters of the names and ending in r for regeneration; circles size correspond to the age category; *p* values are given

most dry forests have been converted into pasture a conservative approach has led to the creation of silvopastoral systems based on grazing and the maintenance of the native tree layer while preserving ecosystem functions (Rejžek et al., 2017). This can be a strategy to maintain or restore natural park forests especially using species like *Aspidosperma quebracho-blanco*, *Prosopis affinis*, *Prosopis nigra* and *Vachellia caven* that are already used in other natural silvopastoral systems (Root-Bernstein & Jaksic, 2013; Rejžek et al., 2017). We propose that floristically diverse park forests have to be protected for conservation and restored whenever possible, without necessarily preventing them from being used for traditional silvopastoralism. An integrated view of the forest–grassland mosaic has to be included in management practices, e.g. by assisting tree establishment and survival in grasslands (Erdős et al., 2018) to create silvopastoral systems.

5 | CONCLUSION

Our study supports the facilitation effect that nurse trees exert on tree regeneration under their canopy, in grazed park forests. Based on our results we suggest that the nurse mechanisms are explained by the provision of shade, the limitation of grass development and therefore the reduction of grass competition, and the attraction of zoochorous seed dispersers. Scattered trees exert parental care in highly modified agricultural and silvicultural park forests of Uruguay and therefore they act as important refugia promoting tree recovery with paramount importance in these ecosystems. Further studies are therefore needed on the outcome of tree–tree regeneration interactions in a scenario of increased magnitude and frequency of grazing. Experimental studies to assess other variables such as humidity, temperature, soil composition and risk of predation under nurse trees and in the open areas will contribute to the understanding of the underlying facilitation mechanism of nurse trees in park forests.

AUTHOR CONTRIBUTIONS
Conceptualization: Paola Pozo and Ina Säumel; implementation and adaptation of the study, Paola Pozo; methodology design and validation, Paola Pozo and Ina Säumel; data acquisition and analysis, Paola Pozo; draft writing, Paola Pozo; review and editing, Paola Pozo and Ina Säumel; visualization, Paola Pozo; supervision and funding acquisition, Ina Säumel.

ORCID
Paola Pozo Inofuentes https://orcid.org/0000-0002-6508-5020
Ina Säumel https://orcid.org/0000-0001-9099-8182

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SUPPORTING INFORMATION

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

Appendix S1. Composition of woody species mean tree density (AD) and mean regeneration density (RD) are given. Abreviations include: BL ('blanqueales', Rio Negro), ALB ('algarrobales', Artigas), ALP ('algarrobales', Paysandú), ES ('espinillares', Tacuarembo).

Appendix S2. Supplementary references for Table 2 on tree and regeneration species composition in park forests in Uruguay are given.