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The use of bird perches and artificial bat roosts to overcome dispersal and establishment limitation in bracken-dominated deforested areas

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ABSTRACT

The failure of seeds to arrive at suitable sites (dispersal limitation) and/or unsuitable conditions for germination, seedling survival and growth (establishment limitation) can impede the regeneration of tropical forests. We installed bird perches and artificial bat roosts in deforested areas dominated by the bracken fern *Pteridium* in the tropical montane forest of Bolivia to evaluate their effect on dispersal and establishment limitations. We also analyzed the relationship between seed size and life-history strategies of plants subject to both limitations. We found that perches reduced dispersal and establishment limitation of all seed sizes (small and large) and life-history strategies (pioneer and non-pioneer). In contrast, bat roosts did not reduce dispersal and establishment limitation in any of the categories. Our results reinforce the observation that dispersal limitation is one of the main filters that plant species must overcome in bracken-dominated deforested areas. The installation of bird perches as well as direct sowing of animal-dispersed seeds and planting of seedlings are strategies that could effectively support the regeneration of these widely distributed deforested areas.

1. Introduction

Seed dispersal and seedling establishment are key processes in the population dynamics of forests (Howe and Miriti, 2000). The failure of seeds to arrive at suitable sites (i.e., dispersal limitation), and unsuitable conditions for germination, seedling survival and growth (i.e., establishment limitation) have consequences in the structure and succession of plant communities (Muller-Landau et al., 2002). The deforestation of tropical forests by human activities can reduce seed dispersal and create unfavorable conditions for seedling growth (Markl et al., 2012; Martínez-Ramos et al., 2016). Therefore, it is important to understand the filters that plant species encounter during forest regeneration in human-modified landscapes.

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Around 90 % of tropical woody plant species produce fruits dispersed by animals, especially by birds and mammals (Howe and Smallwood, 1982). Deforestation and fragmentation of tropical forests leads to differences in the species composition of frugivorous birds between forests and open deforested areas (Maya-Elizarrarás and Schondube, 2015). These differences may reduce the arrival of forest species' seeds in open areas, hindering forest recovery (Gallegos et al., 2024). For frugivorous bats, forest loss can reduce both functional and species richness, which in turn affect ecological processes such as seed dispersal (García-Morales et al., 2016). Due to the importance of seed dispersal by animals, some restoration techniques aim to increase the arrival of animal-dispersed seeds in deforested areas, e.g. through bird perches (Alencar and Guilherme, 2020; Holl, 1998) and artificial bat roosts (Kelm et al., 2008). However, these techniques should not only enhance seed rain, but also should promote seedling establishment to ensure restoration success (Reid and Holl, 2013).

The establishment of seedlings depends on biotic and abiotic factors (Comita et al., 2009). Deforestation alters both factors, that could affect forest regeneration (Martínez-Ramos et al., 2016). For example, the presence of ferns of the genus *Pteridium* (hereafter referred to as bracken) that dominate several deforested areas after fire or land abandonment, leads to high humidity, low temperature, and low light conditions under their fronds and litter (Gallegos et al., 2015; Ssali et al., 2019). These environmental conditions in bracken-dominated areas could be favorable for certain non-pioneer, shade-tolerant plant species (Gallegos et al., 2015; López et al., 2024; Ssali et al., 2019) that are usually dispersed by animals. However, there is evidence of dispersal limitation, especially for animal-dispersed seeds in bracken-dominated areas (Saavedra et al., 2015), which could be one of the main reasons for the slow forest regeneration in these environments.

Depending on the environment, traits such as seed size can influence the establishment of seedlings (Dalling and Hubbell, 2002; Moles and Westoby, 2004). In bracken-dominated areas, large-seeded, shade-tolerant species are favored in their establishment (Gallegos et al., 2015; Ssali et al., 2019). Small-seeded species have lower germination, survival and seedling growth than large-seeded species in these deforested areas (López et al., 2024; Ssali et al., 2019). Although there is information on the effects of bird perches and artificial bat roosts on seed rain, little is known about their impact on dispersal and establishment limitation. Additionally, the relationship between these limitations, seed size, and life-history strategies in bracken-dominated areas remains poorly understood.

The aim of this study is to analyze the effects of bird perches and artificial bat roosts on the dispersal and establishment limitations of animal-dispersed plant species in bracken-dominated areas. Furthermore, it will be evaluated which seed size (small and large) and which life-history strategy (pioneer and non-pioneer) is favored by the presence of the animal attractants, especially with regard to the reduction of dispersal and establishment limitation. To this end, we used data from seed rain and seedling counts to calculate the dispersal and establishment limitations of 37 plant species and addressed the following questions: 1) What influence do bird perches and artificial bat roosts have on the extent of dispersal and establishment limitation in bracken-dominated areas? We expected both techniques to reduce these limitations, as bird perches and artificial bat roosts increase seed dispersal and seedling establishment of animal-dispersed plants (Abreu et al., 2020; Mayta et al., 2024). 2) How do bird perches and artificial bat roosts affect dispersal and establishment limitation of non-pioneer and pioneer species? In bracken-dominated areas, seeds of non-pioneer species are scarce (Saavedra et al., 2015); therefore, we expected dispersal limitation for non-pioneer species to be higher than for pioneer species. However, the presence of bird perches would reduce the limitation of non-pioneer plants (de Almeida et al., 2016; Pausas et al., 2006). In contrast, we did not expect artificial bat roosts to reduce dispersal limitation of non-pioneer species, as bats primarily disperse pioneer seeds (De La Peña-Domene et al., 2014; Muscarella and Fleming, 2007). In terms of establishment limitation, we expected the establishment of non-pioneer species to be less limited, because the establishment of shade-tolerant non-pioneer species is favored by the presence of bracken (Gallegos et al., 2015; López et al., 2024; Ssali et al., 2019). 3) How do bird perches and artificial bat roosts affect dispersal and establishment limitation of small and large-seeded species? For dispersal limitation, we predicted that small seeds would be less limited than large seeds, even with the presence of bird perches and artificial bat roosts, because large seeds are usually dispersed by large birds that are rare in deforested areas (Sodhi and Smith, 2007), and bats mainly disperse small seeds (Muscarella and Fleming, 2007). In terms of establishment limitation, we expected large-seeded species to be less limited in bird perches and artificial bat roosts, as large seeds are favored when establishing in bracken-dominated areas (Gallegos et al., 2015; Ssali et al., 2019).

2. Material and methods

2.1. Study area

We conducted the study in the tropical montane region of Bolivia, in the Sud Yungas province near the town of Chulumani, La Paz (16°24'37''S, 67°31'37''W) between 1900 and 2350 m a.s.l. The mean annual temperature is 20.4 ± 1.3°C, and the mean annual precipitation is 1341.3 ± 182.1 mm (SENAMHI, 2024). The montane humid forests in the area are highly fragmented by agricultural expansion of coca (*Erythroxylum coca*) and human-induced fires (Beck et al., 2024). The remnant forests are restricted to the top of the mountains and surrounded by deforested areas dominated mostly by bracken fern (*Pteridium esculentum* subsp. *arachnoideum*) and shrubs of Asteraceae and Melastomataceae (Lippok, Beck, et al., 2013).

2.2. Experimental design

To test the effect of bird perches and artificial bat roosts in dispersal and establishment limitations, we established eight study sites separated by at least 1 km (Fig. S1). In each site we installed four treatments: Forest, Bracken, Perch and Roost. For the perch treatment, three perches of approximately 5 m were installed, consisting of large stakes with branches of *Erythrina falcata* and *Ficus* spp. Both genera are capable of resprouting and serve as remnant trees in open areas (Zahawi, 2008). Moreover, this type of perch is visited

more frequently than other types, such as crossbar perches (Holl, 1998). The three perches were placed 50 m from the forest edge in bracken-dominated areas, with a distance of 10 m between them (Fig. S2). For the roost treatment, we installed an artificial bat roost (hereafter roost) 50 m from the forest edge in the bracken-dominated area. We designed the roosts following Kelm et al. (2008) with some modifications that can be found in Mayta et al. (2024). At each site, two treatments were used as controls, one in the bracken-dominated area and one at the forest (hereafter bracken and forest). Both treatments without perch or roost were located at a distance of 50 m from the forest margin (Fig. S2).

2.3. Seed rain and seedling establishment

Since birds defecate seeds while perched (Ferguson and Drake, 1999), we placed two seed traps under each perch and four seed traps at a distance of 4 m from each perch. We doubled the number of seed traps with increasing distance to maintain a constant sampling effort and to detect clumping, following a point-source design using concentric annuli (Bullock et al., 2006). On the other hand, bats defecate seeds in flight (Muscarella and Fleming, 2007). Therefore, we placed two seed traps near the roost entrance, four seed traps 4 m away from the roost and eight seed traps 8 m away from the roost. We installed more seed traps around the roosts to cover a larger area and capture more seeds. The controls in bracken and forest had similar arrangements of seed traps as the roost (Fig. S2). Each seed trap consisted of a conic acrylic mesh sewn around a metal ring with a diameter of 0.5 m, placed 80 cm above the ground with two plastic tubes. The seed traps were emptied and seeds were processed four times at each site between April 2020 and June 2021. More frequent sampling was not possible, but seed predation is low in our study area (Gallegos et al., 2014), and we rarely observed decomposed or germinated seeds in the seed traps. Seeds were identified using a reference collection from the study area deposited at the Santiago de Chirca Biological Station. We measured the length of at least five seeds per species, and only seeds of plant species dispersed by animals were included in the analysis.

To assess seedling establishment, we installed a 1 × 1 m plot next to each seed trap, in which all seedlings were removed at the start of the experiment. After 15 months, we registered all seedlings above 2 cm in each plot. For the purposes of this study, we define "establishment" as seedlings that have germinated and survived to at least 2 cm in height. However, we acknowledge that seedlings of this size are still likely dependent on seed reserves and may have a high chance of mortality. Therefore, these individuals may not yet represent fully established seedlings but rather early-stage sprouted seedlings. We collected seedlings of the same morphospecies outside the plots for identification, and if no similar seedlings were found, seedlings were collected inside the plots. Samples were dried and identified in the Herbario Nacional de Bolivia (LPB). Seeds and seedlings were classified as pioneer and non-pioneer species based on previous studies in the study area (Gallegos et al., 2016; Lippok et al., 2013; Lippok et al., 2014; López et al., 2024) and on expert knowledge and information at the LPB.

2.4. Statistical analysis

All analyses were limited to plant species recorded in both seed traps and seedling recruitment plots, as both datasets are required to calculate establishment limitation. Dispersal and establishment limitations were calculated following Muller-Landau et al. (2002) as follows:

$$\textit{Dispersal limitation} = 1 - a/n$$

$$\textit{Establishment limitation} = 1 - r/am$$

Where a is the number of seed traps receiving seeds of a given species, n is the total number of seed traps in each treatment, r represents the number of seed traps and recruitment plots where both seeds and seedlings of a species occurred, and m is the area in which seedlings were recorded. Both indices range from 0 (no limitation) to 1 (complete limitation).

For all the analysis we used generalized mixed-effects models (GLMMs). To analyze the effect of perches and roosts in dispersal and establishment limitation we used the indices of dispersal and establishment limitation as response variables, treatment (forest, bracken, perch and roost) was the fixed effect, and site was the random effect. To evaluate the differences between pioneer and non-pioneer species in terms of their dispersal and establishment limitation, dispersal and establishment limitation indices were the response variables, treatment, life-history strategy (pioneer and non-pioneer) and their interaction were the independent fixed effects, and site was the random effect. To assess the differences in the limitation indices between small and large seeds, the models included dispersal and establishment limitation indices as response variables, treatment, size (small: <3 mm and large:>3 mm), and their interaction as independent fixed effects, and site as the random effect. Each model used an ordbeta distribution of errors. In total, we performed 6 models using the *glmmTMB* package (Brooks et al., 2017). To determine significant differences among treatments, we performed Tukey *post hoc* tests using the *emmeans* package (Russell et al., 2024). In all models, significance of the fixed factors was determined by Likelihood Ratio Tests (LRT) between models with and without the term of interest. We calculated marginal R^2 values to assess the proportion of variance explained by the fixed factors using the r.squaredGLMM function of the *MuMin* package (Barton, 2023). All statistical analyses were conducted in R 4.2.2 (R Core Team, 2022).

3. Results

We calculated dispersal and establishment limitation indices for 37 plant species, of which five species occurred in bracken, 30 species in forest, 20 at perch and three at roost (Table S1).

3.1. Dispersal limitation

On average, we found that 33 species had a dispersal limitation higher than 60 %, three species had a dispersal limitation of about 50 %, and *Miconia hygrophila* had a limitation of 38 %. Dispersal limitation was significantly different between forest and bracken, as well as between perch and bracken ($X^2 = 17.68$, $p < 0.001$). It was 23 % lower in forest (mean = 0.68, CI = 0.64–0.72) and 24 % lower in perch (mean = 0.67, CI = 0.61–0.72) compared to bracken (mean = 0.88, CI = 0.78–0.94) (Fig. 1a, Table 1). No significant differences were observed between bracken and roost (mean = 0.81, CI = 0.71–0.85), and perch exhibited similar dispersal limitation to forest (Fig. 1a, Table 1). We found significant differences in dispersal limitation between pioneer and non-pioneer species ($X^2 = 17.45$, $p < 0.001$), and between large and small-seeded species ($X^2 = 19.22$, $p < 0.001$), across forest, perch and bracken. For non-pioneer species, dispersal limitation was 23 % lower in forest (mean = 0.70, CI = 0.65–0.75) and 22 % lower in perch (mean = 0.71, CI = 0.63–0.79) compared to bracken (mean = 0.91, CI = 0.73–0.98) (Fig. 1b, Table 1). Pioneer species showed similar patterns, with dispersal limitation 23 % lower in forest (mean = 0.67, CI = 0.62–0.72) and 26 % lower in perch (mean = 0.64, CI = 0.58–0.710) relative to bracken (mean = 0.87, CI = 0.74–0.93) (Fig. 1b, Table 1). Roosts did not differ significantly from bracken in either successional type (non-pioneer mean = 0.85, CI = 0.75–0.92; pioneer mean = 0.79, CI = 0.66–0.87) (Fig. 1b, Table 1).

For seed size, large-seeded species exhibited 22 % lower dispersal limitation in forest (mean = 0.71, CI = 0.65–0.76) and 22 % lower in perch (mean = 0.71, CI = 0.63–0.79) compared to bracken (mean = 0.91, CI = 0.73–0.98). Dispersal limitation in roosts did not differ significantly from bracken (mean = 0.898, CI = 0.697–0.971) (Fig. 1c, Table 1). Similarly, small-seeded species showed 23 % lower dispersal limitation in forest (mean = 0.67, CI = 0.62–0.71) and 26 % lower in perch (mean = 0.64, CI = 0.57–0.71) relative to bracken (mean = 0.87, CI = 0.74–0.94), whereas roosts showed values not significantly different from bracken (mean = 0.77, CI = 0.69–0.84) (Fig. 1c, Table 1).

3.2. Establishment limitation

In general, most species had a high establishment limitation (higher than 70 %), only *Myrcia* sp. had an establishment limitation of less than 70 %. Establishment limitation was significantly different among forest, bracken and perch ($X^2 = 32.21$, $p < 0.001$). It was 26 % lower in forest (mean = 0.76, CI = 0.72–0.80) compared to bracken (mean = 0.95, CI = 0.89–0.97), and approximately 25 % lower in perch (mean = 0.71, CI = 0.65–0.77) relative to bracken. No significant differences were detected between bracken and roost (mean = 0.91, CI = 0.82–0.96), nor between forest and perch (Fig. 2a, Table 2). We found significant differences in dispersal limitation between pioneer and non-pioneer species ($X^2 = 37.26$, $p < 0.001$), and between large and small-seeded species ($X^2 = 33.96$, $p < 0.001$), across forest, perch and bracken (Fig. 2a, Table 2). For non-pioneer species, establishment limitation was 25 % lower in forest (mean = 0.713, CI = 0.663–0.759) and 23 % lower in perch (mean = 0.739, CI = 0.649–0.813) compared to bracken (mean = 0.955, CI = 0.884–0.984). Roosts did not differ significantly from bracken (mean = 0.908, CI = 0.782–0.965). For pioneer species, establishment limitation was 8 % lower in forest (mean = 0.879, CI = 0.826–0.918) and 25 % lower in perch (mean = 0.716, CI = 0.642–0.780) relative to bracken (mean = 0.952, CI = 0.876–0.982), while roosts again showed values not significantly different from bracken (mean = 0.941, CI = 0.788–0.986) (Fig. 2b, Table 2).

For large-seeded species, establishment limitation was 26 % lower in forest (mean = 0.71, CI = 0.65–0.75) and 23 % lower in perch (mean = 0.73, CI = 0.65–0.81) compared to bracken (mean = 0.95, CI = 0.88–0.98), whereas roosts did not differ significantly from bracken (mean = 0.89, CI = 0.70–0.94) (Fig. 2c, Table 2). Small-seeded species showed 7 % lower establishment limitation in forest (mean = 0.88, CI = 0.83–0.92) and 24 % lower in perch (mean = 0.72, CI = 0.64–0.78) relative to bracken (mean = 0.95, CI = 0.87–0.98), whereas roosts showed values not significantly different from bracken (mean = 0.96, CI = 0.85–0.99) (Fig. 2b, Table 2).

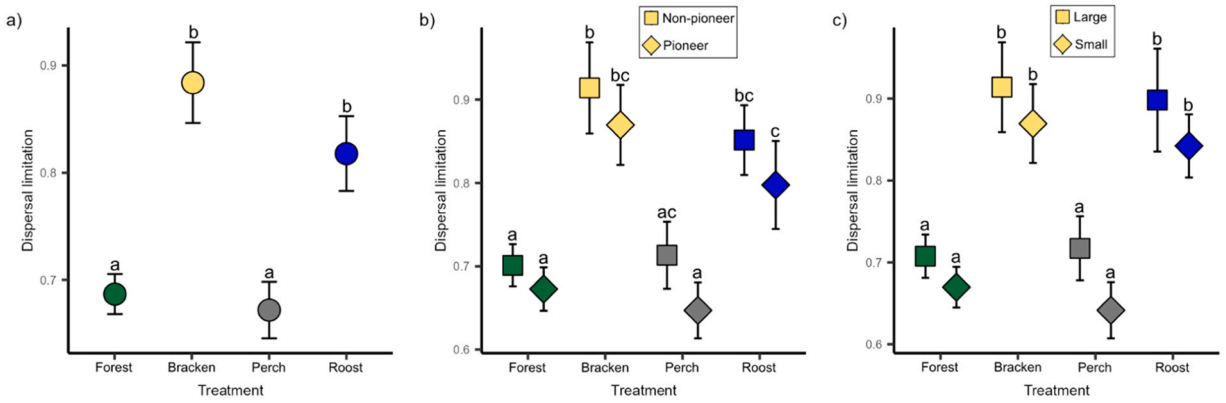

Fig. 1. Indices of dispersal limitation for a) forest, bracken, perch and roost, and for the same treatments considering b) life-history strategy, and c) seed size. The colors represent the different treatments, and the symbols represent characteristics of life-history strategy (non-pioneer or pioneer) and seed size category (large or small). Different letters indicate significance differences at the 0.05 level. Circles, squares and diamonds with error bars denote the mean values ± SE estimated by GLMMs.

Table 1
Results of the generalized linear mixed models for dispersal limitation in general and according to their life-history strategy (pioneer and non-pioneer), and seed size (small and large). Bracken, non-pioneer and large seeds are in the intercept. P-values ≤ 0.05 are denoted in bold.

		Estimate	Standard error	Z value	P value	LRT test p-value	R2 marginal
Dispersal limitation	(Intercept)	2.03	0.36	5.58	**< 0.001**	**< 0.001**	0.16
	Forest	-1.25	0.37	-3.36	**< 0.001**		
	Perch	-1.32	0.38	-3.47	**< 0.001**		
	Roost	-0.69	0.40	-1.72	0.09		
Dispersal limitation life history	(Intercept)	2.37	0.69	3.41	**< 0.001**	**0.003**	0.21
	Forest	-1.51	0.70	-2.15	**0.03**		
	Perch	-1.47	0.72	-2.05	**0.04**		
	Roost	-0.58	0.78	-0.75	0.45		
	Pioneer	-0.47	0.81	-0.58	0.56		
	Forest: Pioneer	0.33	0.82	0.40	0.68		
	Perch: Pioneer	0.17	0.85	0.21	0.83		
	Roost: Pioneer	-0.14	0.90	-0.15	0.87		
Dispersal limitation life history	(Intercept)	2.37	0.69	3.42	**< 0.001**	**< 0.001**	0.21
	Forest	-1.48	0.71	-2.10	**0.03**		
	Perch	-1.44	0.71	-2.00	**0.04**		
	Roost	0.32	1.21	0.26	0.79		
	Small	-0.46	0.80	-0.51	0.56		
	Forest: Small	0.29	0.82	0.35	0.72		
	Perch: Small	0.12	0.83	0.14	0.89		
	Roost: Small	-0.94	1.29	-0.73	0.46		

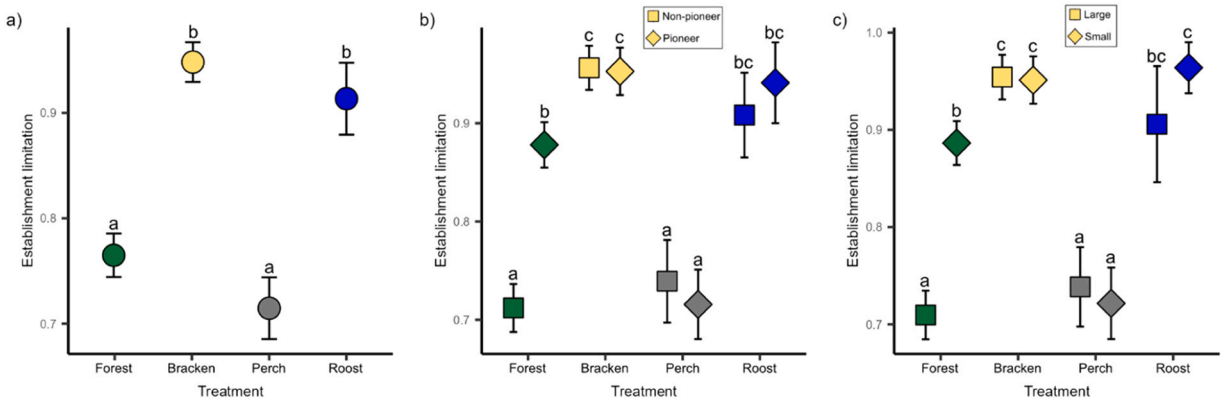

Fig. 2. Indices of establishment limitation for a) forest, bracken, perch and roost, and for the same treatments considering b) life-history strategy, and c) seed size. The colors represent the different treatments, and the symbols represent characteristics of life-history strategy (non-pioneer or pioneer), and seed size category (large or small). Different letters indicate significance differences at the 0.05 level. Circles, squares and diamonds with error bars denote the mean values ± SE estimated by GLMMs.

4. Discussion

Our results indicate that the installation of bird perches is an effective method to reduce dispersal and establishment limitations of bird-dispersed plant species in bracken-dominated areas. Compared to artificial bat roosts, bird perches show a greater reduction in both limitations, with values at perches comparable to those found in forest. Bird perches reduced the dispersal and establishment limitation of pioneer and non-pioneer plants as well as small and large-seeded species. The positive effect of bird perches highlights the importance of attracting animal seed dispersers to deforested areas to overcome dispersal and establishment limitations and thus potentially contribute to the regeneration of tropical montane forests.

4.1. The effect of bird perches and artificial bat roosts in dispersal and establishment limitation

In our study, the installation of bird perches significantly reduced dispersal limitation to a level comparable to that observed in forested areas. Our results support previous studies showing that perches increase the abundance of bird-dispersed seeds in the seed rain in deforested areas (de Almeida et al., 2016; Saavedra et al., 2015). The availability of some food resources in open areas and the presence of bird species that can tolerate deforested habitats are important for the effectiveness of perches (Guidetti et al., 2022). In our study area, there are plants from the Melastomataceae and Ericaceae families in bracken-dominated areas (Lippok et al., 2013) that could be attractive as food resources for birds. Moreover, the abundance and richness of generalist frugivorous birds, which cope well

Table 2
Results of the generalized linear mixed models for establishment limitation in general and according to their life-history strategy (pioneer and non-pioneer) and seed size (small and large). Bracken, non-pioneer and large seeds are in the intercept. P-values ≤ 0.05 are denoted in bold.

		Estimate	Std error	Z value	P-value	LRT test p-value	R2 marginal
Establishment limitation	(Intercept)	2.95	0.38	7.76	**< 0.001**	**< 0.001**	0.51
	Forest	-1.74	0.38	-4.52	**< 0.001**		
	Perch	-2.00	0.40	-5.03	**< 0.001**		
	Roost	-0.55	0.56	-0.97	0.32		
Establishment limitation life history	(Intercept)	3.11	0.52	5.96	**< 0.001**	**< 0.001**	0.71
	Forest	-2.18	0.53	-4.13	**< 0.001**		
	Perch	-2.04	0.56	-3.65	**< 0.001**		
	Roost	-0.59	0.72	-0.82	0.41		
	Pioneer	-0.0.7	0.72	-0.11	0.91		
	Forest: Pioneer	1.17	0.75	1.56	0.12		
	Perch: Pioneer	-0.04	0.77	-0.05	0.95		
	Roost: Pioneer	-0.82	0.90	-0.90	0.36		
Establishment limitation seed size	(Intercept)	3.10	0.52	5.92	**< 0.001**	**< 0.001**	0.72
	Forest	-2.19	0.53	-4.14	**< 0.001**		
	Perch	-2.05	0.56	-3.67	**< 0.001**		
	Roost	-0.97	0.71	-1.37	0.17		
	Small	-0.07	0.72	-0.11	0.91		
	Forest: Small	1.24	0.75	1.64	0.10		
	Perch: Small	-0.02	0.77	-0.02	0.98		
	Roost: Small	-0.32	0.90	-0.35	0.72		

with the loss of forested areas (Gomes et al., 2008), are higher in bracken areas than at forest edges (Gallegos et al., 2024).

We found that the installation of bird perches reduced the index of establishment limitation in bracken areas. The presence of bird perches in deforested areas commonly increases the abundance of bird-dispersed seeds, however, this increase is not always accompanied by an increase in seedling establishment (de Almeida et al., 2016; Heelemann et al., 2012; Holl, 1998). The success of this restoration technique depends on the biotic and abiotic factors where perches are installed. In grass-dominated areas the soil compaction, the lack of nutrients or the competition with grasses could impede the establishment of bird-dispersed species (Florentine and Westbrooke, 2004; Holl, 1998). Contrary, bracken areas have abiotic conditions (high humidity, low light, low soil compaction) favorable for the establishment of some bird-dispersed plants (López et al., 2024). The similar levels of establishment limitation observed in both, forest and perches, indicate that seed arrival is a primary filter for plant species in these deforested areas.

In tropical forests bats are important seed dispersers for forest regeneration, however, in our study the presence of artificial bat roosts did not reduce the dispersal limitation of bat-dispersed species. Kelm et al. (2008) reported an increase in the seed rain of bat-dispersed species around artificial bat roosts installed in tropical forests in Costa Rica. In contrast to their study, where roosts were installed in continuous forests and small forest patches, we installed our roosts in open, deforested bracken areas. It is possible that the light or temperature conditions in the roosts located in the bracken did not attract many bats, which could explain the low quantity of bat-dispersed seeds found in our seed traps. A similar result was reported by Reid et al. (2013), whose artificial bat roosts were also placed in open, deforested areas. Future applications of artificial bat roosts should explore alternative designs that improve micro-climatic conditions and enhance their effectiveness as a restoration technique. Furthermore, our results could be related to the scarcity of food resources for bats, since bat-dispersed species in bracken areas, such as *Piper* and *Vismia* are rare (Lippok, Beck, et al., 2013). The presence of roosts did not reduce the establishment limitation either. This result show that this technique has limited effectiveness to assist forest regeneration in bracken areas.

4.2. The effect of bird perches and artificial bat roosts in the dispersal and establishment limitation of non-pioneer and pioneer species

Regarding life history, perches allowed the reduction of dispersal limitation of non-pioneer and pioneer species. In contrast to our expectation that non-pioneer species would show higher dispersal limitation, since these seeds are typically more restricted in deforested areas (de Almeida et al., 2016; de la Peña-Domene et al., 2018) and usually have large seeds (Guzmán-Luna and Martínez-Garza, 2016; Martínez-Garza and Howe, 2003), that are dispersed by large birds that are scarce in deforested areas (Sodhi and Smith, 2007). We did not find differences between both life-history strategies. This may be due to the ability of some birds to move between forest and open areas. Species such as *Mionectes striaticolis, Pipreola frontalis* and *Catharus ustulatus* were captured in forest and bracken areas (Gallegos et al., 2024), these and other birds could be the responsible of dispersing non-pioneer species from forest to bracken.

The presence of perches reduced the establishment limitation of non-pioneer and pioneer species. We expected that the reduction will be lower for pioneer species compared to non-pioneer species, because pioneer plants usually need high light levels for germination (Everham et al., 1996; Pearson et al., 2002). However, López et al. (2024) found that the presence of bracken reduces the density of seedlings of early-successional herbs, but did not reduce the density of early and late-successional trees and shrubs. Under the perches we did not register any pioneer herb, and the majority of pioneer species belonged to the family Melastomataceae, that is a common element in these deforested areas (Lippok et al., 2013).

Roosts were unable to reduce dispersal and establishment limitation of non-pioneer and pioneer species. The values of dispersal and

establishment limitation for both categories were comparable to those found in bracken. In our study area, frugivorous bats are less abundant than omnivorous/frugivorous birds (Gallegos et al., 2024), and there are more bird-dispersed than bat-dispersed plant species in forest and bracken areas (Lippok et al., 2013; Lippok et al., 2014). Also, bats defecate while flying (Muscarella and Fleming, 2007) and although we increased the number of seed traps and recruitment plots in this treatment to improve the possibility of detecting dispersed seeds and established seedlings, it may be possible that we did not find all the seeds and seedlings.

4.3. The effect of bird perches and artificial bat roosts in the dispersal and establishment limitation of small and large-seeded species

Concerning seed size, we hypothesized that large-seeded species will have higher dispersal limitation than small-seeded species in perches. We did not find significant differences between both size categories; however large seeds tended to be more limited than small seeds in all treatments. Large frugivorous birds are scarce in deforested areas (Markl et al., 2012), but we observed that the perches installed in this study were used by large bird species such as *Penelope montagnii* (approximately 706 g) and *Aulacorhynchus coeruleicintis* (approximately 208 g). These species could handle fruits that have large seeds that are important in the regeneration of bracken-dominated areas (Ssali et al., 2019). We also did not find differences in establishment limitation between small and large-seeded species, both being reduced by the presence of perches. Although seedling composition between forest and bracken areas with bird perches in our study area is different (Mayta et al., 2024), under perches we found seedlings of species such as *Nectandra cuspidata, Hedyosmum racemosum* and *H. angustifolium* that are common in forest and have large seeds. In bracken areas, seed size is positively related to seedling establishment and survival (Gallegos et al., 2025). Large-seeded species tend to better tolerate shaded conditions (Walters and Reich, 2000) and thick litter layers (Wang et al., 2022), both of which are characteristic of bracken areas. Nevertheless, some small-seeded species, particularly from the genera *Miconia* and *Gaultheria*, are also common in bracken habitats (Lippok et al., 2013), indicating that species within these genera may tolerate the environmental conditions created by bracken.

Roosts were unable to reduce dispersal and establishment limitation of small and large-seeded species. Bats usually disperse small seeds of the genera *Piper* and *Vismia* that are important in the early stages of tropical forest succession (Muscarella and Fleming, 2007). However, both are light demanding species for germination and seedling establishment (Daws et al., 2002; Wieland et al., 2011). It is possible that light conditions under bracken fronds and litter were not favorable for the establishment of bat-dispersed species. Thus, this technique could probably yield better results in grass-dominated areas, where the conditions, particularly of light, may favor the establishment of bat-dispersed species. However, the interpretation of the roost results should be made with caution because only three species were recorded in this treatment. This low richness may reduce the statistical power of the comparisons and limits the generalizability of our findings for roosts. Nevertheless, the low number of species itself indicates strong environmental filtering for bat-dispersed plants in bracken-dominated areas, which likely contributes to the high dispersal and establishment limitation we detected.

Although the presence of roosts was able to increase the density of bat-dispersed seeds and seedlings (Mayta et al., 2024), this technique was not able to reduce the indices of dispersal and establishment limitation. The inability of roosts to reduce dispersal and establishment limitations may be related to how these limitations are calculated. The indices used do not only account for the density or abundance of seeds and seedlings; they also consider the number of seed traps and plots where species are detected. The dispersal limitation index reflects the proportion of sites reached by seeds and can indicate whether dispersal limitation results from the restricted distribution of available seeds (Muller-Landau et al., 2002). In the case of establishment limitation, the index also incorporates the number of seed traps and recruitment plots where both seeds and seedlings of a species occur. At certain sites, we observed hundreds of bat-dispersed seeds, but typically in just one of the 14 seed traps installed around the roost, and the co-occurrence of bat-dispersed seeds and seedlings was low. Thus, the establishment limitation index allows us to infer that when seeds arrive but no seedlings establish, the limitation must occur at the establishment stage (Muller-Landau et al., 2002). It is also important to note, as described in the Methods, that both indices were calculated only for species present in both the seed traps and the recruitment plots. In our study sites, we identified 70 species of animal-dispersed seeds and 160 species of animal-dispersed seedlings (Mayta et al., 2024). However, the indices in this study were calculated for only 37 species. Several abundant seed-rain species, such as *Cecropia* sp. and *Ficus* sp., could not be included because they were recorded in the seed traps but were absent from the recruitment plots (Mayta et al., 2024). As a result, some of our findings should be interpreted in light of this methodological constraint. For example, although bracken areas have a higher abundance of bird-dispersed pioneer species compared to forest (Mayta et al., 2025), our analyses of dispersal and establishment limitation did not detect differences between pioneer and non-pioneer species.

It is important to evaluate the techniques that aim the recovery of forest in sufficient periods of time (Holl et al., 2024). However, our study had a relatively short duration (15 months), and some seeds may require more time to germinate or for seedlings to establish successfully. This limited time frame may underestimate longer-term germination and establishment processes. It is also worth mentioning that in our study area the constant burning makes it very difficult to maintain plots for long periods of time. From the eight sites evaluated, three were burned again after our last monitoring, reducing the possibility of obtaining data for more than two years. Future studies could also focus on identifying the characteristics of birds and bats that are attracted to perches and roosts. Animal traits, such as body mass, wing morphology, and gape width that are related to the capacity of disperse large or small seeds and the distance that a bird or bat is capable of traveling, may help to understand which plants are favored by both techniques. Although dispersal limitation differed among treatments and plant traits, the marginal R^2 values were low (0.16–0.21), indicating that much of the variation remains unexplained. This likely reflects the influence of unmeasured factors, such as the local abundance of animal-dispersed plants or environmental heterogeneity that could affect seed dispersal processes (Villegas et al., 2024).

Our results reinforce the idea that dispersal limitation is one of the most important filters that plant species must overcome in bracken-dominated areas. Techniques aimed at attracting seed-dispersing animals can facilitate forest regeneration. However, the lack

of long-term studies may limit our understanding of the ecological processes that contribute to the slow regeneration of these deforested areas. The installation of bird perches, along with direct sowing and planting of seedlings of animal-dispersed seeds, are strategies that could effectively support the regeneration of these widely distributed deforested areas.

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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.

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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.gecco.2026.e04064.

Data availability

Data will be made available on request.

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