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Disentangling the roles of bracken fronds and litter on natural seedling recruitment in fire-disturbed tropical montane habitats

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ABSTRACT

Tropical montane forests are diverse ecosystems often affected by uncontrolled human-induced fires causing tree mortality and creating large deforested areas. After fires, *Pteridium* spp. ferns (bracken) often dominate, and forest regeneration in these areas is slow. In this study, we evaluated the effects of bracken fronds and litter, as well as the micro-environmental conditions created by the fern, on the density and species diversity of naturally recruiting seedlings. At eight sites, 120 experimental plots were established among forest and bracken-dominated areas with the following treatments: (a) fronds and litter intact (F+L+); (b) fronds intact and litter removed (F+L-); (c) fronds removed and litter intact (F-L+); and (d) fronds and litter removed (F-L-). After one year, all seedlings were registered, identified and classified according to their life-form (tree, shrub, herb, vine), dispersal vector (wind- or animal-dispersed) and successional status (early-, mid-, and late-successional). For all treatments we assessed 12 micro-environmental variables. We identified 3649 naturally-recruiting seedlings corresponding to 278 species from 70 families. We found positive effects of bracken fronds particularly on tree seedling recruitment: treatments with fronds had greater densities of both animal- and wind-dispersed tree seedlings, 1.8 and 1.4 fold higher, respectively, compared to treatments without fronds. Similarly, the density of early-, mid- and late-successional tree species was 1.3, 1.7 and 1.9 times higher in treatments with than without fronds. Furthermore, species diversity of early-, mid- and late-successional tree species was higher in the treatments with fronds. The environmental conditions generated by bracken presence, such as photosynthetically active radiation, soil temperature, live bracken biomass and litter depth, had positive effects on seedling density of all, animal-dispersed and early-successional tree species, and negative effects on seedling recruitment of other life-forms, notably from early successional stages. To promote forest regeneration in bracken-dominated areas, active restoration measures such as direct seed addition and transplants of nursery-raised seedlings of mid- and late-successional species should be considered. Since bracken can hinder the establishment of some life forms and species but favor others, it is recommended to include a trait-based approach to understand species responses to

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environmental factors and select species that are optimally adapted to bracken-dominated habitat conditions to promote forest regeneration.

1. Introduction

Tropical montane forests are exposed to a variety of threats that are primarily attributable to human activities (Gardner et al., 2009; Laurance et al., 2012). Agricultural expansion through slash-and burn and uncontrolled fires has led to extensive fire-disturbed areas (Gardner et al., 2009; Laurance et al., 2012). After fire, ferns of the genus *Pteridium* (hereafter referred as bracken) rapidly dominate the landscape for a long time (Carvalho et al., 2022; Hartig & Beck, 2003). Bracken is widespread worldwide (Marrs et al., 2000) and is generally difficult to control (Stewart et al., 2008).

In tropical fire-disturbed areas dominated by bracken, forest regeneration is slow (K. Hartig & Beck, 2003; Palomeque et al., 2017), and is related to the fern's resilience and success as a competitive species (Roos et al., 2010). Bracken's success is mainly attributed to its dense fronds and deep litter accumulation, which shades other species and prevents their establishment (Marrs et al., 2000), and to allelopathic effects that affect the growth and development of particular seedling species (Jatoba, 2023; Silva Matos & Belinato, 2010). This suggests establishment limitation (i.e. failure in seed germination, seedling survival and/or growth due to biotic or abiotic factors) (Muller-Landau et al., 2002; Münzbergová & Herben, 2005). Alternatively, slow forest regeneration in bracken-dominated areas may also be linked to dispersal limitation (i.e., a failure of seeds to reach a site, Gallegos et al., 2016), which may be related to the lack of natural perches and food sources for birds, the main seed dispersers in these areas (Saavedra et al., 2015).

To reduce establishment limitation, some experimental efforts in temperate and tropical climates have tried to reduce bracken's dominance and biomass by cutting and using herbicides (Milligan et al., 2016; Pakeman et al., 2002; Xavier et al., 2023).The most effective strategies for reducing bracken density in the tropics consisted of cutting bracken fronds every 2–4 weeks and planting fast-growing pioneer trees or shrubs by seed broadcasting, direct sowing or nursery-raised-seedling transplants (Douterlungne et al., 2010, 2013; Toledo-Aceves et al., 2022; Vleut et al., 2013). However, maintaining repeated cutting of fronds is costly (Aguilar-Dorantes et al., 2014; Xavier et al., 2023). Additionally, other factors such as the incorporation of mid- and late-successional animal-dispersed species should be considered to ensure the recovery of forest function (Levy-Tacher et al., 2015). Determining the most effective management strategy requires a better understanding of the ecology of bracken-dominated areas in tropical environments.

In bracken-dominated areas, factors such as light availability (Ssali et al., 2019) and soil properties (Lippok et al., 2013; Valdez-Ramírez et al., 2020) can influence forest succession (Guariguata & Ostertag, 2001). Plants can be classified as early-, mid- and late-successional species according to their abundance at each successional stage, which is determined by its physiological characteristics such as shade-tolerance (Bazzaz, 1979). The direction and speed of succession in secondary tropical forests depends mainly on the arrival and establishment of seeds (de la Peña-Domene & Martínez-Garza, 2018), because most species do not form a seed bank (Palma et al., 2021; Wijdeven & Kuzee, 2000). Given the unfavorable conditions in most deforested tropical areas, many forest species have limited ability to establish (de la Peña-Domene & Martínez-Garza, 2018; Martínez-Ramos et al., 2016) Martínez-Ramos et al., 2016). Surprisingly, Gallegos et al. (2016) found high seedling survival and growth of tree and non-tree species in bracken-dominated areas, and bracken fronds were found to increase seed germination, seedling growth and survival of late-successional tropical species (Gallegos et al., 2015, 2016; Ssali et al., 2019), suggesting little establishment limitation. Nevertheless, bracken litter can form a physical barrier reducing seed bank germination, preventing seeds from reaching the ground, and inhibiting natural recruitment in temperate zones (Ghorbani et al., 2006). However, the role of bracken fronds and litter have not been disentangled in tropical ecosystems, and their effects should be assessed to improve our understanding of forest regeneration processes in fire-disturbed tropical montane forests. Furthermore, analysis of environmental conditions could help to understand the specific effects of bracken fronds and litter on the seedling community.

We conducted an experimental study to gain a better understanding of the effects of traditional management strategies for bracken control on natural seedling recruitment and the specific micro-environmental conditions that allow seedling recruitment of different species in tropical bracken-dominated areas. We addressed the following questions: (i) What are the effects of bracken fronds and litter on density and species diversity of naturally recruiting seedlings? We expected higher seedling recruitment of mid- to late-successional species with bracken fronds and litter than early-successional species, due to their higher shade-tolerance (Gallegos et al., 2015; Ssali et al., 2019). Additionally, given the dispersal limitation and the lack of perches in bracken-dominated areas (Gallegos et al., 2016; Saavedra et al., 2015), we also expected recruitment of animal-dispersed species to be lower in bracken than in forest, but higher in treatments with fronds and litter than in their absence. (ii) How do the micro-environmental conditions generated by bracken affect density and species richness of naturally recruiting seedlings? We expected that the increasing shade and soil moisture generated by bracken will negatively affect the density and species diversity of early-successional seedlings, whereas mid- and late-successional species would benefit from these micro-environmental conditions (Gallegos et al., 2016; Ssali et al., 2019).

2. Materials and methods

2.1. Study area

The study was conducted in the vicinity of Chulumani, province Sud Yungas, La Paz, Bolivia (16°24'37" S, 67°31'37" W), in a tropical montane forest located on the eastern slope of the Andes, between 1900 and 2400 m asl. The mean annual temperature is 20.5°C and the mean annual precipitation is about 1390 mm (Molina-Carpio et al., 2019). The forests in this area have become highly fragmented as a direct consequence of uncontrolled and frequent anthropogenic fires (Killeen et al., 2005) and agricultural expansion of *Erythroxylum coca* for traditional use (Killeen et al., 2008). The landscape consists of two large remnants of continuous old forests, of approximately 1500 and 3000 ha, surrounded by vast areas dominated by bracken fern (*Pteridium esculentum* subsp. *arachnoideum* (Kaulf.) J. A. Thomson) (Schwartsburd et al., 2018), wind-dispersed shrubs of Asteraceae and Melastomataceae, and some bird-dispersed species of Ericaceae (Lippok et al., 2013). At the forest edges, the most common tree species are *Hedyosmum racemosum* (Chlorantaceae), *Clusia elongata* (Clusiaceae) and *Hieronyma fendleri* (Phyllantaceae); while species from the Rubiaceae, Piperaceae, Melastomataceae and Lauraceae families are abundant in the forest interior (see Lippok et al., 2014). Most woody species are dispersed by birds and bats (Lippok et al., 2014; 2013), although terrestrial mammals such as *Mazama americana* and *Dasyprocta variegata* can also disperse seeds (Gallegos et al., 2024).

2.2. Experimental design

At eight sites, each separated by at least 1 km, 50 ×50 m plots were established in bracken-dominated areas, at 100 m from the forest edge.

The bracken-dominated areas were last burned 5–15 years before the start of the experiment and since have been dominated by bracken and a few scattered shrubs. To assess the effect of bracken fronds and litter on natural seedling recruitment, each plot was divided in four subplots of 25 ×25 m, with the following treatments: (a) with fronds and with litter (F+L+); (b) with fronds, without litter (F+L-); (c) without fronds, with litter (F-L+) and (d) without fronds, without litter (F-L-) (Fig. 1). To maintain these treatments, fronds were cut carefully with a machete at ground level and litter was removed manually every four months, during one year. Within each of the four subplots, three 1 m^2 plots were randomly established to assess seedling density and species richness (Fig. 1). To provide a reference for seedling recruitment in the forest interior, we also established three 1 m^2 plots in the forest interior of each site. In order to have similar conditions at the beginning of the experiment, we removed seedlings and saplings from all the 1 m^2 plots.

2.2.1. *Seedling sampling*

One year after the establishment of the experiment, all seedlings above 2 cm of height were measured and recorded in each plot. Similar seedlings for each morphospecies per site were collected out of the plots and compared. Saplings and adults near our plots were also collected for reference. All vouchers were dried and taken to the Herbario Nacional de Bolivia (LPB) for identification. We also used a seedling reference collection of more than 100 species sown in the tree nursery of the Santiago de Chirca Biological Station deposited at the LPB. After seedling comparison and identification, all species were classified according to their life-form (tree, shrub, herb or vine), dispersal vector (wind- or animal-dispersed) and successional status (early-, mid- and late-successional), according to the abundance of each species in plots established at different successional stages in previous studies (Gallegos et al., 2016; Lippok et al., 2014; Lippok et al., 2013), and based on expert knowledge, personal observations, and information at the LPB (Table S1).

2.2.2. *Environmental factors*

We measured environmental factors once, during both the wet and dry seasons. We collected two soil samples in each subplot using a metal ring of 3.5 cm in diameter and 5 cm in height. The soil samples were stored in hermetic bags to obtain their wet weight and then dried to obtain the dry weight and calculate soil moisture (ISRIC 2002). Additional soil composite samples of each subplot were sent to the "Laboratorio de Calidad Ambiental" at the Universidad Mayor de San Andres (La Paz, Bolivia), for analyses of soil pH, exchangeable potassium, available phosphorus, soil organic matter, carbon and total nitrogen, following the ISRIC 4, ISRIC 9, ISRIC 14–3, ISRIC 5 and ISRIC 6 methods, respectively (ISRIC, 2002). The soil temperature was measured at three random points per subplot with a soil thermometer (ScienceFirst, Florida, USA). At five points per subplot we also measured the photosynthetically active radiation (PAR) with a PAR quantum sensor (Delta Ohm, Padova, Italy) connected to a photoradiometer (HD2102.2). For calibration, a reference data point was taken at 2 m height, pointing to a clearing (2 m-PAR). Subsequently, PAR data were taken at 20 cm from the ground (20 cm-PAR). To assess the relative PAR available for seedlings, we calculated DeltaPAR as (20 cm-PAR/2 m-PAR) x 100 (Gallegos et al., 2015). Litter depth was measured at the end of the study using a metal ruler from the ground to the top of the litter in at least three points of each 1 m^2 plot where litter was present. Since the above-ground biomass consisted mostly of living and dead bracken fronds, we established two additional 1 m^2 plots in each subplot where we collected all the above-ground bracken biomass, and then separated the living and dead fronds, which were dried and weighed separately.

2.3. *Data analysis*

To characterize the species diversity, we calculated the q1 Hill number, which represents the Shannon diversity, interpreted as the exponential of the Shannon index, and measures the effective number of common species, using the *iNEXT* package (Hsieh et al., 2016). We

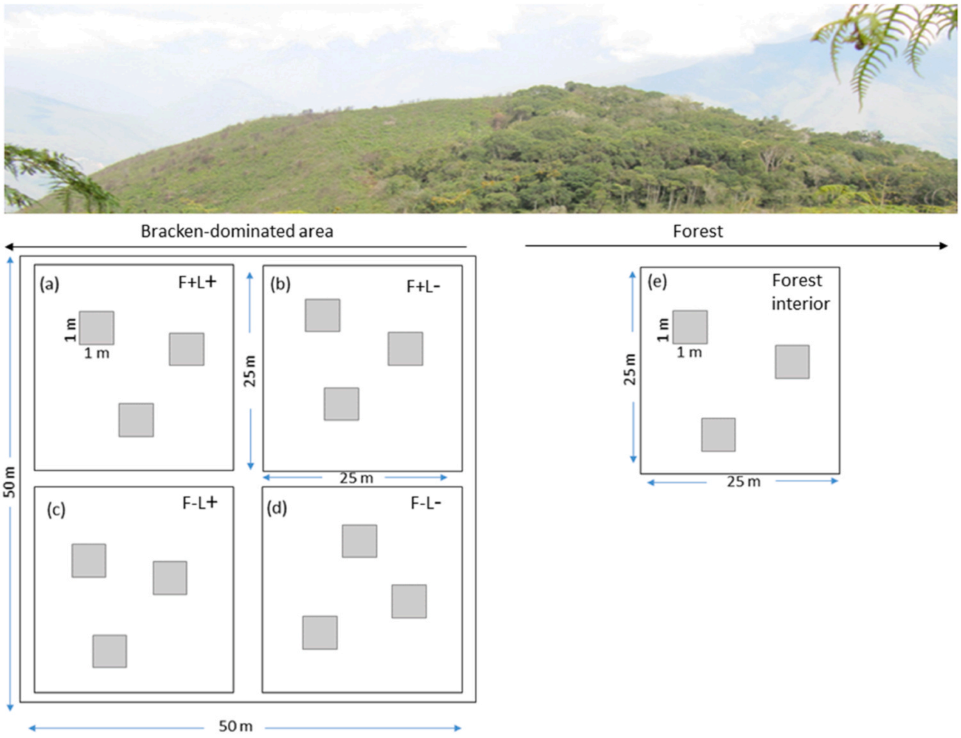

Fig. 1. Details of the experimental design. Left: Arrangement of experimental subplots for treatments (25 ×25 m) and plots for natural recruitment (1 ×1 m) in the bracken-dominated areas: were (F+) represent bracken fronds presence, (F-) bracken fronds removal, (L+) bracken litter presence, and (L-) bracken litter removal. Right: plots for natural recruitment (1 ×1 m) in the forest interior.

assessed the effect of bracken fronds and litter on seedling density and species diversity among treatments using generalized linear mixed-effects models (GLMM). We calculated the mean density and species diversity of the three 1 m^2 plots in each subplot, and included seedling density and species diversity of the following life-forms as response variables in separate models: total, animal-, wind-dispersed, and early-, mid-, and late-successional trees, shrubs, herbs and vines (vines and lianas were pooled). In all models, we included treatment (F+L+, F+L-, F-L+, F-L-) as the fixed effect, and site as the random effect. Post hoc comparisons among treatments were performed in the emmeans package. All models were performed with the *glmmTMB* package (Brooks et al., 2017) and assumed a negative binomial distribution for density a Gaussian distribution for diversity. Each model was validated analyzing residuals in the *DHARMa* package (Hartig, 2022). Given our interest in evaluating the effect of bracken fronds and litter, seedlings recruiting in the forest interior were not included in the models, and were only used as a reference in figures. To assess the relationship of environmental variables with density and species diversity of naturally recruiting seedlings, we performed a Principal Component Analysis (PCA) on 12 environmental variables: soil pH, potassium, phosphorus, nitrogen, carbon, organic matter, soil temperature, soil moisture, litter depth, dead- and live-bracken biomass and photosynthetically active radiation,

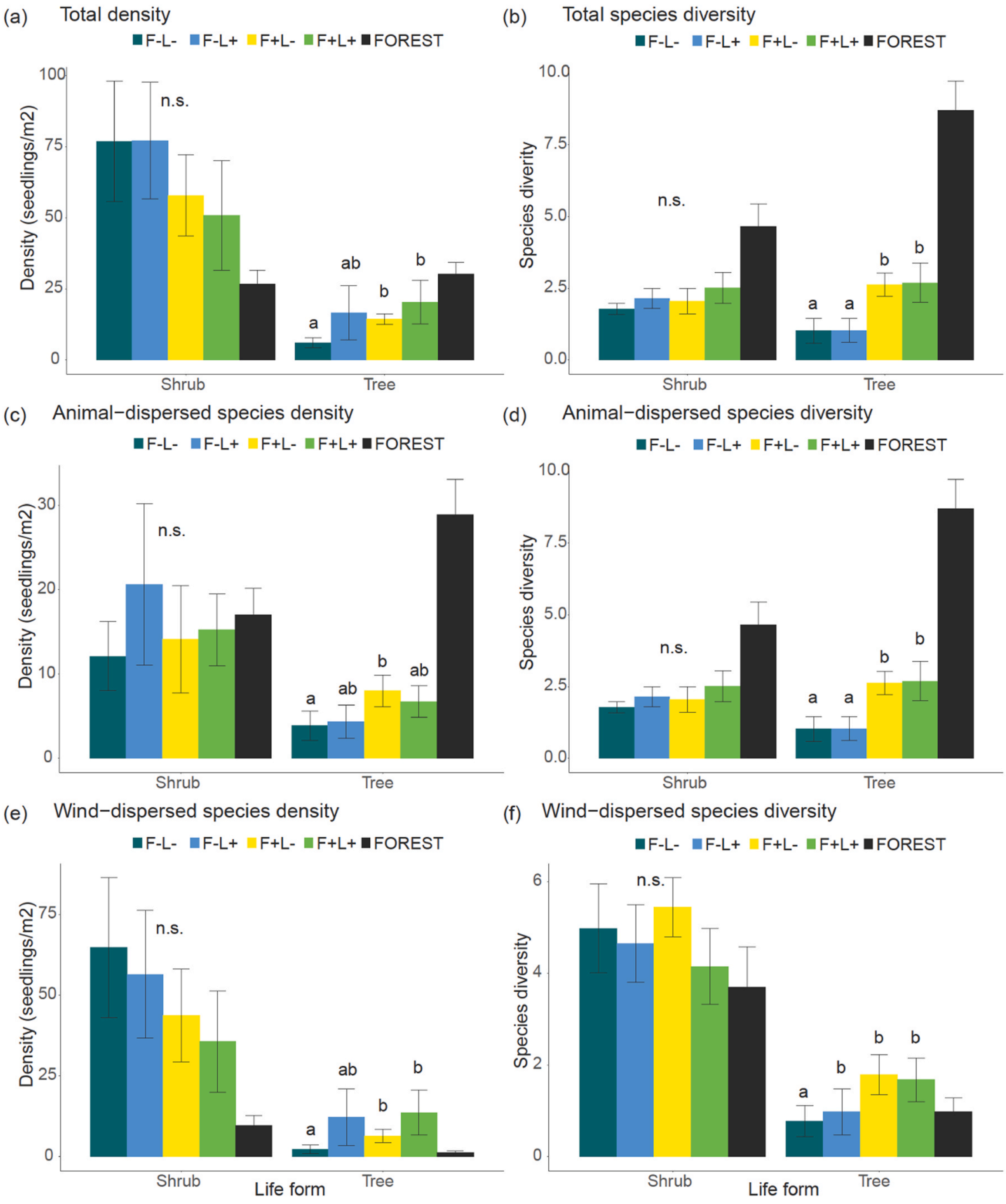

Fig. 2. Density (left panels) and species diversity (Hill number q1, right panels) of: (a-b) total, (c-d) animal-dispersed, and (e-f) wind-dispersed naturally recruiting seedlings under different bracken treatments: with fronds (F+), without fronds (F-, after bracken fronds' removal), with bracken litter (L+), without bracken litter (L-, after bracken litter removal), in comparison to forest (FOR), according to their life-form. Different letters denote significant differences among treatments ($p < 0.05$), n.s. indicates no significant differences ($p>0.05$). NA denotes no feasible comparison. Shown are means ± SE.

using the princomp function in the *stats* package. Prior to the ordination, all variables were scaled. We identified the environmental variables that contributed most to the variance in each axis. Finally, we use the first two axes to conduct linear regressions. All statistical analyses were performed in R 4.2.1 (R Core Team, 2022).

3. Results

3.1. Seedling recruitment

In the 120 plots established in the forests and bracken-dominated areas, we found a total of 3649 naturally recruited seedlings from 278 morphospecies and 70 families. Most morphospecies (75.55 %) were identified at the species level, 16.9 % at the genus level, 7.55 % at the family level, and 3.6 % were not identified and were discarded from all analyses. A comparison of the number of seedlings registered in forests and bracken-dominated areas, according to their life-form, successional status and dispersal vector is shown in Table S2.

The most common tree species that recruited naturally in the forest were *Nectandra cuspidata*, *N. acutifolia* (Lauraceae) and *Clusia elongata* (Clusiaceae), and in the bracken-dominated areas were *Clethra scabra* (Clethraceae), *Myrsine coriacea* (Primulaceae) and *Weinmannia sorbifolia*

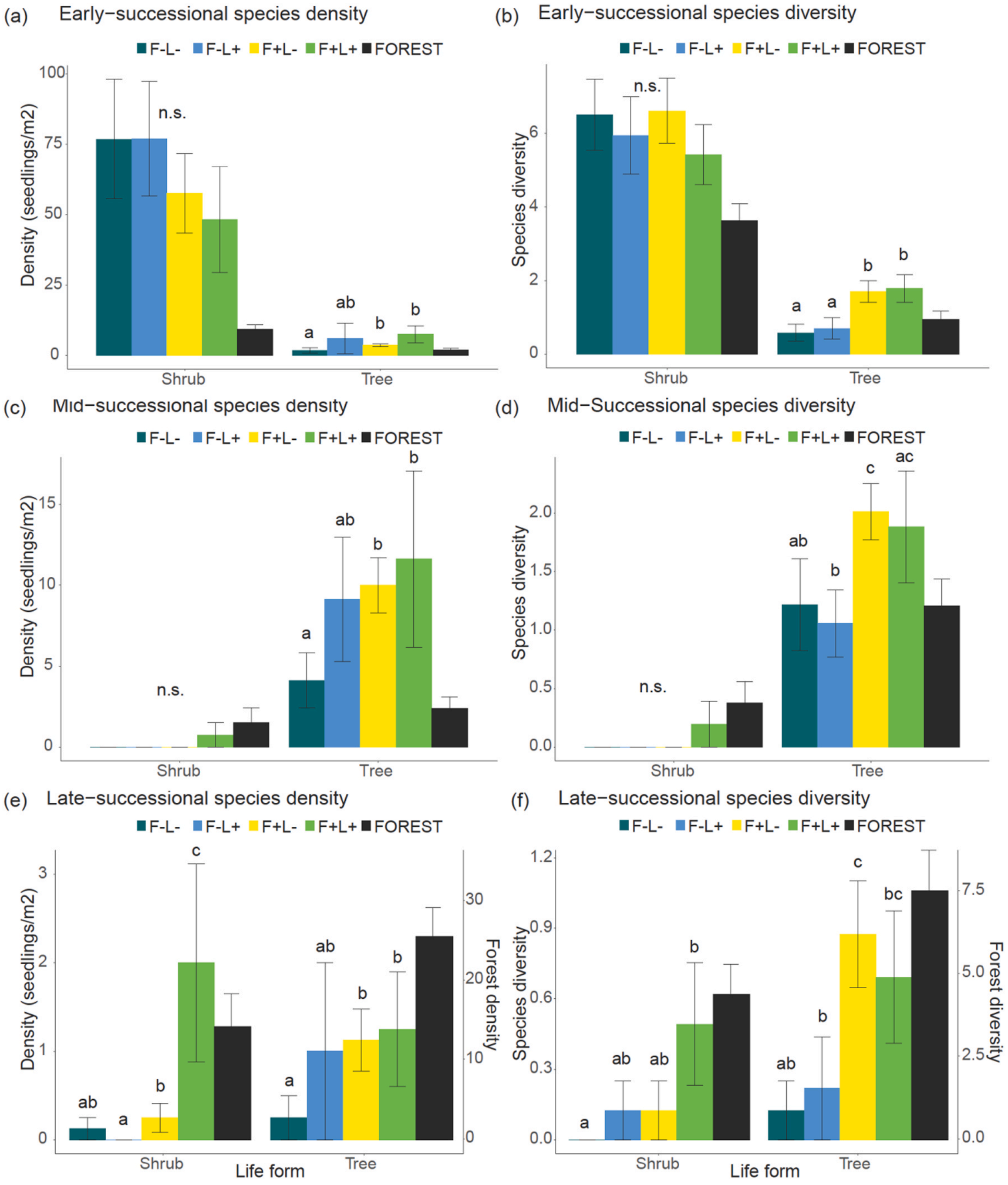

Fig. 3. Density (left panels) and species diversity (Hill number q1, right panels, right panels) of: early- (a-b), mid-(c-d), and late-successional (e-f) naturally recruiting seedlings under different bracken treatments: with fronds (F+), without fronds (F-, after bracken fronds' removal), with bracken litter (L+), without bracken litter (L-, after bracken litter removal), in comparison to forest (FOR), according to their life-form. Different letters denote significant differences among treatments ($p < 0.05$), n.s. indicates no significant differences ($p>0.05$). NA denotes no feasible comparison. Shown are means ± SE.

(Cunoniaceae) (Table S1).

3.2. Effects of fronds and litter removal on natural seedling recruitment

The total density of tree seedlings were 3.3 times higher in the treatment with fronds and litter (F+L+) than without fronds and without litter (F-L-). The same pattern was detected for their species diversity (Fig. 2a-b). Similarly, animal- and wind-dispersed tree species diversity were significantly higher in treatments with than without fronds (Fig. 2d,f). Seedling density and species diversity of early-, mid- and late-successional tree species in the treatment with fronds and litter (F+L+) were 4.3, 2.8 and 5 times higher, respectively, than in the treatment without fronds nor litter (F-L-) (Fig. 3). The same pattern was observed for their diversity, and for density and species diversity of late-successional shrubs (Fig. 3). We did not find any other significant difference among treatments for shrubs (Figs. 2 and 3). Seedling density and diversity of herbs was 1.95 times higher in the treatment without fronds and without litter (F-L-) than the treatment with fronds and litter (F+L+) for wind-dispersed species (Fig S1e-f). Seedling density of animal-dispersed and early-successional herbs were 1.6 and 2 times higher, respectively, in the treatment with fronds and without litter (F+L-) than in the treatment with fronds and litter (F+L+), the same pattern was observed for their diversity (Fig. S1a-d, S2a-b). Vines were not different among bracken treatments (Fig. S1, S2).

3.3. Effects of micro-environmental conditions created by bracken on natural seedling recruitment

The first two axes of the PCA explained 60.5 % of the variation of environmental variables among 96 plots (Fig. S3). The PCA axis 1 was positively related to photosynthetically active radiation (PAR) (0.41 of correlation with the axis) and soil temperature (0.40), both variables explained 16.6 % and 16.20 % of the variance in this axis, respectively. PCA axis 1 was negatively related to live bracken biomass (-0.41) and litter depth (-0.41), these variables explained 17.5 % and 16.9 % of the variance of this axis, respectively. The PCA axis 2 was positively related to dead bracken biomass (0.57) and litter depth (0.42), and these variables explained 32.7 % and 17.7 % of the variance of this axis. PCA axis 2 was negatively related to soil moisture (-0.44) and carbon (-0.34) and these variables explained 19.6 % and 12.03 % of the variance of this axis. The correlations of each environmental variable with each axes and the percentage explained by each variable can be found in Table S3.

Regarding naturally recruiting tree seedlings, the first axis was significantly and negatively correlated with the total species diversity, animal-dispersed species diversity and early-successional species diversity (Fig. 4a-c). For shrub species, the first axis was significantly and negatively correlated with the density of late-successional species (Fig. 4d). The other categories of shrubs and trees were not significantly correlated with any PCA axes.

For herbs, the first axis was not correlated with any category. The second axis was negatively correlated with the density and species diversity of all naturally recruiting herbs, wind-dispersed and early-successional species of herbs (Fig. S4). Regarding vines, nor of the two PCA axes were correlated to any category.

4. Discussion

Our results show positive effects of bracken fronds and litter on the seedling density and species diversity in all categories of naturally recruited tree seedlings. Removal of bracken fronds and litter had negative effects on density and species diversity of tree seedlings, and contrastingly positive effects on the density and diversity of wind-dispersed herb species. The positive effect of bracken on tree species was related to environmental conditions created by the bracken.

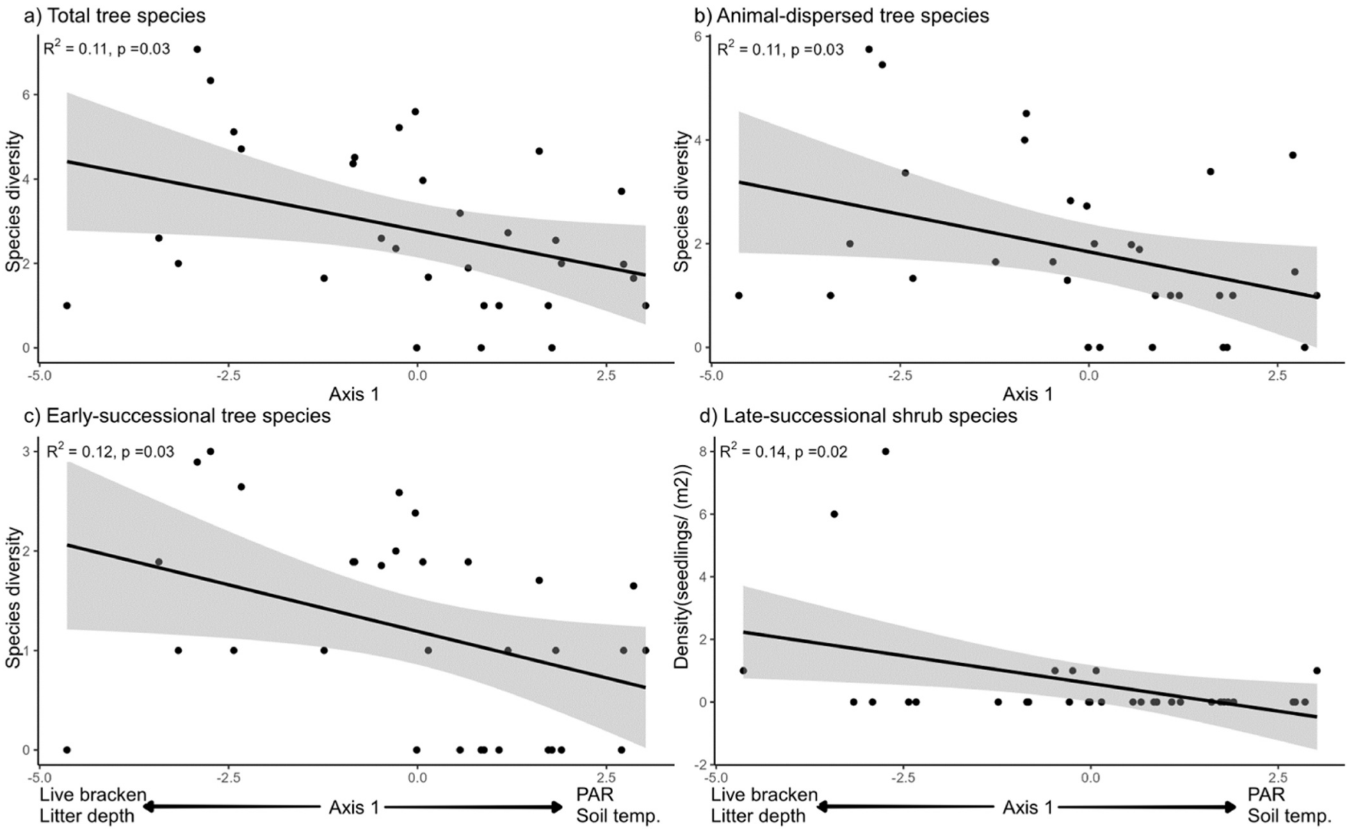

Fig. 4. Significant regressions of (a) total tree species diversity, (b) animal-dispersed tree species diversity, (c) early-successional tree species diversity, and (d) late-successional shrub species density, as a function of PCA scores of environmental variables.

Bracken fronds' and litter shading was positively related to the species diversity of all, animal-dispersed and early-successional tree seedlings and late-successional shrubs. In contrast, the density and species richness of all, wind-dispersed and early-successional herbs were negatively affected by environmental conditions generated by bracken, such as litter depth and dead bracken biomass. Given the favorable micro-environmental conditions created by bracken for animal-dispersed as well as for mid- and late-successional tree species, the inclusion of trees from these categories in active restoration strategies would be promising to promote forest regeneration.

4.1. *Effects of fronds and litter on seedling recruitment*

Although several studies suggest that bracken fronds could shade and inhibit establishment and recruitment of other species (Humphrey & Swaine, 1997; Marrs et al., 2000; Paz et al., 2022), and that litter acts as a physical barrier that prevents the arrival of seeds to the ground inhibiting natural recruitment (Ghorbani et al., 2006; Pakeman & Hay, 1996), we found that seedling density and species diversity of naturally recruiting early-, mid- and late-successional tree species were higher under bracken fronds and litter than after their removal. These results are consistent with previous studies in the Neotropics (Gallegos et al., 2016, 2015) and in the Afrotropics (Ssali et al., 2019), suggesting that bracken is a potential facilitator for shade-tolerant and late-successional tree species. Thus, in contrast to other studies that found bracken to have a negative effect on seedling establishment (Carvalho et al., 2022; Paz et al., 2022), our experimental results show that bracken creates the environmental conditions necessary for the establishment of shade-tolerant and late-successional seedlings, and reduces harsh conditions of open areas.

With respect to bracken litter, previous studies have reported that litter accumulation acts as a barrier and prevents seed germination of herbs, grasses and shrubs in temperate zones (Amouzgar et al., 2020; Ghorbani et al., 2006). Our results are consistent with this pattern for herbs showing that seedling density and diversity of early-successional and wind-dispersed species of herbs decrease with increasing litter depth and dead bracken biomass. However, we did not find an effect of these variables on tree species diversity or density. Given that bracken litter biomass almost doubles in volume within one year (Rivas-Alonso et al., 2021), our results may be related to the fact that litter accumulation modifies environmental conditions, such as shading, moisture retention and temperature maintenance, which could either improve or hinder seedling establishment depending on their specific requirements (Jessen et al., 2023; Ssali et al., 2019).

Our results support that bracken acts as an ecological filter mainly mediated by shading, as previously suggested by Ssali et al. (2019). The low seedling recruitment of early-successional species in bracken-dominated areas could be related to their light requirements, life-form and dispersal syndrome. Early-successional species in general require high light conditions for germination and growth (Everham et al., 1996), but depending on their life-form, non-tree species may have lower establishment probabilities (Garcia et al., 2015, 2016). Although some species of Melastomataceae and Asteraceae can persist on the soil seed bank in bracken-dominated areas (Xavier et al., 2016), previous studies found that the species richness and density in the soil seed bank is low (Lippok et al., 2013; Ssali et al., 2018), and that seedling density and species richness is not associated with the seed bank but is associated to the seed rain (Gallegos et al. 2016, Ssali et al. 2018). Early-successional species tend to have smaller seeds than mid- or late-successional species (De La Peña-Domene et al., 2016; Rivas-Alonso et al., 2021), and their germination rates are higher only under high-light conditions (Pearson et al., 2002). Moreover, smaller seeds exhibit reduced competition during establishment and lower seedling vigour than larger seeds, which generally have greater resources to support seedling development (Murali, 1997; Westoby et al., 1996).

Although wind-dispersed seeds are able to move long distances in open areas, animal-dispersed seeds reach open areas only when their dispersal agents are present (Pearson et al., 2002). For bracken-dominated areas, Saavedra et al., 2015 reported severe seed limitation, mainly due to the lack of perching structures for birds, resulting in poor arrival of animal-dispersed seeds, especially for large-seeded and late-successional species. Most animal-dispersed seeds from the forest interior do not arrive in open areas until their dispersal agents find perches, shelter or food (Estrada & Coates-Estrada, 2005). Contrary to our expectations, early-successional trees, also benefited from bracken fronds and litter presence. In our study, *Miconia* (Melastomataceae) species were frequent in bracken-dominated areas. We found the highest abundance of *M. hygrophila* and *M. theazans*, both classified as early-successional species, in the treatment with bracken fronds and litter. *Miconia* species are considered keystone plant resources for frugivorous birds and are the most species-rich zoochorous genus with long fruiting periods (Blendinger et al., 2011; Maruyama et al., 2013). Mid- and late-successional tree species, such as *Nectandra cuspidata*, *Rhamnus shaerosperma*, *Symplocos arechea*, and species from *Clusia,* like *C. trochiformis*, *C. lechleri* and *C. elongata,* all of them dispersed by birds, were also present in treatments with fronds and with litter (F+L+). Therefore, including *Miconia* and other animal-dispersed species in restoration strategies could foster the arrival of seed-dispersing birds to the bracken-dominated area.

This strategy could help to reduce the differences in species composition of seed-dispersing birds and bats between the forest and bracken-dominated areas, pointed as one of the main causes of dispersal limitation (Gallegos et al., 2024).

4.2. *Effects of micro-environmental conditions on seedling recruitment*

Micro-environmental conditions determine the success of seed germination and seedling establishment (Herzog et al., 2002; Martínez-Garza et al., 2016). We did not find differences in soil nutrients among treatments. This could be related to the short duration of the experiment, which may not have been sufficient to produce differences in nutrients among treatments and to show differences in seedling density and species richness in relation to soil properties.

Our treatments with bracken fronds and litter reduced soil temperature, maintained soil moisture and likely reduced tree seedling mortality. Contrarily, the treatments without fronds and without litter had low tree seedling density and species diversity, probably due to the low humidity and higher temperatures in open areas causing seedling mortality due to desiccation (Alvarez-Aquino et al., 2004; Khurana and Singh, 2001).

Plant species vary in their light requirements to germinate, establish, and grow (Montgomery & Chazdon, 2002; Yu et al., 2008). In our study, lower levels of photosynthetically active radiation were associated with higher tree density and species diversity, suggesting that tree species tolerate shade under a bracken canopy and their recruitment could be improved by bracken fronds. Although few of the seedlings recorded in the bracken-dominated areas corresponded to late-successional species, we found evidence that bracken allows their recruitment and their low density is likely related to dispersal limitation (Gallegos et al., 2016). Most of the tree species surveyed in bracken fronds and litter presence were dispersed by animals, indicating their potential to become established, and to promote forest regeneration by providing food sources and perching structures for birds.

5. Implications for management

The succession of montane forests in bracken-dominated areas is frequently disrupted and remains arrested (Christmann et al., 2023). Our results highlight the importance of the micro-environmental conditions generated by bracken for natural recruitment of tree species, in particular for animal-dispersed tree species. Therefore, to promote forest regeneration in bracken-dominated areas, active ecological restoration strategies such as direct seed addition, and transplants of nursery-raised seedlings of mid- and late-successional animal-dispersed shrub and tree species should be considered. Since light availability reduces under long-term bracken-dominance, some strategies to reduce bracken density to ensure tree establishment should be evaluated. If seedlings are transplanted from the nursery and the bracken fronds are not cut, a significant amount of combustible material remains, posing a fire risk. Therefore, seedlings should be transplanted soon after a fire to promote forest regeneration from the beginning and to take advantage of the amelioration in environmental conditions provided by bracken fronds shortly after the fire. These strategies must be accompanied by a socialization of fire management in local communities, as they are key to restoration programs. Furthermore, our results highlight that dispersal limitation could be the main factor hindering forest regeneration, so the inclusion of attractants for seed dispersers should be evaluated.

CRediT authorship contribution statement

Alfredo F. Fuentes: Writing – review & editing, Data curation. **Cesar Mayta:** Writing – review & editing, Methodology, Investigation, Data curation. **Cecilia L. López:** Writing – original draft, Software, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Isabell Hensen:** Writing – review & editing, Validation, Supervision, Funding acquisition. **Victor Vasquez:** Writing – review & editing, Data curation. **Emili Jimenez:** Writing – review & editing, Investigation, Data curation. **Mariana Villegas:** Writing – review & editing, Investigation. **Silvia C. Gallegos:** Writing – review & editing, Validation, Supervision, Project administration, Investigation, Funding acquisition, Data curation, Conceptualization.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.foreco.2024.122056.

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