






## RESEARCH ARTICLE

# Bird perches and artificial bat roosts increase seed rain and seedling establishment in tropical bracken-dominated deforested areas

Cesar Mayta<sup>1,2,3,4</sup> , Cecilia L. López<sup>1,2,3</sup> , Mariana Villegas<sup>3,5</sup> , Luis F. Aguirre<sup>6</sup>,  
Isabell Hensen<sup>1,7</sup> , Silvia C. Gallegos<sup>1,2,3</sup> 

Tropical forests are being reduced by human activities. The use of fire for agricultural expansion generates areas dominated by the bracken fern *Pteridium*, where forest regeneration is slow. This may be caused by seed limitation, especially of animal-dispersed seeds, due to the absence of seed dispersers from the forest in deforested areas, calling for restoration strategies to assist forest regeneration. We installed bird perches and artificial bat roosts to evaluate their effect on the density, species richness, and composition of animal-dispersed seeds and seedlings of tree and non-tree species in bracken-dominated areas in the tropical montane forest of Bolivia. We found that perches and bat roosts increased the density and species richness of animal-dispersed seeds and established seedlings. The seeds and seedlings dispersed by birds were clumped under the perches, while the seeds and seedlings dispersed by bats were distributed around the roosts. Perches had a higher density and species richness of seeds and seedlings compared to bat roosts, suggesting that the use of perches could be a better option as a restoration tool in bracken-dominated areas. The increase in seed rain and seedling establishment of animal-dispersed species in perches and bat roosts supports seed limitation, hindering forest succession in bracken-dominated areas. The use of bird perches accompanying other restoration techniques is a promising restoration strategy to accelerate forest regeneration in tropical areas dominated by *Pteridium*, which are widely distributed.

**Key words:** animal-mediated seed dispersal, disturbance, ecological restoration, forest regeneration, *Pteridium*

## Implications for Practice

- Seed limitation in bracken-dominated areas is one of the first limiting factors in the process of forest regeneration; restoration programs should focus on techniques to overcome this filter.
- The installation of bird perches and artificial bat roosts increased seed arrival and seedling establishment of animal-dispersed species in bracken-dominated areas.
- Bird perches had higher effectiveness than artificial bat roosts. Bird perches should be included in restoration strategies to foster forest regeneration in bracken-dominated areas.

## Introduction

Tropical montane forests harbor much of Earth's terrestrial biodiversity but are under severe threat, primarily due to human activities (Gardner et al. 2009). The use of fire for agricultural expansion reduces forest cover and results in altered and fragmented ecosystems (Laurance et al. 2014). Burned areas can become dominated by grasses and/or ferns, hindering forest regeneration (Chazdon 2003; Hartig & Beck 2003). Globally, ferns in the genus *Pteridium* (hereafter bracken) are common elements in burned/deforested landscapes (Alday et al. 2013).

Slow forest regeneration in tropical bracken-dominated areas may be due to seed limitation and/or unfavorable conditions for seedling establishment (Marrs & Watt 2006). Since bracken can shade other plants, shade-tolerant species, commonly dispersed by animals, can be facilitated by the micro-environmental conditions (high humidity, low temperature,

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<sup>1</sup>Institute of Biology/Geobotany and Botanical Garden, Martin Luther University Halle-Wittenberg, Große Steinstraße 79/80, D-06108, Halle, Germany

<sup>2</sup>Herbario Nacional de Bolivia, Instituto de Ecología, Universidad Mayor de San Andrés, Campus Universitario Cota-Cota, Calle 27, La Paz, Bolivia

<sup>3</sup>Santiago de Chirca Biological Station, La Paz, Sud Yungas, Bolivia

<sup>4</sup>Address correspondence to C. Mayta, email [cesarmaytarocabado@gmail.com](mailto:cesarmaytarocabado@gmail.com)

<sup>5</sup>Instituto de Ecología, Universidad Mayor de San Andrés, Campus Universitario Cota-Cota, Calle 27, La Paz, Bolivia

<sup>6</sup>Centro de Biodiversidad y Genética, Universidad Mayor de San Simón, Cochabamba, Bolivia

<sup>7</sup>German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Puschstraße 4, 04103, Leipzig, Germany

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and low-light conditions) generated by bracken (Gallegos et al. 2015; Ssali et al. 2019). Despite the possible facilitative effects of bracken on animal-dispersed species, the density of seeds and seedlings is lower in bracken-dominated areas than in the forest (Saavedra et al. 2015; Gallegos et al. 2016; Ssali et al. 2018). This pattern could be related to differences in the species composition of seed dispersers between both habitats or to a lower abundance of animal seed dispersers in bracken-dominated areas (Gallegos et al. 2024). Therefore, it is important to study the impact of the use of animal artificial attractants as a forest restoration strategy to increase seed dispersal and reduce seed limitation.

Seed dispersal by animals is an important ecological function in tropical forests, and is related to the maintenance of plant diversity and forest regeneration processes (Sekercioglu 2006). However, increasing deforestation and habitat fragmentation decreases animal-mediated seed dispersal, as several seed disperser species are sensitive to deforestation and the subsequent simplification of vegetation structure (Morante-Filho et al. 2018). Additionally, the scarcity of natural perches and food resources in deforested areas can cause a reduction in the number of birds in deforested sites (Athie & Dias 2016). Bats are also important seed dispersers (Kunz et al. 2011), and several plant species rely almost exclusively on them for seed dispersal (Muscarella & Fleming 2007), highlighting their importance for forest regeneration.

About 90% of woody species in the tropical forest bear fruits that are attractive to animals (Howe & Smallwood 1982). Frugivorous birds and bats, among other animal seed dispersers, move seeds into deforested areas, fostering forest regeneration (Galindo-González et al. 2000). Birds and bats differ in their seed deposition patterns: birds usually defecate seeds while perched, whereas bats defecate seeds while flying (Muscarella & Fleming 2007). The differences in their seed deposition behavior produce differences in the spatial distribution of seeds and seedlings; while bird-dispersed seeds and seedlings are found principally under perches (Zwiener et al. 2014), bat-dispersed seeds and seedlings could be found in open areas.

Active ecological restoration strategies that help increase seed dispersal into deforested areas can accelerate forest regeneration (Holl 1998). There are different techniques to increase the rain of animal-dispersed seeds, such as the use of perches (Holl 1998; Alencar & Guilherme 2020) and the construction of artificial roosts for bats (Kelm et al. 2008). However, as seed rain is only one of many steps in the cycle of forest regeneration (Dent & Estrada-Villegas 2021), the effects of artificial perches and bat roosts on seedling establishment must also be considered (Reid & Holl 2013; Holl et al. 2022). Although several studies found an increase in seed density and species richness in the seed rain under perches installed in pastures, most of them did not find an increase in seedling establishment (Holl 1998; de Almeida et al. 2016; but see Mcclanahan & Wolfe 1993). Accordingly, de Oliveira Bahia et al. (2023) found in a meta-analysis that perch structures did not increase seedling richness and only weakly increased seedling abundance in open vegetation areas. These results could be related to the low germination and establishment of some species due to the competition with grasses (Holl 1999) and to the harsh microclimatic conditions

in open, deforested environments. On the contrary, the presence of bracken can favor the establishment of several species, such as *Myrsine coriacea*, *Clusia elongata*, *Clethra scabra*, and *Psychotria mahonii* (Gallegos et al. 2016; Ssali et al. 2019). This could be due to the micro-environmental conditions created by bracken that allow the establishment of shade-tolerant tree species (Gallegos et al. 2015; Ssali et al. 2019). Therefore, the inclusion of perches has the potential to be an effective restoration method in bracken-dominated areas.

The construction of artificial bat roosts for frugivorous bats is a technique that has not been as extensively tested in tropical regions (Mering & Chambers 2014), probably due to the low benefit–cost rates observed in previous experiences. A study in Costa Rica found that artificial bat roosts did not accelerate the regeneration of tropical forests in grass-dominated abandoned pastures (Reid et al. 2013), but the effects of artificial bat roosts in other deforested areas need further study, both in terms of seed rain and seedling establishment.

This study aims to analyze and compare the effect of bird perches and artificial bat roosts on seed rain and seedling establishment of species dispersed by birds and bats in bracken-dominated landscapes. We hypothesized that (1) given the favorable micro-environmental conditions that bracken provides for several animal-dispersed species, both techniques will increase seed rain and seedling establishment in terms of density and species richness; (2) due to the greater number of plant species dispersed by birds in our study area (bird/bat ratio approximately 3:1; Lippok et al. 2013, 2014), bird perches are expected to generate a greater density and species richness of seeds and seedlings compared to roosts; (3) given the behavior of both animal groups with respect to seed deposition patterns, birds will generate the highest seed rain and seedling establishment under the perches, while bats will disperse seeds beyond the immediate vicinity of roosts; (4) if perches and bat roosts attract seed dispersers from the forest, it can be assumed that both techniques promote the occurrence of animal-dispersed forest species in deforested areas.

## Methods

### Study Area

The study was conducted in the tropical montane region of the Bolivian Andes between 1900 and 2350 m a.s.l. in an area of 17 by 13 km, near the town of Chulumani (16°24'37"S, 67°31'37"W). The topographical heterogeneity and elevational gradient in this ecosystem generate high plant diversity (Lippok et al. 2014). The mean annual temperature is  $20.4 \pm 1.3^\circ\text{C}$ , and the mean annual precipitation is  $1341.3 \pm 182.1$  mm (SENAMHI-INADHI 2024). Forests around Chulumani are highly fragmented due to agricultural expansion and human-induced fires. The landscape is composed of two large forest fragments (of about 1500 and 3000 ha, respectively; Fig. S1) surrounded by deforested areas dominated by the bracken fern *Pteridium esculentum* subsp. *arachnoideum* and shrubs of Asteraceae and Melastomataceae, such as *Tibouchina brittoniana* and *Pleroma stenocarpa*, most of them dispersed by wind, and also

some *Gaultheria* species (Ericaceae) dispersed by birds (Lippok et al. 2013). Forest edges are characterized by the presence of *Myrsine coriacea* (Primulaceae), *Cecropia elongata* (Urticaceae) and *Vismia glaziovii* (Hypericaceae) (Lippok et al. 2014).

### Study Design

To test the effect of bird perches and artificial bat roosts on seed rain and seedling establishment, we established eight study sites separated by at least 1 km (Fig. S1). At each site, we implemented four treatments: perches, artificial bat roosts, bracken, and forest (Fig. S2) between December 2019 and February 2020. For the perch treatment, in bracken-dominated areas, we installed three perches of approximately 5 m height, consisting of stakes with branches of *Erythrina falcata* and *Ficus* spp. (Zahawi 2008). We used this type of perch because it is more frequently visited by birds than artificial crossbar perches (Holl 1998), and because the stakes of both genera can resprout and serve as remnant trees in open deforested areas (Zahawi 2008). The three perches were located 50 m from the forest edge in bracken-dominated areas, with a distance of 10 m between them (Fig. S2). In the roost treatment, an artificial bat roost (hereafter roost) was placed 50 m from the forest edge in bracken-dominated areas. The roosts were designed following Kelm et al. (2008), with modifications for a lighter design (see Fig. S3 for design details). There were two controls at each site, one in the bracken-dominated area and one at the forest edge (hereafter bracken and forest). Both treatments were located at a distance of 50 m from the forest edge, with no perches or artificial bat roosts installed.

### Seed Rain and Seedling Establishment

We placed two seed traps under each perch (distance 0 m) and four seed traps, forming a cross, at 4 m from each perch (distance 4 m; Fig. S2). We doubled the number of seed traps with increasing distance to maintain a constant sampling effort and to detect clumping, following the design for point sources in concentric annuli (Bullock et al. 2006).

We placed two seed traps near the roost entrance (distance 0 m), four seed traps at 4 m from the roost (distance 4 m), and eight seed traps at 8 m from the roost (distance 8 m; Fig. S2). Since bats defecate seeds in flight (Kunz et al. 2011), we added a distance 8 m to cover more area and capture more seeds (Bullock et al. 2006). The controls had similar arrangements of the seed traps as the roosts (Fig. S2).

For each bracken and forest treatment, we placed 14 seed traps in the same arrangement, but without perches and roosts. 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. 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 in our study site, seed predation is low (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. The assignment into a seed dispersal category (bird, bat, or both) was based on previous studies about the diet of frugivorous birds and bats in tropical ecosystems (Snow 1981; Loayza et al. 2006; Saavedra et al. 2014; Castaño et al. 2018). We also measured the length of at least five seeds per species. Only seeds of plant species dispersed by birds or bats were included in the analysis.

To monitor seedling establishment, we installed a  $1 \times 1$  m plot next to each seed trap, where all seedlings were removed at the start of the experiment without disturbing the soil. Between July and August 2021, we registered all seedlings above 2 cm in each plot. For identification, seedlings of the same morphospecies were collected outside the plots, and if no similar seedlings were found, seedlings were collected inside the plots. Samples were dried and taken to the Herbario Nacional de Bolivia (LPB) for identification. Seeds and seedlings were then classified according to their life form as tree and non-tree species (including herbs and shrubs <2 m height). We made this classification because bracken-dominated areas have a dominance of non-tree species, while tree species are rare (Lippok et al. 2013; Ribeiro et al. 2013), but are very important for the forest regeneration process (Holl 2012).

In total, we set up 144 seed traps and recruitment plots around perches, 112 around roosts, 112 in the bracken area, and 112 in the forest.

### Data Analysis

To evaluate the effects of perches and roosts on the density and species richness of seeds and seedlings, we used generalized linear mixed-effects models (GLMMs). We used the density and species richness of bird- and bat-dispersed seeds and seedlings for tree and non-tree species as the response variables, in separate models, giving a total of 16 models. In each model, we included treatment (perches, roosts, bracken, and forest), distance (0 and 4 m for birds; and 0, 4, and 8 m for bats), and their second-order interaction as the independent fixed effects, and site and Perch or Roost id nested within the site as the random effects. We then performed model selection for each full model to select the most important variables, using the package MuMIn (Barton 2023) and the Akaike information criterion corrected for small sample size (AICc) to select the best models ( $\Delta AIC < 2$ ) (Burnham & Anderson 2002). To compare perches and roosts, we used GLMM, including the density and species richness of seeds and seedlings of animal-dispersed species as the response variables, in separate models, considering treatment (perch and roost) as the independent fixed effect and site as the random effect. We used a Poisson distribution of errors for species richness of seeds and seedlings, and a negative binomial distribution for density of seeds and seedlings due to overdispersion. To assess the difference in seed size among treatments, we used a linear mixed model including the community weighted means of seed length as the response variable,

treatment (bracken, roost, forest, and perch) as an independent fixed effect, and site as a random effect. All models were performed using the *glmmTMB* package (Brooks et al. 2017). To determine significant differences between treatments and distances, we performed Tukey post hoc tests for multiple-comparisons using the *emmeans* package (Russell et al. 2024). Additionally, we performed Likelihood Ratio Tests to test the significance of the variables included in the best models compared to the null models for each case.

We evaluated the effects of perches and roosts on the species composition of seeds and seedlings with a permutational multivariate analysis of variance (PERMANOVA) using the *adonis2* function in the *vegan* package (Oksanen et al. 2022), with the Bray–Curtis dissimilarity measure and 1000 permutations to calculate p-values. To assess the difference between treatments, we used the *pairwise.adonis* function in the *pairwiseAdonis* package (Martinez Arbizu 2020). To visualize seed and seedling composition, we used non-metric multidimensional scaling (NMDS) with Bray–Curtis dissimilarity index using the function *metaMDS*

from the *vegan* package. All statistical analyses were conducted in R 4.2.2 (R Core Team 2022).

## Results

### Seed Rain

After 15 months, we collected a total of 22,997 animal-dispersed seeds from 70 morphospecies (Table S1, hereafter referred to as species) in the 480 installed seed traps. We collected 13,202 (57.4%) seeds from tree species such as *Cecropia*, *Ficus*, and *Myrsine*, among others, and 9795 (42.6%) seeds from non-tree species such as *Gaultheria erecta*, *Miconia* spp., and *Piper* spp. We found 11,240 (48.9%) seeds that could be dispersed by both animal groups, 10,830 (47.1%) seeds dispersed by birds, and 927 (4.0%) seeds dispersed by bats.

The best model for seed density and species richness of tree and non-tree bird-dispersed species in the seed rain included

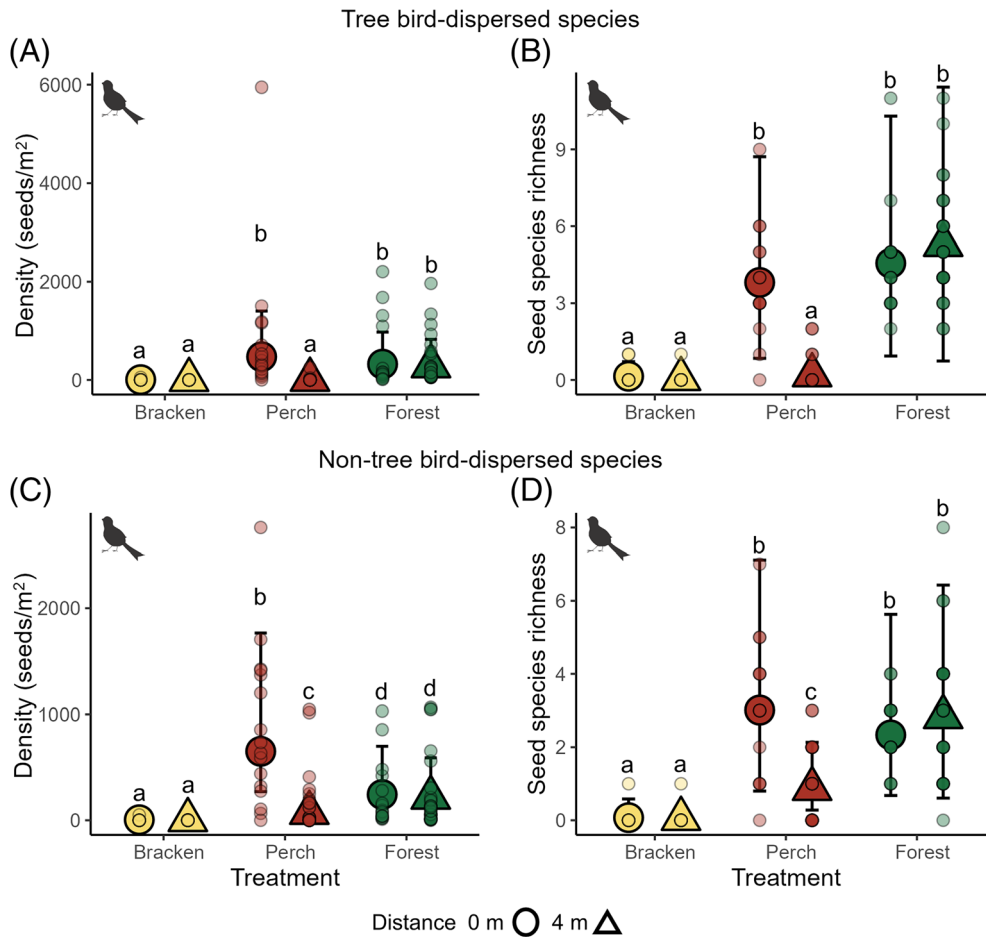


Figure 1. Seed density and seed species richness of bird-dispersed species per seed trap in bracken, perches, and in the forest. (A) Seed density and (B) species richness of tree species, and (C) seed density, and (D) species richness of non-tree species. The colors represent the different treatments, and the symbols represent the distance category of the seed traps: circle = under the perch (distance 0 m), triangle = 4 m away from the perch (distance 4 m). Different letters indicate significant differences at level 0.05 based on post hoc Tukey tests for multiple comparison among treatments and distances. Large circles and triangles with error bars denote means  $\pm$ 95% CI estimated by the GLMMs, small circles denote observed values.



the treatment, distance, and their second-order interaction (Table S2). Seed density and richness of bird-dispersed seeds from tree species were 201.7 and 22.1 times higher under perches (distance 0 m), respectively, and 190.3 and 54.4 times higher in the forest compared to bracken (Table S3; Fig. 1A & 1B). Seed density of non-tree species under the perches (distance 0 m) was significantly and 4.1 times higher than in the forest (Fig. 1C). Notably, seed density and richness of non-tree species were 29.8 and 4.8 times higher, respectively, under perches than in bracken (Fig. 1C & 1D), and 87 and 17.4 times higher, respectively, at 4 m from perches than in bracken.

The best model for seed density and species richness of bat-dispersed species included only the treatment (Table S2; Fig. S4). Seed density and richness were 16.1 and 8.3 times higher, respectively, for tree species, and 222.6 and 9.5 times higher, respectively, for non-tree species, in roosts compared to bracken (Table S3; Fig. 2A–D). Seed density and species richness were 12.5 and 5.1 times higher, respectively, in perches than in roosts (Table S4; Fig. S5). The animal-dispersed seeds found in perches, roosts, and forest were significantly larger than seeds found in bracken (Table S5; Fig. S6).

### Seedling Establishment

After 15 months, we recorded a total of 6162 animal-dispersed seedlings from 160 species (Table S6), of which 2959 (48.0%) corresponded to tree species and 3203 (52.0%) to non-tree species. We recorded 5654 (91.7%) seedlings of bird-dispersed species, 439 (7.1%) seedlings that could be dispersed by both animal groups, and 75 (1.2%) seedlings belonging to bat-dispersed species. Seedling density was independent of seed density for bird-dispersed species ( $r = -0.45$ ,  $p = 0.27$ ) and bat-dispersed species ( $r = 0.2$ ,  $p = 0.64$ ).

The best model for seedling density and richness of species dispersed by birds included treatment and distance as well as the second-order interaction only for tree species (Table S7). Seedling density and richness of tree and non-tree species were significantly higher in perches (at 0 and 4 m) than in bracken (Table S8; Fig. 3A–D); tree density and richness were 16.2 and 8.3 times higher, respectively; and non-tree density and richness were 3.3 and 2.2 times higher, respectively. Seedling density and richness of tree species were higher under perches than at 4 m from perches, while density and richness of non-tree species were similar under perches than at 4 m from perches (Fig. 3A–D). Seedling density of tree species and density and

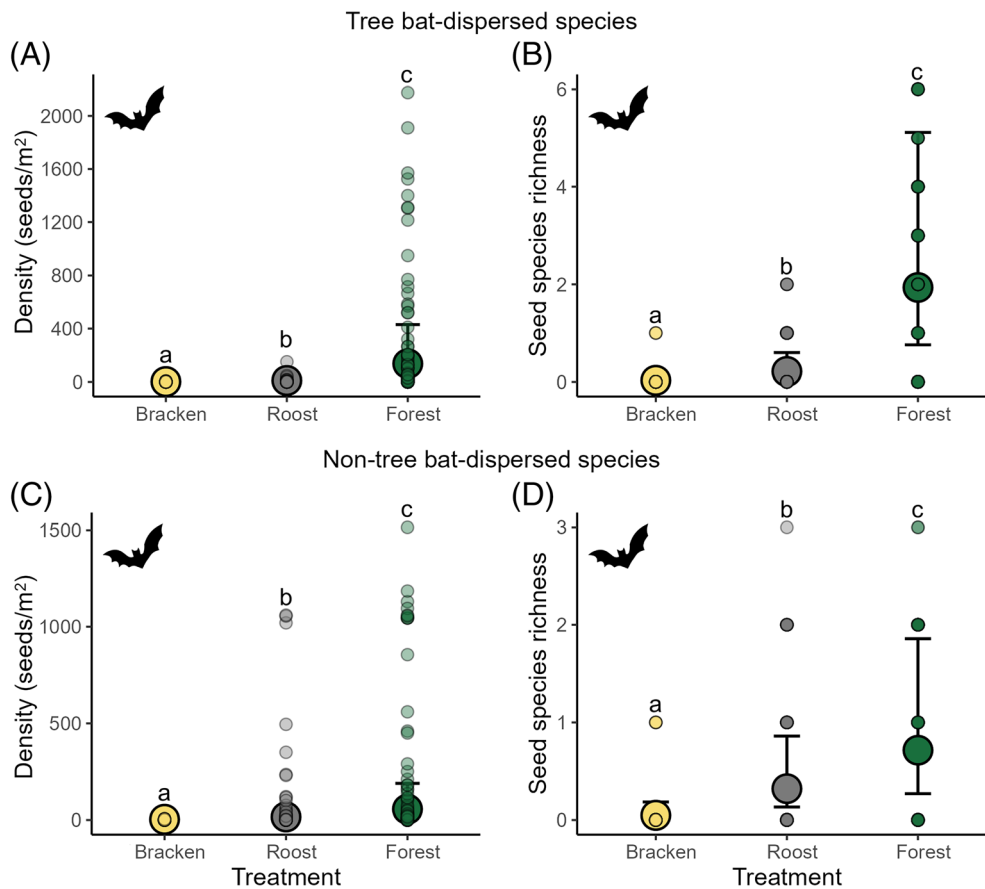


Figure 2. Seed density and species richness of bat-dispersed species per seed traps in bracken, at roosts and in forest. (A) Density and (B) species richness of non-tree seeds, (C) density, and (D) species richness of tree seeds. The colors represent the different treatments. Different letters indicate significant differences at level 0.05 based on post hoc Tukey among treatments. Large circles with error bars denote means  $\pm 95\%$  CI estimated by the GLMMs of seed density (A and C) and species richness (B and D), small circles denote observed values.

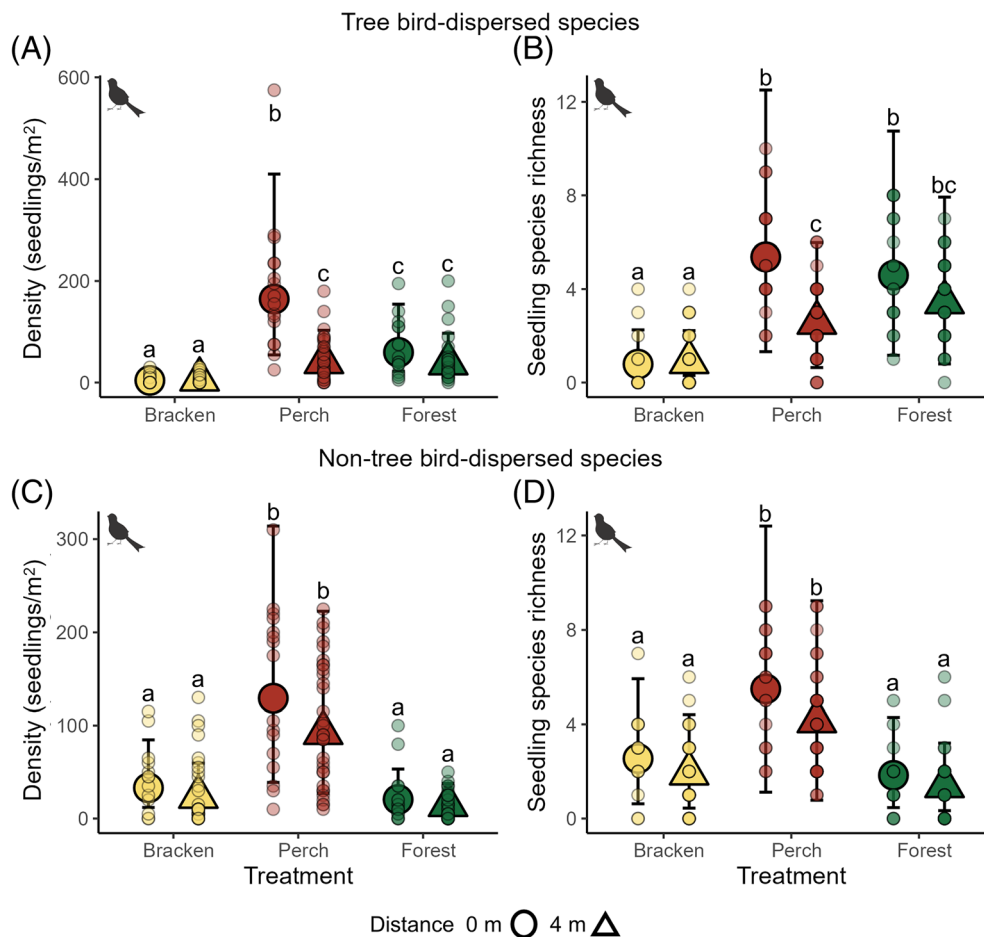


Figure 3. Seedling density and species richness of bird-dispersed species per recruitment plot in bracken, at perches and in forest. (A) Density and (B) species richness of non-tree seedlings, (C) density, and (D) species richness of tree seedlings. The colors represent the different treatments, and the symbols represent the distance category of the recruitment plots: circle = under the perch (distance 0 m), triangle = 4 m away from the perch (distance 4 m). Different letters indicate significant differences at level 0.05 based on post hoc Tukey tests for multiple comparison among treatments and distances. Large circles and triangles with error bars denote means ±95% CI estimated by the GLMMs, small circles denote observed values.

richness of non-tree species were significantly higher under perches (distance 0 m) than in forests (Fig. 3A–C); density of tree species was 2.1 times higher, and density and richness of non-tree species were 6.7 and 3.1 times higher, respectively.

The best model for density and species richness of bat-dispersed seedlings included only the treatment (Table S7; Fig. S7). Seedling density and richness of tree and non-tree species were significantly higher in the forest compared to bracken and roosts (Fig. 4A–D). Seedling density and richness of tree species were 3.7 and 3.1 times higher in roosts compared to bracken (Table S8; Fig. 4A & 4B). Seedling density and species richness were 72.9 and 27.5 times higher in perches than in roosts, respectively (Table S4; Fig. S5).

### Seed and Seedling Composition

Composition of bird-dispersed species in the seed rain differed between bracken, forest, and perches (PERMANOVA analysis:  $r^2 = 0.37$ ,  $p = 0.001$ , NMDS stress = 0.17; Fig. 5A). Forest sites were grouped separately in the upper part of axis 2, while

sites related to bracken and perches were grouped in the lower part (Fig. 5A). Species such as *Alchornea glandulosa*, *A. triplinervia* (Euphorbiaceae), *Beilschmiedia tovarensis* (Lauraceae), and *Faramea candelabrum* (Rubiaceae) were found exclusively in forest (Fig. 5A). Most bird-dispersed seeds found exclusively in forests corresponded to the tree life form. Seeds of *Rubus* sp. (Rosaceae) and *G. erecta* (Ericaceae) were found in greater quantities in perches and bracken (Fig. 5A). Seeds of *Miconia minutiflora* and *M. brittonii* (Melastomataceae) were common under perches (Fig. 5A). Some tree species were frequently found in forests and were also found under perches, such as *Hedyosmum racemosum* (Chloranthaceae), *Trema micrantha* (Cannabaceae), and *Myrcia* sp. (Myrtaceae).

Species composition of seedlings emerged from bird-dispersed seeds in forests was different from that of bracken and perches ( $r^2 = 0.54$ ,  $p < 0.001$ , NMDS stress = 0.18; Fig. 5B). Seedling communities were distinguished along axis 1, with bracken and perches communities on the left and forest community on the right (Fig. 5B). Tree species such as *A. glandulosa* (Euphorbiaceae), *Beilschmiedia latifolia*, and

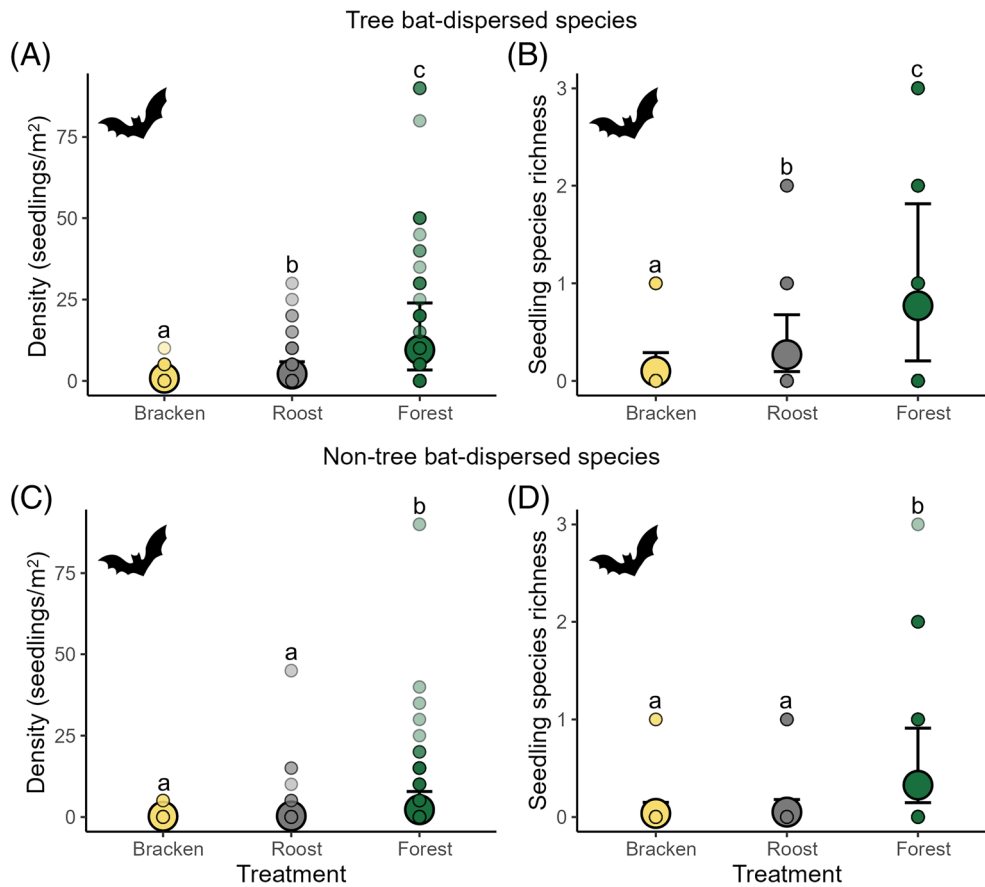


Figure 4. Seedling density and species richness of bat-dispersed species per recruitment plot in bracken, at roosts and in forest. (A) Density and (B) species richness of non-tree seedlings, (C) density, and (D) species richness of tree seedlings. The colors represent the different treatments. Different letters indicate significant differences at level 0.05 based on post hoc Tukey among treatments. Large circles with error bars denote means  $\pm$  95% CI estimated by the GLMMs of seed density (A and C) and species richness (B and D), small circles denote observed values.

*Ocotea comata* (Lauraceae) were found exclusively in forests (Fig. 5B). The non-tree seedlings of *G. erecta*, *G. vaccinioides* (Ericaceae), and *Galium hypocarpium* (Rubiaceae) were found exclusively in bracken and perches (Fig. 5B). Some tree species that were common in forests, were also present under perches, such as *Alchornea brittonii* (Euphorbiaceae), *H. racemosum* (Chloranthaceae), *Myrcia paivae* (Myrtaceae), *Myrsine coriacea* (Primulaceae), and *Clusia elongata* (Clusiaceae).

Composition of bat-dispersed seeds was different between roosts and forests, but bracken and roosts were not different ( $r^2 = 0.58$ ,  $p < 0.001$ , NMDS stress = 0.11; Fig. 5C). Along axis 1, forest species clustered on the right, and bracken and roosts clustered on the left (Fig. 5C). Species found only in forest were *Ficus cuatrecasiana* (Moraceae), *Solanum betaceum* (Solanaceae), and *Vismia rusbyi* (Hypericaceae) (Fig. 5C). All species found in bracken and at roosts also occurred in forests. *Piper* sp. 1, *Piper trigoniastriifolium* (Piperaceae) and *Solanum albidum* (Solanaceae) were the most abundant species around roosts. *Cecropia* sp. 1 (Urticaceae) and *Vismia* sp. (Hypericaceae) were common in forests and were also found around roosts.

Bat-dispersed seedlings showed no differences in species composition between bracken and roosts, but the composition

of forests differed in comparison to the other two treatments ( $r^2 = 0.32$ ,  $p = 0.01$ , NMDS stress = 0.11, Fig. 5D). *Anthurium weberbaueri*, *A. ottobuchtienii*, and *A. acebeyae* (Araceae) were found only in forests (Fig. 5D). *Solanum maturecalvans* (Solanaceae) was found exclusively around roosts (Fig. 5D). The species that had higher densities around roosts were *P. trigoniastriifolium*, *P. pubiovarium* (Piperaceae), and *Vismia crassa* (Hypericaceae).

## Discussion

Bird perches and artificial bat roosts increased the density and species richness of animal-dispersed seeds and seedlings in bracken-dominated areas. The effect was higher under perches highlighting their potential application in forest restoration strategies. In our study, the density of tree seeds and seedlings in perches was 201.7 and 16.2 times higher than in bracken, respectively. Several large-seeded tree species, such as *Alchornea brittonii*, *A. grandiflora* (Euphorbiaceae), and *Nectandra cuspidata* (Lauraceae), were found in perches, and were absent in deforested areas without perches. These species are characteristic of forest interior, and could be important in the forest

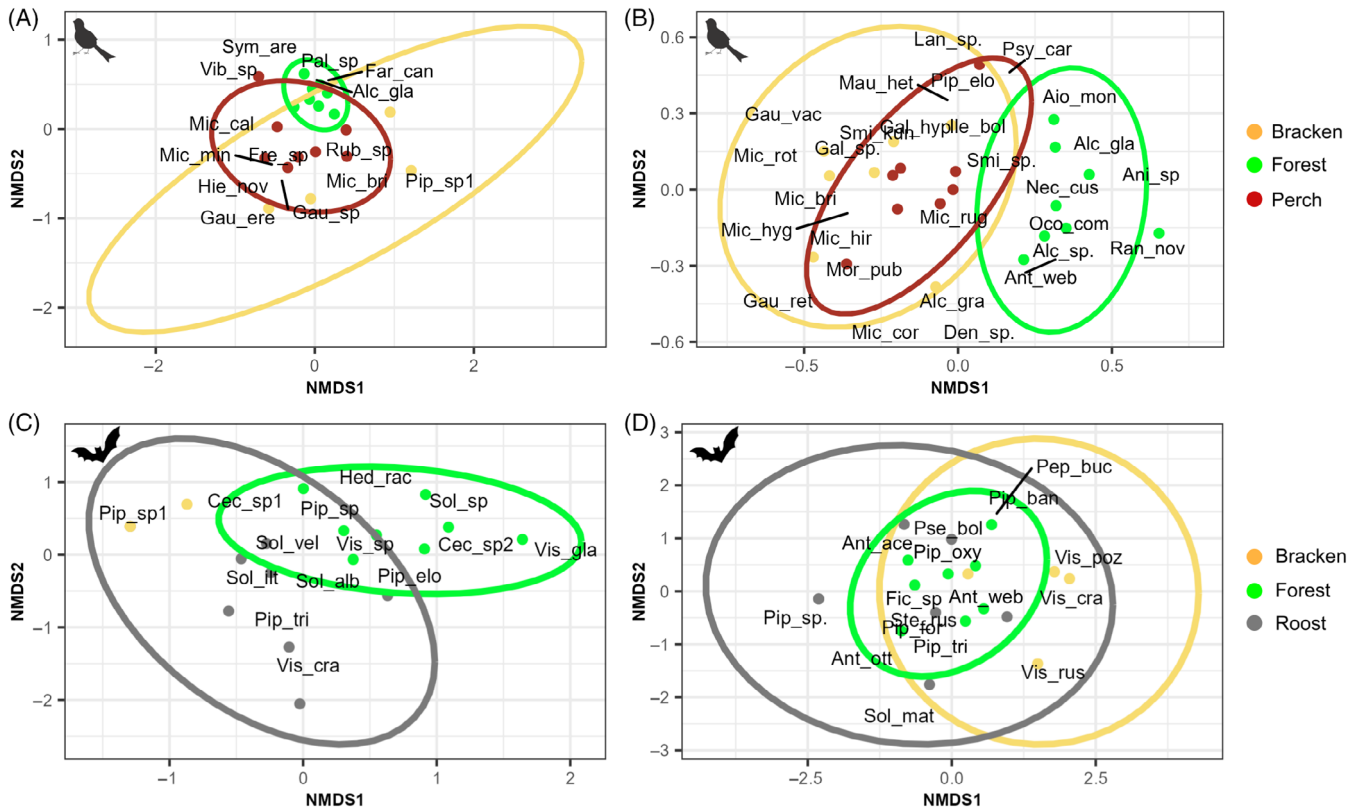


Figure 5. Non-metric multidimensional scaling (NMDS) ordination plots considering Bray–Curtis distances for (A) bird-dispersed seeds, (B) bird-dispersed seedlings, (C) bat-dispersed seeds, and (D) bat-dispersed seedlings. Ellipses are 95% CI for treatment centroids. Yellow for bracken areas, green for forest, brown for perches, and gray for roosts.

regeneration process because they produce fleshy fruits that are attractive to frugivorous seed dispersers and could help overcome seed limitation.

**Bird Perches**

Several studies have shown that the use of perches increases the density of bird-dispersed seeds in the seed rain (Holl 1998; La Mantia et al. 2019; Alencar & Guilherme 2020). We found not only an increase in the density, but also in the species richness of bird-dispersed seeds. This result supports the findings of Saavedra et al. (2015) from the same study area. However, the positive effect of perches on species richness in seed rain was not observed in some studies carried out in deforested areas dominated by grasses (Holl 1998; Zwiener et al. 2014). The differences in the results between bracken-dominated and grass-dominated areas could be related to the higher density of birds in bracken-dominated areas compared to pastures, and pastures with shrubs, as found by Maya-Elizarrarás and Schondube (2015) in an evergreen tropical rainforest in Mexico.

Independently of seed density, we found that perches also increased the density and species richness of bird-dispersed seedlings compared to bracken and forests, highlighting their potential for forest restoration. Our results are consistent with studies in the Brazilian Atlantic Forest (Zwiener et al. 2014;

Abreu et al. 2020; but see de Almeida et al. 2016) and in disturbed temperate ecosystems (McClanahan & Wolfe 1993), where perches increased seedling establishment.

After classifying bird-dispersed seeds in the seed rain, we found the highest seed density of non-tree species under perches, whereas non-tree species richness was similar under perches and in forests. Saavedra et al. (2015) reached a similar conclusion regarding the density and richness of non-tree species. Regarding seedling establishment, we recorded the highest density and richness of non-tree seedlings under perches. The most abundant species belonged to *Miconia* and *Gaultheria*. The highest density of non-tree seeds and seedlings under perches in bracken-dominated areas may be related to the presence of non-tree vegetation of Melastomataceae and Ericaceae in these environments (Zanforlini et al. 2007). These families have numerous non-tree species that produce fleshy fruits attractive to birds, which could explain why we found a great density and richness of non-tree seeds and seedlings from these families in deforested areas.

In relation to tree life form, the most abundant tree seeds under perches corresponded to *Cecropia* sp1, *Morella pubescens*, and *Myrsine* sp. These species had small and intermediate seeds (<10 mm length), while we found few species with large seeds (≥ 10 mm length) under perches. However, the density of seeds and seedlings of large-seeded species was still higher



under perches than in bracken. Large seeds require large birds to be dispersed, and large birds are usually rare in tropical deforested areas (Thiollay 1992; Sodhi & Smith 2007), but can be important seed dispersers of species with large seeds in tropical forests under high disturbance (Moreira et al. 2017) and in deforested areas in temperate and Mediterranean regions (González-Varo et al. 2023). Accordingly, in a parallel study with camera traps, we registered large bird species such as *Aulacorhynchus coeruleicinctis* (Ramphastidae, approximately 208 g) and *Penelope montagnii* (Cracidae, approximately 706 g) using the perches, indicating their potential to attract large birds and increase the density of large seeds.

The majority of bird-dispersed seeds were found under the perches, while the seed traps 4 m away received fewer seeds. This pattern is related to birds' behavior that defecate while sitting (Da Silva et al. 1996), and bird-dispersed seeds usually fall near the perching site. This behavior limits the presence of bird-dispersed seeds in deforested areas to perch sites. However, we found that 4 m away from the perches there were also more seeds and seedlings than in the bracken-dominated area without perches. This could be related to the fact that in bracken-dominated areas some species can be secondarily dispersed by animals, e.g. by ants (Gallegos et al. 2014), and some seeds might be moved a few meters from the perches and germinate, or that some seeds might be ejected while birds take off from or land on the perches.

The most abundant genera under perches were *Myrsine* and *Clusia*. Lippok et al. (2013) found that *Myrsine coriacea* was the most abundant tree growing in bracken-dominated areas, and suggested that this species could be important for forest restoration because it resprouts after fire and its fleshy fruits are attractive to birds. *Clusia* species were among the main fruit resources for birds in the forest interior and forest edge in our study area (Saavedra et al. 2014) and these species have high germination and establishment rates in bracken-dominated areas (Gallegos et al. 2015).

### Artificial Bat Roosts

Our results showed that roosts increase the density and species richness of bat-dispersed seeds in the seed rain. Kelm et al. (2008) found a similar result in Costa Rica, although they placed roosts in forest fragments and not in deforested areas. Also in Costa Rica, Reid et al. (2013) placed artificial roosts in deforested areas and found lower detection of bats in roosts installed in grass-dominated areas than in roosts installed in the forest, probably because the temperature inside the roosts of grass-dominated areas was not suitable for bats, resulting in a lack of use, and thus, less seed dispersal. In our study, we aimed to insulate the roost structure by including a 2 cm thick polystyrene in the interior of each panel while building the roosts, which probably worked favorably in reducing the temperature inside. We confirmed bat visitation to roosts from signs such as droppings and fruit remains in seven of the eight roosts we installed. Although none of the roosts were permanently colonized, they were frequently used as foraging sites.

Seeds of tree and non-tree species had higher densities and species richness near roosts than in bracken areas. The most abundant bat-dispersed genera found in the seed rain around the roosts were *Piper* and *Solanum*. These genera were also common in the seed rain at isolated trees in deforested areas in a tropical rainforest in Mexico (Galindo-González et al. 2000) and on forest slopes and landslides in a montane rainforest in Ecuador (Lindner & Morawetz 2006). These non-tree species are important for forest regeneration because they usually colonize deforested areas (Galindo-González et al. 2000). The tree genera with the highest number of seeds in the seed rain around roosts were *Cecropia* and *Vismia*. Both genera have tree species that colonize deforested areas and can facilitate forest regeneration (Nascimento et al. 2006). In addition, *Vismia* is capable of resprouting after fire (Mesquita et al. 2015), which could be an advantage in areas where fire is a major cause of deforestation. We found that seed density and species richness were not limited by distance to roosts. This pattern could be related to bats' behavior, where they defecate seeds in flight (Kunz et al. 2011). Therefore, bat-dispersed seeds are scattered, unlike the seeds dispersed by birds that are clumped under the perches (Corlett 2002).

The density of tree seedlings was higher near roosts compared to bracken areas. This result shows the potential of this technique to support the forest regeneration process in bracken-dominated areas. For example *Vismia crassa*, *V. pozuzoensis*, and *V. rusbyi* had higher densities near roosts than in bracken-dominated areas without the roosts. Density and species richness of non-tree seedlings were similar between roosts and bracken, which is possibly associated with the characteristics of seed germination of bat-dispersed species. The genera *Piper* and *Solanum* have higher germination in light conditions similar to gaps than under the canopy (Ferraz et al. 2001; Pearson et al. 2002). Bracken-dominated areas probably have lower light conditions than those needed by some bat-dispersed species for germination and recruitment. Thus, the presence of roosts increases the density of bat-dispersed seeds, but not all species seem to be able to establish. In our study, we did not remove the soil in the recruitment plots prior to the experiment. While there is a possibility that some of the observed seedlings originated from the seed bank, previous studies have shown that few species are stored in the soil seed bank in tropical bracken-dominated areas (Lippok et al. 2013; Ssali et al. 2018).

### Species Composition of Bird and Bat-Dispersed Seeds and Seedlings

Species composition in the seed rain of bird-dispersed and bat-dispersed seeds varied among perches, roosts, bracken, and forest. In all cases, forests were different compared to the other treatments, and there were no differences between perches and bracken, and roosts and bracken. In general, large seeds ( $\geq 10$  mm in length) were scarce in bracken areas. The scarcity of large-seeded species beyond the forest could be related to the scarcity of large dispersers in deforested areas. However, the presence under perches of *A. brittonii*, *Hedyosmum racemosum*, and *Clusia elongata*, species that are abundant at forest edges

(Lippok et al. 2014), showed that this technique could favor the recruitment of forest tree species in bracken-dominated areas. On the other hand, the seeds of *Piper*, *Solanum*, and *Vismia* were the most abundant near the roosts. Although the species composition of bird and bat-dispersed seedlings was different among forest, perches, and roosts; there were several genera shared among these treatments, including *Clusia*, *Myrsine*, *Myrcia*, *Hedyosmum*, and *Vismia*. All these genera are from trees that produce fruits attractive to birds or bats. The higher establishment of tree species demonstrates the importance of perches and roosts to overcome barriers to forest regeneration.

Comparing both techniques, we observed that the perches had a higher density and species richness of seeds and seedlings than roosts. This result could be related to the fact that in our study site there are more plants that are dispersed by birds (Lippok et al. 2013, 2014). Furthermore, the installation of perches is easier and less expensive than the installation of artificial roosts. These characteristics are important in choosing restoration techniques, and in bracken-dominated areas, the use of perches may be a better option than the use of artificial roosts.

The increase in seed rain and seedling establishment by bird perches and artificial bat roosts supports seed limitation as one of the main barriers to forest regeneration in bracken-dominated areas (Lippok et al. 2013; Saavedra et al. 2014, 2015; Gallegos et al. 2015, 2016). In turn, the greater establishment of seedlings in both perch and roost treatments suggests that the bracken fern may not inhibit the seedling establishment of some tree species. To better understand the process of forest succession in bracken-dominated areas, it is necessary to evaluate other aspects, such as the functional traits of animal seed dispersers and their ability to disperse over long distances (Selwyn et al. 2023). The size of the remaining forest area and the landscape configuration, which could influence the functional traits of animal seed dispersers (Bovo et al. 2018), could also have an impact. In addition, it is necessary to evaluate the fate of establishing seedlings over a longer period than that evaluated in this study to determine if there are other filters (e.g. intra- and interspecific competition, resource limitation, seed predation, or herbivory) that delay the process of forest regeneration in these widely distributed degraded habitats.

In our study, we placed the perches and artificial bat roosts 50 m from the forest edge, which may be too close to the forest. However, in our study area, seed dispersal and seedling recruitment decrease at 20 m from the forest edge, and this pattern persists at least up to 80 m from the forest edge (Saavedra et al. 2015; Gallegos et al. 2016). However, other studies in the tropics have shown that seed dispersal decreases between 8 m (Cubiña & Aide 2001) and 30 m from the forest edge (Teegalapalli et al. 2010). Therefore, our results reflect how perches can increase seed rain and seedling establishment in near-forest areas, but further studies are needed to assess whether this pattern is maintained at greater distances. We were unable to determine the identity of seed dispersers and visitation rates. Future studies could use meta barcoding and point observations to identify the

seed disperser species and determine their visitation rates. In addition, our study was of short duration, which could influence the seedling composition determined, as some species take a longer time to germinate. It is also important to analyze the relationship between environmental variables such as precipitation, temperature, and seedling establishment to improve the design of future restoration programs in bracken-dominated areas. All these caveats raise new questions that can be clarified in future studies.

So far, some techniques, such as the mechanical removal of fronds (Levy-Tacher & Morón-Ríos 2023; Xavier et al. 2023), and nursery-seedling transplants (Xavier et al. 2023) helped to reduce the dominance of bracken in tropical ecosystems. However, these methods are expensive and could be accompanied by other tools, such as bird perches, that are cheaper and have the potential to attract seed dispersers, promote the arrival of hundreds of seeds, their seedling establishment and promote the forest regeneration process.

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## Supporting Information

The following information may be found in the online version of this article:

**Figure S1.** (a) Map of the study area located in the Municipality of Chulumani, Sud Yungas province, La Paz, Bolivia.

**Figure S2.** Experimental design showing the arrangements of (a) Perches, artificial bat roosts and controls in the forest edge (green) and bracken-dominated area (orange).

**Figure S3.** Details of the construction of the artificial bat roosts.

**Figure S4.** Seed density and species richness of bat-dispersed species per seed traps in bracken, at roosts and in forest.

**Figure S5.** Comparison of (a) density, (b) richness of animal-dispersed seeds, and (c) density, (d) richness of animal-dispersed seedlings between perches and artificial bat roosts.

**Figure S6.** Comparison of seed sizes from animal-dispersed seeds among treatments.

**Figure S7.** Seedling density and species richness of bat-dispersed species per recruitment plot in bracken, at roosts, and in forest.

**Table S1.** List of animal-dispersed seed species captured in seed traps.

**Table S2.** Model selection table ordered by the Akaike information criterion (AIC) for bird- and bat-dispersed seeds.

**Table S3.** Variables included in the best GLMM models for (a) bird- and (b) bat-dispersed seeds.

**Table S4.** Results from the generalized linear mixed-effects models (GLMM) comparing perches and artificial bat roosts.



**Table S5.** Results from a generalized linear mixed-effects models (GLMM) comparing seed size between treatments.

**Table S6.** List of seedling species registered in the recruitment plots.

**Table S7.** Model selection table ordered by the Akaike information criterion (AIC) for bird- and bat-dispersed seedlings.

**Table S8.** Variables included in the best GLMM models for (a) bird- and (b) bat-dispersed seedlings.

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