The role of animal-mediated seed dispersal in the forest regeneration of tropical areas dominated by bracken fern

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Chapter 1 Introduction

1.1 General Introduction

Tropical montane forests harbor a vast diversity (Myers, 1997). These forests provide various ecosystem services, including water regulation and purification, carbon storage and sequestration (Soh et al., 2019). Tropical montane forests are among the most diverse and richest ecosystems, due to their spatial and environmental gradients (Richter, 2008). However, like other tropical forests, they are under severe threat from deforestation caused by agricultural expansion, logging, and human-induced fires (Lewis et al., 2015; Phillips, 1997). Land use intensification can slow or arrest forest succession, either by reducing soil fertility due to deforestation or by promoting the dominance of grasses and ferns in deforested areas, which increases the risk of fires (Lamb et al., 2005).

Ferns of the genus *Pteridium*, commonly known as bracken, are among the most successful species in colonizing fire-disturbed areas (Alday et al., 2013). The dominance of bracken can persist for several years, and its presence is associated with slow forest regeneration (Hartig and Beck, 2003). The filters that plant species must overcome in bracken-dominated areas are not well understood. Some authors report that in these areas the establishment of plant species is hindered by the conditions created by the accumulation of litter and the dense fronds of bracken (Da Silva and Silva Matos, 2006; Ghorbani et al., 2006; Marrs et al., 2000). Other studies suggest that the primary factor limiting forest regeneration is the lack of animal-dispersed seeds in these deforested areas (Gallegos et al., 2016, 2024; López et al., 2024; Saavedra et al., 2015). Given the impact of bracken on forest succession and its widespread distribution in the tropics, it is important to study the main ecological processes involved in forest regeneration. The relationship between bracken-dominated areas and animal-mediated seed dispersal is particularly important to study, as this ecological interaction plays a key role in forest regeneration.

1.2 Forest regeneration in human-modified landscapes

Large extents of tropical forest are being deforested to create agricultural lands (Malhi et al., 2014). Once these lands are abandoned, forest regeneration processes can take place, eventually leading to the formation of secondary forests (Jakovac et al., 2021). The regeneration process varies across deforested areas, depending on biophysical conditions, landscape characteristics, and land use history (Jakovac et al., 2021). It is also the combination of processes in different spatio-temporal scales, ranging from local to regional scales (Arroyo-Rodríguez et al., 2017).

Climate, geomorphology, species extinction and migration, among others, are forces that influence forest regeneration at a regional scale (Arroyo-Rodríguez et al., 2017; Moran et al., 2000; Poorter et al., 2016). At landscape context, the forest remnants, the land-use history, and the matrix characteristics influence forest regeneration, and have consequences for local processes that affect the successional pathways (Arroyo-Rodríguez et al., 2017; Poorter et al., 2024, 2023). For example, in areas with intensive and extensive land use and low forest cover, forest regeneration depends mainly on local processes such as seed dispersal and seedling establishment (Herrera and García, 2010; Martínez-Ramos et al., 2016). Contrarily, in areas dominated by forest matrices, forest regeneration depends mainly on environmental factors such as soil characteristics and microclimate (Arroyo-Rodríguez et al., 2017; Jakovac et al., 2021). Since several tropical montane zones are comprised of few forest remnants embedded within an agricultural or deforested matrix (Beck et al., 2024; Schneider and Fernando, 2010; Velazco et al., 2024), fostering seed dispersal and seedling establishment of forest tree species in deforested areas is crucial for forest regeneration.

1.3 Animal seed dispersal in deforested habitats

In deforested areas, there are many factors that could impede forest recovery. One of the most important is the lack of seed dispersal (Holl, 1999; Wunderle, 1997). Seed dispersal is a fundamental process for plant population dynamics (Ruxton and Schaefer, 2012; Wenny, 2001). It could help to reduce mortality and competition related to the distance to parents (Clark and Clark, 1984), and it gives plants the opportunity to colonize new sites (Cain et al., 2000). Seeds can be dispersed by abiotic (i.e., wind) or biotic (i.e., animals) vectors (Nathan et al., 2008). In the humid tropics, the predominant form of seed dispersal is mediated by animals (Howe and Smallwood, 1982). In tropical humid forests, around 90% of woody plants produce fleshy fruits that are dispersed principally by birds and mammals (Howe and Smallwood, 1982). Birds are considered an important group of seed dispersers that share some characteristics with bats (Medellín and Gaona, 1999). Both can cover long distances and connect deforested areas with forest fragments, which is important for forest regeneration (Galindo-González et al., 2000; Ingle, 2003; Whittaker and Jones, 1994).

Fragmented landscapes are characterized by the presence of different habitats such as forest interior, forest edges and more disturbed open areas (Hardwick et al., 1997). These habitats usually harbor different animal communities and properties; for example, bird species richness, abundance and composition differ between forest interior and deforested areas (Maya-Elizarrarás and Schondube, 2015; Tchoumbou et al., 2020). At disturbed forest edges, birds that require specific habitat conditions and food resources may be lost (Jankowski et al., 2021; Menke et al., 2012), and generalist species gain in richness and abundance (Morante-

Filho et al., 2015). In addition, as a result of deforestation and forest fragmentation, large frugivores tend to disappear (Markl et al., 2012; Renjifo, 1999), while small frugivores and omnivores seem to better tolerate such disturbances (Gomes et al., 2008; O'Dea and Whittaker, 2007). Tropical forest disturbance could also generate differences in the trait composition of bird communities between forested and deforested areas (García-Morales et al., 2016; Newbold et al., 2013). For instance, bird species of disturbed habitats tend to be smaller and have a higher capacity to flight long distances than birds of less disturbed habitats (Camargo et al., 2020; Falconí-López et al., 2024; Messina et al., 2021). In birds, traits such as body mass, gape width, and wing morphology are linked to the quantity and size of seeds they can disperse, as well as the distance they can flight (Bovo et al., 2018; Campagnoli et al., 2024). On the other hand, the abundance of frugivorous bats has been shown to increase in fragmented habitats (Cleary et al., 2016), while the trait composition of bat communities can be stable (Díaz-B et al., 2023; Farneda et al., 2020). It is likely that small frugivorous and omnivorous birds, as well as frugivorous bats, are particularly important for seed dispersal and forest regeneration in disturbed forest habitats (Carlo and Morales, 2016; Muscarella and Fleming, 2007), but their joint effects on tropical forest regeneration remain poorly understood.

Deforestation not only affects the diversity and traits of animal seed dispersers, but it can also have an effect on the interaction between plants and their animal seed dispersers (González-Varo et al., 2023). Some studies showed that disturbed habitats had fewer pairwise bird-plant interactions (Menezes Pinto et al., 2021), but other studies found the opposite pattern (Menke et al., 2012; Saavedra et al., 2014). In deforested areas, little is known about the communities of seed-dispersing animals that move between deforested and forested areas, the plant species they disperse, and their impact on forest regeneration.

1.4 Dispersal and establishment limitation

The failure of seeds to reach sites for germination is related to a source limitation (insufficient seed number), and/or dispersal limitation (non-uniform or limited dispersal) (Beckman and Rogers, 2013). In deforested areas, a lower abundance and different composition of seed-dispersing animals could contribute to dispersal limitation (Duncan and Chapman, 2002; Gallegos et al., 2024). The lower abundance of seed-dispersing animals could be related to a lack of perches, limited food availability, and insufficient shelters (Athie and Dias, 2016; Kelm et al., 2008). Additionally, deforestation limits the movement of certain animals, which in turn reduces seed dispersal to open areas (McConkey and O'Farrill, 2016).

In addition to dispersal limitation, deforested areas may also face establishment limitation. This occurs when there is a lack of suitable sites for seedling establishment (Muller-Landau et al., 2002). Some authors suggest that the shade and soil characteristics in bracken-dominated areas could reduce seedling establishment and thus prevent forest regeneration (Levy-Tacher et al., 2015; Marrs et al., 2000; Paz et al., 2022). In contrast, other studies show that the microclimatic and soil humidity conditions generated by bracken can favor the establishment of certain species, especially shade-tolerant species (Gallegos et al., 2015; López et al., 2024; Ssali et al., 2018). These differing results highlight the complex role of bracken, whose presence can either hinder or support forest regeneration, depending on the species involved. For example, bracken may be detrimental to species that require high light for germination and establishment, such as pioneer herbs (López et al., 2024). Conversely, bracken can benefit the establishment of shade-tolerant species, including non-pioneer trees and shrubs (Gallegos et al., 2015; López et al., 2024). Gaining a better understanding of which processes—whether dispersal limitation or establishment limitation—drive slow forest regeneration in bracken-dominated areas can help to design strategies to restore these widely distributed deforested areas.

1.5 Restoration techniques

In order to address the scarcity of animal-dispersed seeds in deforested areas, bird perches and/or artificial bat roosts have been installed in some studies (Heelemann et al., 2012; Holl, 1998; Kelm et al., 2008; Shiels and Walker, 2003; Vogel et al., 2018). These techniques allow to increase the number of animal-dispersed seeds in the seed rain of deforested/open areas (Guidetti et al., 2016; Kelm et al., 2008). Bird perches provide structural complexity to the landscape, which increases the abundance and species richness of bird communities (Horgan et al., 2017; Vogel et al., 2018). Since most birds need to perch to defecate and disperse seeds, the presence of perches has a high potential to increase bird-mediated seed dispersal (Alencar and Guilherme, 2020; La Mantia et al., 2019; Mcclanahan and Wolfe, 1993). The installation of artificial bat roost provides shelter to frugivorous bats, and increases the seed rain around the roosts (Kelm et al., 2008). However, the increase of animal-dispersed seeds is not always accompanied with an increase in the establishment of seedlings (de Almeida et al., 2016; Reid et al., 2013). Other factors, such as light, soil nutrients and humidity, competition with existing vegetation, influence the effectiveness of these restoration techniques (Florentine and Westbrooke, 2004; Holl, 1998). In bracken-dominated areas, the installation of bird perches increased both the density and species richness of non-pioneer and pioneer seeds in the seed rain (Saavedra et al., 2015). However, the effect of this technique on seedling establishment was not tested, nor was the impact of artificial bat roosts on seed rain and seedling establishment. Furthermore, the evaluation of the effectiveness of different restoration techniques on reducing dispersal and establishment limitations is urgently needed.

1.6 Thesis aim

The main aim of this thesis is to analyze the role of animal seed dispersers in forest regeneration in bracken-dominated areas in tropical montane forests. For this purpose, I present an analysis of bird and bat traits related to seed dispersal, animal-plant interactions, their effect on seed rain and seedling establishment, how seed dispersal and seedling establishment can be enhanced by the inclusion of animal attractants, and what effects these attractants have on dispersal and establishment limitations in forested and deforested areas. I addressed the following questions:

- How do the composition of functional traits of birds and bats, the abundance and richness of animal-plant interactions, and the characteristics related to the life strategy (pioneer or non-pioneer) of dispersed seeds change between forests and bracken-dominated areas? I expected that birds recorded in bracken-dominated areas would have a lower body mass, smaller gape width and morphological characteristics in the wings that allow them to flight larger distances than birds captured in the forest (Camargo et al., 2020; Falconí-López et al., 2024; Messina et al., 2021), whereas I did not expect differences in the trait composition of bats between both habitats (Farneda et al., 2020). Regarding seed-dispersal interactions, I expected to find more seed-dispersal interactions in bracken-dominated areas due to their high bird species richness and higher abundance compared to forests, and the opposite pattern for bats due to their high abundance in forest compared to bracken-dominated areas (Gallegos et al., 2024). Regarding life strategy of dispersed seeds, I expected to find more seeds of pioneer species in the feces of animals captured in bracken-dominated areas than in animals captured in forests because of the expected changes in trait composition, particularly in birds. Birds with small gape width usually disperse small seeds (Bovo et al., 2018; Wheelwright, 1985), and small seeds are characteristic of pioneer species (Valio and Scarpa, 2001).
- What are the effects of installing bird perches and artificial bat roosts on the density and species richness of animal-dispersed seeds and seedlings of tree and non-tree species in bracken-dominated areas? Given the positive effects of both techniques on the seed rain of animal-dispersed species (Guidetti et al., 2016; Kelm et al., 2008; Shiels and Walker, 2003), and the favorable micro-environmental conditions provided by bracken for several animal-dispersed species (Gallegos et al., 2015; Ssali et al., 2018), I expected that both techniques will increase seed rain and seedling establishment in terms of density and species richness.
- What influence do bird perches and artificial bat roosts have on the extent of dispersal and establishment limitation of pioneer and non-pioneer species, as well as species

with small and large seeds in bracken-dominated areas? I expected that both techniques would reduce these limitations, as bird perches and artificial bat roosts increase seed dispersal (Abreu et al., 2020; Alencar and Guilherme, 2020; Guidetti et al., 2016; Kelm et al., 2008) and the establishment of seedlings of animal-dispersed plants is promoted by the presence of bracken (Gallegos et al., 2015; Ssali et al., 2018). Regarding life strategy, in bracken-dominated areas, seeds of non-pioneer species are scarce (Saavedra et al., 2015); therefore, I expected dispersal limitation for non-pioneer species to be higher than for pioneer species. However, the presence of bird perches would alleviate the limitation of non-pioneer plants (de Almeida et al., 2016; Pausas et al., 2006). In contrast, I 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, I 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). Finally, I expected that small seeds to 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 primarily disperse small seeds (Muscarella and Fleming, 2007). In terms of establishment limitation, I expected that large-seeded species would 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).

Chapter 2 Materials and methods

2.1 Study area

The study was conducted in a tropical montane humid forest in the Bolivian Andes between 1,900 and 2,350 m a.s.l. near the town of Chulumani (16º24’37” S, 67º31’37” W), in the Sud Yungas province from La Paz. The topographical heterogeneity and elevational gradient in this ecosystem generate high plant diversity (Lippok et al., 2014). The mean annual temperature is 20.5 °C, and mean annual precipitation is 1390 mm (Molina-Carpio et al., 2019). In this region, montane forests have been deforested due to logging, human induced fires and the extension of coca (*Erythroxylum coca*) plantations (Killeen et al., 2005). The landscape is composed by two large forest fragments of about 1500 and 3000 ha, the remnant forests are highly fragmented, and are restricted to the top of the mountains. Forest fragments are surrounded by deforested areas dominated mostly by bracken fern (*Pteridium esculentum* subsp. *arachnoideum*) and shrubs of Asteraceae, Ericaceae and Melastomataceae (Lippok et al., 2013a). The majority of plant species in bracken-dominated areas are dispersed by wind, however there are species such as *Myrsine coriacea* (Primulaceae), *Gaultheria erecta* (Ericaceae) and *Leandra carassana* (Melastomataceae) that are dispersed by birds and are common in these deforested habitats (Lippok et al., 2013a). There are also some species of Solanaceae and Piperaceae that are dispersed by bats in bracken-dominated areas, although they are scarce (Lippok et al., 2014; López et al., 2024). The most common species at the forest edge of the study area are *Hedyosmum racemosum* (Chloranthaceae), *Clusia elongata* (Clusiaceae) and *Hieronyma fendlerii* (Phyllanthaceae), among those dispersed by birds, and *Piper pilirameum*, *P. trigonastrifolium* and *Vismia glaziovii* among those dispersed by bats(Lippok et al., 2014). Birds and bats are the main seed dispersers for woody vegetation (Lippok et al., 2014, 2013a), although other terrestrial mammals such as *Mazama americana* and *Dasyprocta variegata* can also disperse seeds (Rumiz, 2010).

2.2 Study design

2.2.1 Bird and bat functional traits and seed sampling

I conducted the study at eight sites located at the borders of remnant forests separated by at least 1 km (Figure 1). At each site, I placed eight mist nets (9 x 2.5 m) at 0.5 m from the ground. Four mist nets were set inside the forest at 20 m from the forest margin (hereafter forest), and four mist nets were set in the bracken-dominated area (hereafter bracken) at 20 m from the forest margin. From March 2020 to June 2021, I visited each site four times and captured birds and bats. Mist nets were placed for 2-3 days on each visit, from 0630 to 1830 h to capture birds, and from 1830 to 2300 to capture bats. Mist nets were closed when it rained. Total sampling effort was 4861 net-hours for birds, and 2576 net-hours for bats.

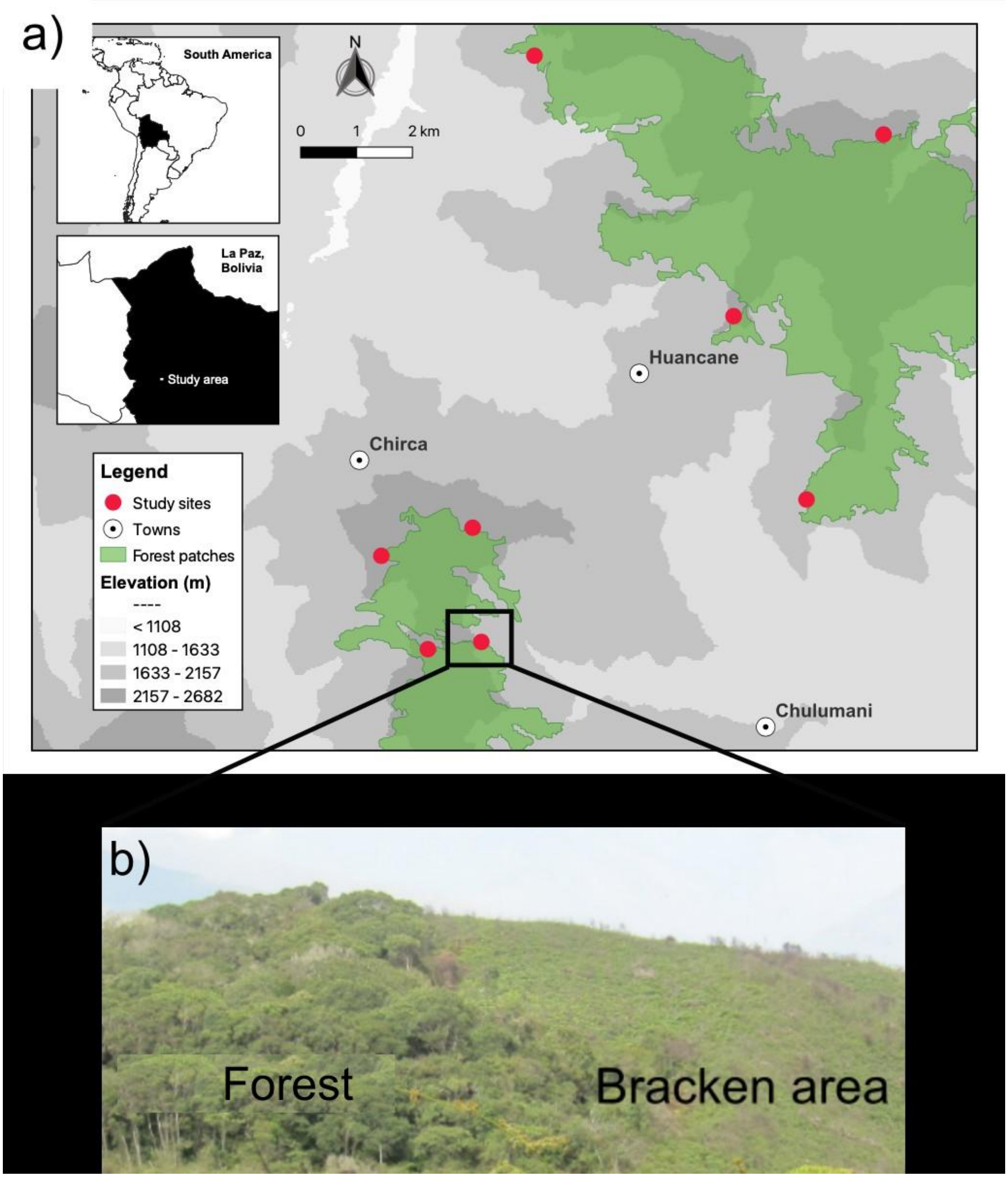


Figure 1. a) Map of the study area located in the Municipality of Chulumani, Sud Yungas province, La Paz, Bolivia. The eight sites are located on the borders of forest remnants. b) Representative image of the eight study sites in which a clear difference in structure is observed between the forest edge and the bracken-dominated area.

Captured birds and bats were placed in cloth bags for 20-30 minutes to collect feces and regurgitates. Captured animals were weighed, measured, marked with color rings, identified to the species level and released. Mariana Villegas contributed to the identification of bird species, while Luis F. Aguirre assisted in the identification of bat species. For each bird species, I measured the following traits: body mass, hand-wing index and gape width, while I could only measure body mass for bats. These traits were chosen because body mass is related to the amount and size of consumed fruits and seeds, as well as the distance of seed dispersal (Wotton and Kelly, 2012). Gape width determines whether a bird species can consume large, medium or small-sized seeds (Wheelwright, 1985). In addition, I recorded the degree of frugivory of bats from the EltonTraits 1.0 database (Wilman et al., 2014). Hand-wind index (HWI) was calculated using the equation HWI = 100 x (D_K/L_W), where D_K is Kipp's distance (the distance between the tip of the first secondary feather and the tip of the longest primary feather) and L_W is wing length. HWI is related to the flight efficiency; high values are related to species that could perform long-distance flights, whereas small values are related to more sedentary species with lower dispersal abilities (Falconí-López et al., 2024; Sheard et al., 2020). Birds and bats were classified into feeding guilds according to Aguirre (2007), Aguirre et al. (2009), Billerman et al. (2022), and Herzog et al. (2016). Because I found seeds in the feces and regurgitates of omnivorous and frugivorous birds and bats (hereafter referred to as birds and bats), functional trait analysis included both guilds.

I collected the seeds carried by birds and bats from the cloth bags. Undamaged seeds were extracted from all droppings and regurgitates, grouped into morphotypes, counted and identified under a dissecting microscope to the lowest possible taxonomical level by comparing them with a reference collection from the study area deposited at the Santiago de Chirca Biological Station. Mariana Villegas assisted in grouping the seeds by their morphotypes. Overall, 321 seed samples (droppings and/or regurgitates) were collected: 267 seeds from birds and 54 from bats. Each of the identified plant species was classified as pioneer or non-pioneer species according to previous studies in the study site (Gallegos et al., 2016; Lippok et al., 2014, 2013a; López et al., 2024), expert knowledge, and information at the Herbario Nacional de Bolivia (LPB). These data were used to calculate the abundance and species richness of plants dispersed by birds and bats in forest and bracken.

2.2.2 Bird perches and artificial bat roosts

To test the effect of bird perches and artificial bat roosts on seed rain and seedling establishment I implemented four treatments: perch, artificial bat roosts, bracken and forest (Figure 2a) between December 2019 and February 2020 in each study site (Figure 1). For perch treatment, three perches of ~5 m height were installed in bracken, consisting of stakes with branches of *Erythrina falcata* and *Ficus* spp. (Zahawi, 2008). This type of perch was used, 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 margin in bracken, with a distance of 10 m between them (Figure 2a). In the roost treatment, an artificial bat roost (hereafter roost) was placed 50 m from the forest margin in bracken. The roosts were designed following Kelm et al. (2008) with modifications for a lighter design (see Figure S1 for design details). There were two controls at each site, one in the bracken and one at the forest. Both control treatments were located at a distance of 50 m from the forest edge, with no perches or roosts installed.

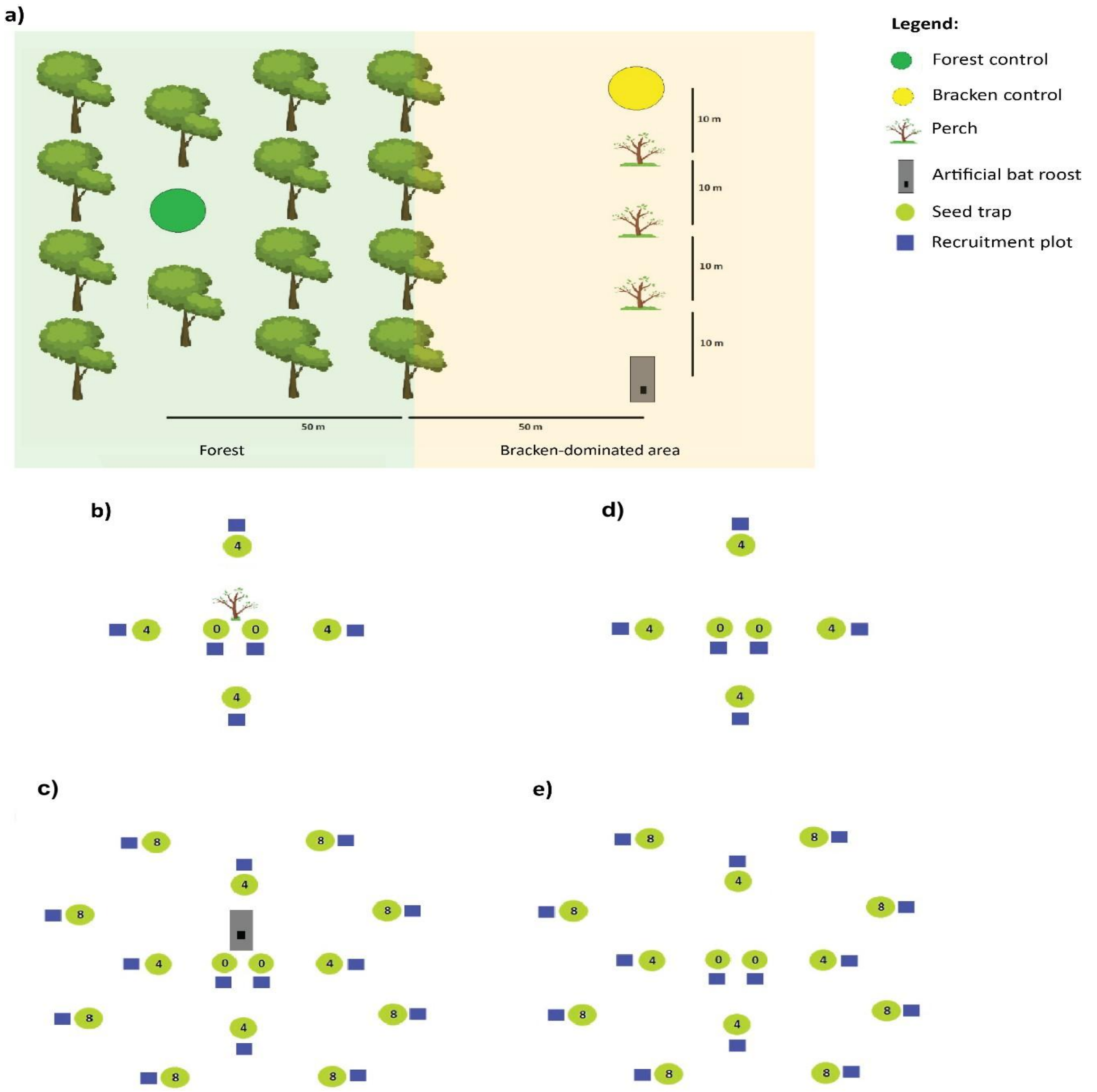


Figure 2. Experimental design showing the arrangements of a) Perch, roost and controls in the forest (green) and bracken area (orange). b-e) Arrangement of seed traps and recruitment plots at b) perch, c) roost, d) control for perch in forests and bracken areas, and e) control for roosts in forest and bracken areas. Numbers (0, 4 and 8) denote the distance in meters from perch or roost. Next to each seed trap there was a 1x1 m recruitment plot. The controls in the bracken and forest had the same arrangement of seed traps and recruitment plots without perch or roost. The same arrangement was replicated at eight study sites.

2.2.2.1 Seed rain and seedling establishment

Under each perch, two seed traps were placed beneath the perch (distance 0m), and four seed traps, arranged in a cross, were placed 4 m away from each perch (distance 4m) (Figure 2b). The doubled number of seed traps with increasing distance helped to maintain a constant sampling effort and allowed to detect clumping, following the design for point sources in concentric annuli (Bullock et al., 2006).

Two seed traps were placed near the roost entrance (distance 0m), four seed traps were placed at 4 m from the roost (distance 4m), and eight seed traps were placed at 8 m from the roost (distance 8m, Figure 2c). Since bats defecate seeds in flight (Kunz et al., 2011), I increased the distance to 8 m to cover more area and capture more seeds (Bullock et al., 2006).

For each control treatment (bracken and forest), 14 seed traps were placed, but without perches and roosts (Figure 2d-e). Each seed trap consisted in 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 the study site seed predation is low (Gallegos et al., 2014) and I 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 (Castaño et al., 2018; Loayza et al., 2006; Saavedra et al., 2014; Snow, 1981). I 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, plots of 1 x 1 m were installed 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, all seedlings above 2 cm in each plot were registered. 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. Cecilia L. Lopez and Silvia C. Gallegos identified the seedlings. Seeds and seedlings were then classified according to their life form as tree and non-tree species (including herbs and shrubs < 2 m height). I made this classification because bracken-dominated areas have a dominance of non-tree species, while tree species are rare (Lippok et al., 2013a; Ribeiro et al., 2013), but are very important for the forest regeneration process (Holl, 2012).

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

2.3 Data analysis

For most of the analysis, I used generalized linear mixed-effects models (GLMMs). However, the models vary in their random effect, and in their distribution of errors that depend on the characteristics of response variables. All GLMMs were performed using the *glmmTMB* package (Brooks et al., 2017). To assess significant differences among treatments, Tukey *post hoc* tests were performed using the *emmeans* package (Russell et al., 2024). For each model, the significance of the fixed factors was determined by Likelihood Ratio Tests (LRT) between models with and without the term of interest. I 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). Overdispersion in model residuals were tested with *DHARMA* package (F. Hartig, 2024). All statistical analyses were conducted in R 4.2.2 (R Core Team, 2022).

2.3.1 Bird and bat functional traits, seed-dispersal interactions and functions

I analyzed differences of bird and bat functional trait composition between habitats testing the community-weighted means (CWM) of gape width, body mass and HWI for birds and body mass and frugivory degree for bats. Community-weighted mean of each trait was calculated as the average of trait values, weighted by the relative abundance of captured bird and bat species in each site and habitat type. Habitat type (forest and bracken) was included as the independent fixed effect, and site was the random effect. The models used a Gaussian distribution of errors, except for bat's frugivory degree that used a Gamma distribution of errors.

I compared the seed-dispersal interactions in separate models for bird and bats, taking interaction richness (number of unique interactions) and interaction abundance (interaction frequency) as the response variables, habitat type (forest and bracken) as the independent fixed effect, and site as the random effect. The models used a Gaussian distribution of errors for interaction richness and Poisson distribution of errors for interaction abundance. The detection of all the species/interactions in natural environments is difficult (Chiu et al., 2023; Jordano, 2016). The observed interactions depend on the sample completeness which difficult the comparison of datasets across different sites (Vizentin-Bugoni et al., 2016). To overcome this problem, I estimated the interaction richness with the iNEXT.link package (Chiu et al., 2023). I used the non-asymptotic coverage-based method, which relies on coverage-based rarefaction and extrapolation (Chiu et al., 2023). This method was applied at each site, within each habitat, and for each animal group. Resulting in a total of 16 estimation of interaction richness for birds and 16 for bats.

Finally, to analyze the function provided by seed dispersers, I compared the abundance and species richness of pioneer and non-pioneer species found in feces and regurgitates of birds and bats captured in bracken and forest. The abundance and species richness of pioneer and non-pioneer species were calculated for each study site. In separate models I tested the abundance of seeds, and seed species richness as the response variables for birds and for bats. For all four models, life strategy (pioneer or non-pioneer), habitat (forest and bracken) and their interaction were the independent fixed effects. Site was the random effect, and the four models used a Poisson distribution of errors. I assessed the sample completeness of animal-plant interaction using method "abundance" with the *iNEXT* package (Hsieh et al., 2016). Matthias Schleuning supervised the statistical analysis of bird and bat functional traits and seed-dispersal interactions.

2.3.2 Bird perches and artificial bat roosts

2.3.2.1 The effect of animal attractants on seed rain and seedling establishment

In the GLMMs I used the density and species richness of bird- and bat-dispersed seeds and seedlings of tree and non-tree species as the response variables, in separate models, giving a total of 16 models. In each model I included treatment (perch, roosts, bracken and forest), distance (0m and 4m for birds; and 0m, 4m, and 8m for bats), and their interaction, as the independent fixed effects, and site and Perch or Roost id nested within the site as the random effects. I then performed model selection for each full model to select the most important variables, using the package *MuMIn* (Barton, 2023) and used the Akaike information criterion corrected for small sample size (AICc) to select the best models (ΔAIC<2) (Burnham and Anderson, 2002). To compare perch and roost, I included 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. I 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, I used a LMM 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 random effect.

2.3.2.2 The effect of animal attractants on dispersal and establishment limitation

To assess the effect of perches and roosts in dispersal and establishment limitation all analyses were limited to plant species registered in both seed traps and seedling recruitment plots, resulting in a total of 37 plant species. Dispersal and establishment limitations were calculated following Muller-Landau et al. (2002) as follows:

Dispersal limitation = 1 – a/n

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).

Indices of dispersal and establishment limitation were the 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, I used dispersal and establishment limitation as response variables, treatment, life strategy (pioneer and non-pioneer) and their interaction as independent fixed effects, and site as a random effect. To assess the differences in the limitation indices between small and large seeds, I used 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, and in total, six models were performed.

Isabell Hensen and Silvia C. Gallegos obtaining the funding, developed the ideas and design the studies that form the basis of this thesis.

Chapter 3 Results

3.1 Functional trait composition, seed-dispersal interactions and functions

3.1.1 Functional traits of birds and bats

During 15 months of sampling, 31 bird species were captured, 27 species (99 individuals) in bracken and 13 species (65 individuals) in forest (Table S1). For bats, 12 species were captured, eight in bracken (23 individuals) and eight in forest (34 individuals) (Table S1). In bracken, the most common bird species were *Elaenia albiceps* and *Mionectes striaticollis*; 23 individuals of both species were recorded. The most common bat species in bracken were *Sturnira oporaphilum* and *Carollia perspicillata*, of which nine and four individuals were recorded, respectively. In forest, *M. striaticollis* and *Chiroxiphia boliviana* were the most abundant bird species, of which 23 and 17 individuals were recorded, respectively. Among the bats, *Carollia perspicillata* and *Carollia brevicauda* were the most common species with 14 and 11 records, respectively.

I found no differences in body mass ($X^2 = 0.83$, $p = 0.36$) and gape width ($X^2 = 0.01$, $p = 0.91$) of birds between bracken and forest (Figure 3a-b, Table S2). The hand-wing index (HWI) was significantly higher in bracken compared to forest ($X^2 = 18.91$, $p < 0.001$, Figure 3c, Table S2). For bats, I found no differences in body mass ($X^2 = 0.77$, $p = 0.38$) and frugivory degree ($X^2 = 0.31$, $p = 0.38$) between the two habitat types (Figure 3d-e, Table S2). The largest bird species such as *Aulacorynchus coeruleicinctis* (~208 g) and *Pyrrhura molinae* (~ 78 g) were only captured in bracken. At forest, *Turdus amaurochalinus* (~ 58 g) and *Pipreola frontalis* (~ 48 g) were the largest bird species. Among the bats, *Sturnira tildae* (~20 g) and *S. oporaphilium* (~17 g) were the largest species in bracken and at forest, respectively.

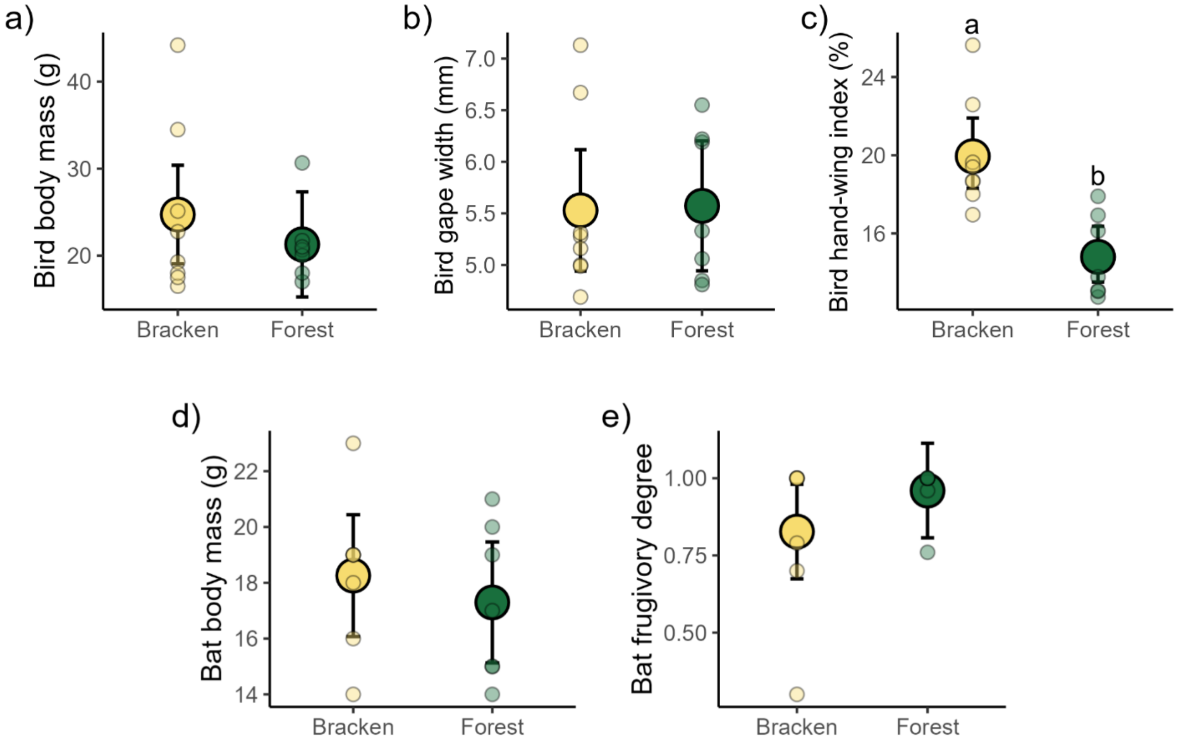


Figure 3. Comparison of community-weighted means of a) bird body mass, b) bird gape width and c) bird hand-wing index between bracken and forest habitats of 31 bird species. Comparison of community-weighted means of d) bat body mass and e) bat frugivory degree between bracken and forest habitats of 12 bat species. Different letters indicate significant differences at level 0.05 based on *post hoc* Tukey comparison among habitats. Large circles with error bars denote the mean values ± 95% CI estimated by GLMMs, small circles denote the observed values at the eight sites per habitat type.

3.1.2 Seed-dispersal interactions

After 7,437 net-hours of sampling effort for birds and bats, I registered a total of 124 interactions between 31 species of seed dispersers (25 birds, 6 bats) and 39 plant species. Of these, 69 interactions were recorded in bracken and 55 at forest. The sampling completeness was 89 % in bracken and 91 % at forest (Figure S2). For birds I found that in bracken the interaction richness and interaction abundance were 2.50 and 2.23 times higher, respectively, compared to forest (X^2 = 7.02, p = 0.008 interaction richness, X^2 = 11.57, p < 0.001 interaction abundance, Figure 4a-b, table S3). For bats I did not find differences for interaction richness between bracken and forest (X^2 = 3.47, p = 0.07, Figure 4c, table S3). The abundance of interactions was 2.7 times higher in bracken than in forest (X^2 = 7.19, p = 0.007, Figure 4d, Table S3).

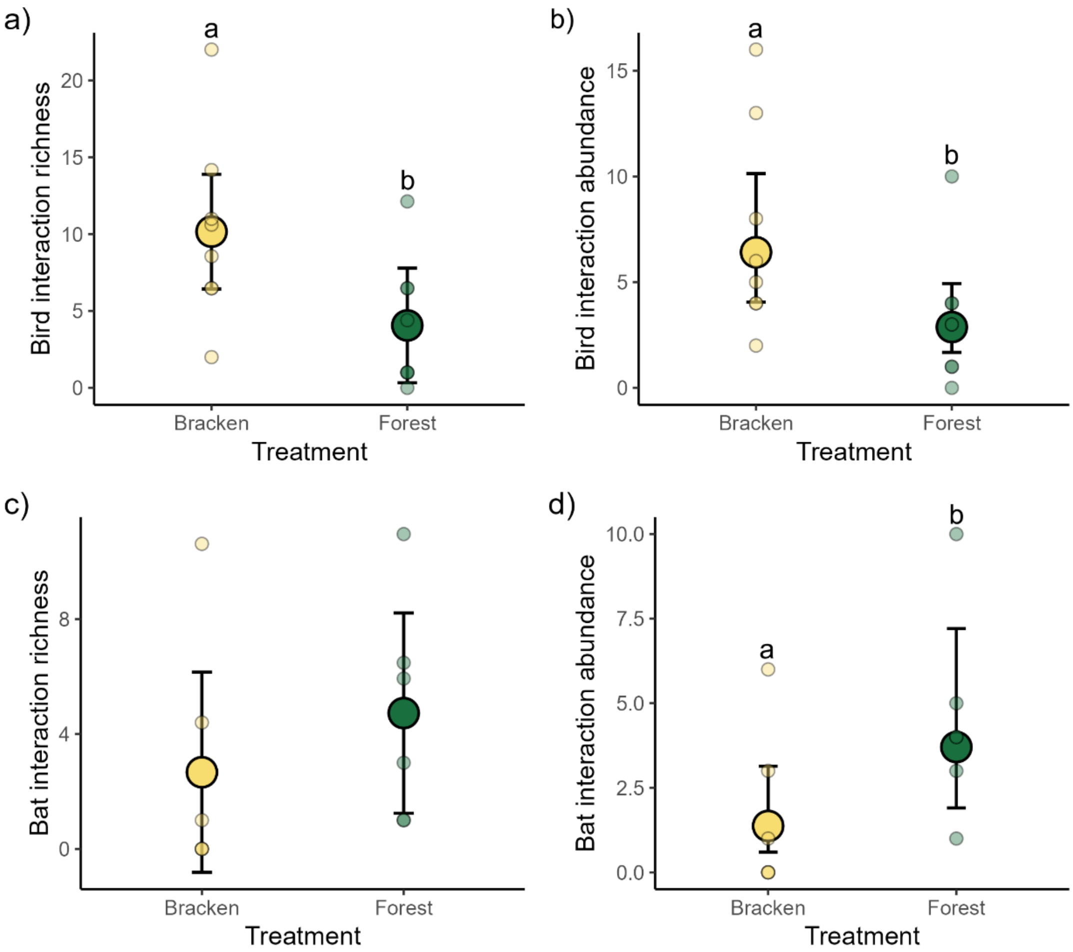


Figure 4. Difference in the a) interaction richness and b) abundance of bird and c) interaction richness and d) abundance of bats between bracken and forest habitats. Different letters indicate significant differences at level 0.05 based on *post hoc* Tukey comparison among habitats. Large circles with error bars denote the mean values ± 95% CI estimated by GLMMs, small circles denote the observed values at the eight sites per habitat type.

3.1.3 Life strategies of animal-dispersed plant species

I found that the abundance and species richness of bird-dispersed pioneer seeds in bracken were 2.85 and 2.15 times higher, respectively, compared to forest (X^2 = 9.13, p < 0.01, Figure 5a-b, Table S4). In bracken the abundance of bird-dispersed pioneer species was 9.54 times higher than the abundance of non-pioneer species in the same treatment (X^2 = 14.01, p < 0.001, Figure 3A, Table S4). Abundance of bat-dispersed pioneer seeds in bracken was 1.41 times higher compared to forest (X^2 = 4.11, p = 0.04, Figure 3A, Table S4), and 1.46 times higher compared to non-pioneer seeds in forest (X^2 = 4.01, p = 0.04, Figure 3A, Table S4). I did not find differences in bat-dispersed richness between habitats and life strategy categories (Figure 3B, Table S4). The most abundant pioneer species in feces were *Gaultheria erecta* (bird-dispersed), *Piper elongatum* (bird and bat-dispersed) and *Gaultheria reticulata* (bird-dispersed) (Table S5).

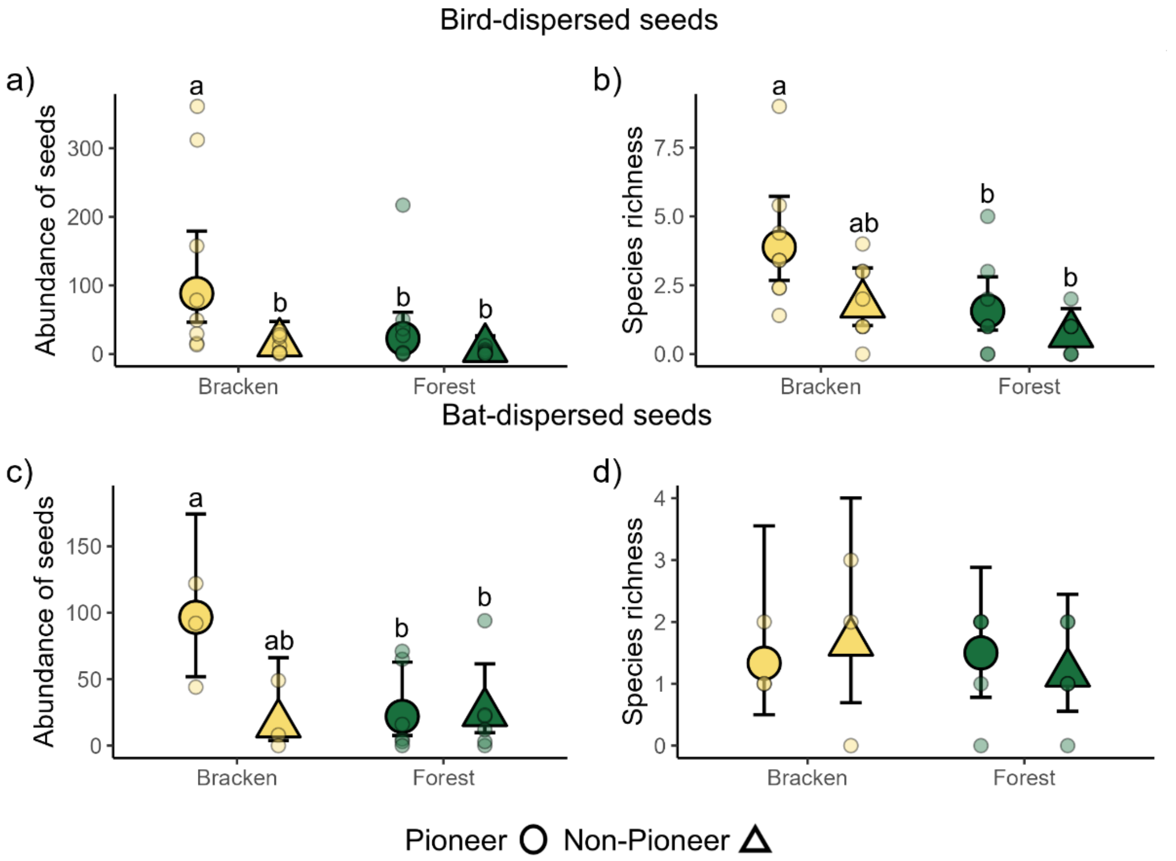


Figure 5. Differences in a) abundance and b) species richness of seeds found in birds and c) abundance and d) species richness of seeds found in bats captured in bracken and forest habitats. Different letters indicate significant differences at level 0.05 based on *post hoc* Tukey multiple comparison among habitats and life strategy. Large circles (Pioneer) and triangles (non-pioneer) with error bars denote means ± 95% CI estimated by the GLMMs, small circles denote the observed values at each of the eight study sites.

3.2 Bird perches and artificial bat roosts

3.2.1 The effect of animal attractants on seed rain

After 15 months, I collected a total of 22,997 animal-dispersed seeds from 70 morphospecies (hereafter referred to as species, Table S6) in the 480 installed seed traps. I collected 13,202 (57.4%) seeds from tree species from *Cecropia*, *Ficus* and *Myrsine,* among others, and 9,795 (42.6%) seeds from non-tree species, such as *Gaultheria erecta, Miconia* spp. and *Piper* spp. I 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 the treatment, distance and their interaction (Table S7). Seed density and richness of bird-dispersed seeds from tree species were 201.7 and 22.1 times higher under perch (distance 0 m), respectively, and 190.3 and 54.4 times higher in the forest compared to bracken ($X^2 = 43.48$, $p < 0.001$ tree seed density, $X^2 = 60.74$, $p < 0.001$ tree seed richness, Figure 6a-b, Table S8). Seed density of non-tree species under perch (distance 0 m) was significantly and 4.1 times higher than in the forest (Figure 6c). Notably, seed density and richness of non-tree species were 29.8 and 4.8 times higher, respectively, under perch than in bracken (X^2 = 34.36, p < 0.001 non-tree seed density, X^2 = 37.94, p < 0.001 non-tree seed richness, Figure 6c-d), and 87 and 17.4 times higher, respectively, at 4 m from perch than in bracken.

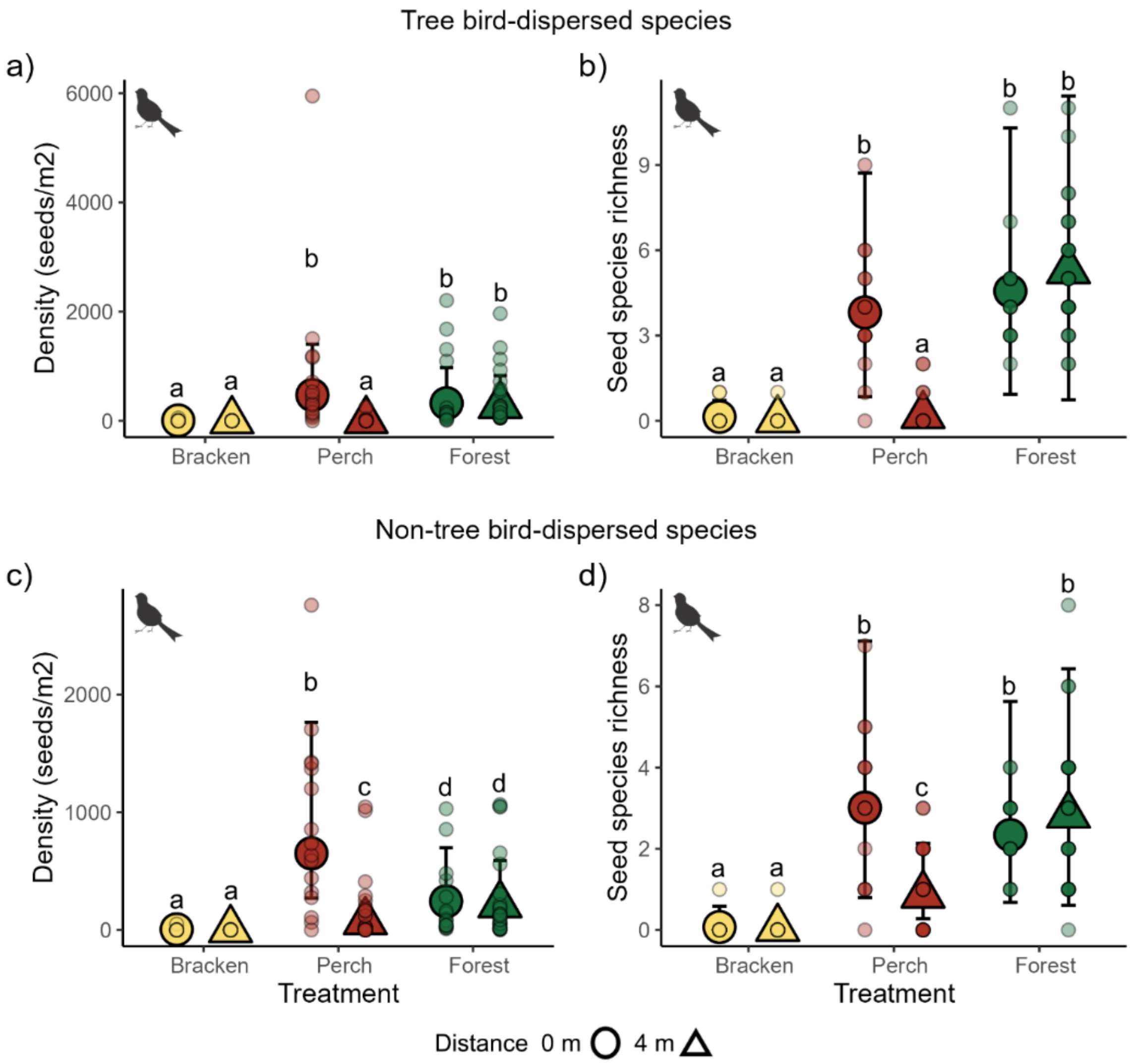


Figure 6. Seed density and seed species richness of bird-dispersed species per seed trap in bracken, perch and in the forest. a) seed density and b) species richness of tree species, and c) seed density and d) species richness of non-tree species. The colors represent the different treatments, and the symbols represent the distance category of the seed traps: circle = under the perch (distance 0 m), triangle= 4m 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.

The best model for seed density and species richness of bat-dispersed species included only the treatment (Table S7, Figure S3), while they did not change with distance. Seed density and richness of tree species around the roost were 16.1 and 8.3 times higher, respectively, compared to bracken ($X^2 = 114.91$, $p < 0.001$ tree seed density, $X^2 = 173.71$, $p < 0.001$ tree seed richness, Figure 7a-d, Table S8). Seed density and richness of non-tree species around the roost were 222.6 and 9.5 times higher, respectively, compared to bracken ($X^2 = 45.93$, $p < 0.001$ non-tree seed density, $X^2 = 45.99$, $p < 0.001$ non-tree seed richness, Figure 7a-d, Table S8). Seed density and species richness were 12.5 and 5.1 times higher, respectively in perch than in roost ($X^2 = 66.01$, $p < 0.001$ seed density, $X^2 = 54.95$, $p < 0.001$ seed richness, Figure S4, Table S9). The animal-dispersed seeds found in perch, roost and forest were significantly larger than seeds found in bracken ($X^2 = 34.03$, $p < 0.001$, Figure S5, Table S10).

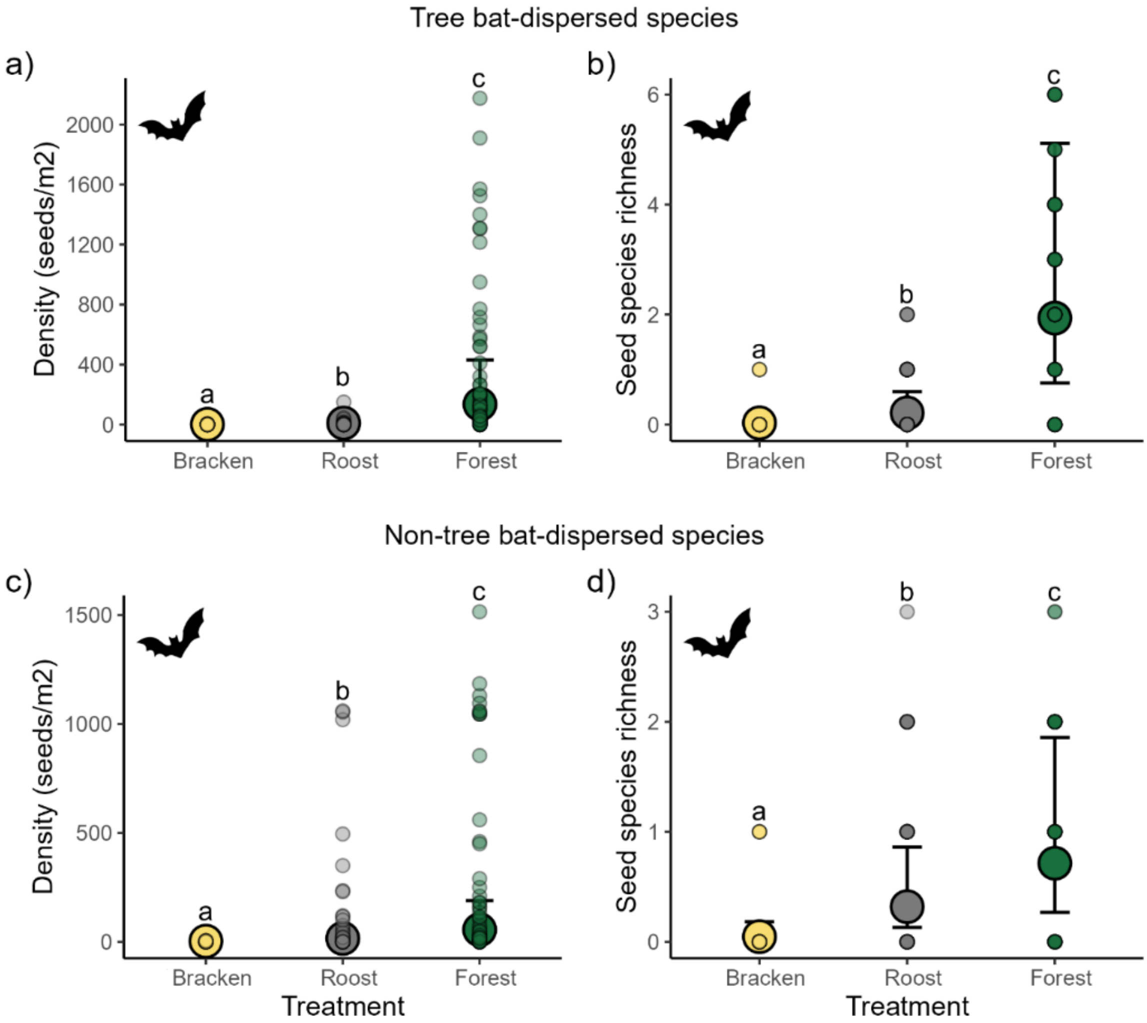


Figure 7. Seed density and species richness of bat-dispersed species per seed traps in bracken, at roosts and in forest. a) density and b) species richness of non-tree seeds, c) density and d) species richness of tree seeds. The colors represent the different treatments. Different letters indicate significant differences at level 0.05 based on *post hoc* Tukey among treatments. Large circles with error bars denote means ± 95% CI estimated by the GLMMs of seed density (figures a and c) and species richness (figures b and d), small circles denote observed values.

3.2.2 The effect of animal attractants on seedling establishment

After 15 months, I recorded a total of 6,162 animal-dispersed seedlings from 160 species (Table S11), of which 2,959 (48.0%) corresponded to tree species and 3,203 (52.0%) to non-tree species. I recorded 5,654 (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 the treatment and distance as well as the interaction only for tree species (Table S12). Seedling density and richness of tree and non-tree species were significantly higher in perch (at 0 and 4m) than in bracken ($X^2 = 89.65$, $p < 0.001$ tree seed density, $X^2 = 69.31$, $p < 0.001$ tree seed richness, $X^2 = 103.86$, $p < 0.001$ non-tree seed density, $X^2 = 79.81$, $p < 0.001$ non-tree seed richness, Figure 8a-d, Table S13). Tree density and richness under perch were 16.2 and 8.3 times higher, respectively, and non-tree density and richness were 3.3 and 2.2 times higher, respectively, than in bracken. Seedling density and richness of tree species were higher under perch than at 4 m from perch, while density and richness of non-tree species were similar under perch than at 4 m from perch ($X^2 = 36.18$, $p < 0.001$ tree seed density, $X^2 = 19.71$, $p < 0.001$ tree seed richness, $X^2 = 3.13$, $p = 0.07$ non-tree seed density, $X^2 = 2.12$, $p = 0.14$ non-tree seed richness, Figure 8a-d). Seedling density of tree species and density and richness of non-tree species were significantly higher under perch (distance 0 m) than in forests (Figure 8a-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, under perch than in forest.

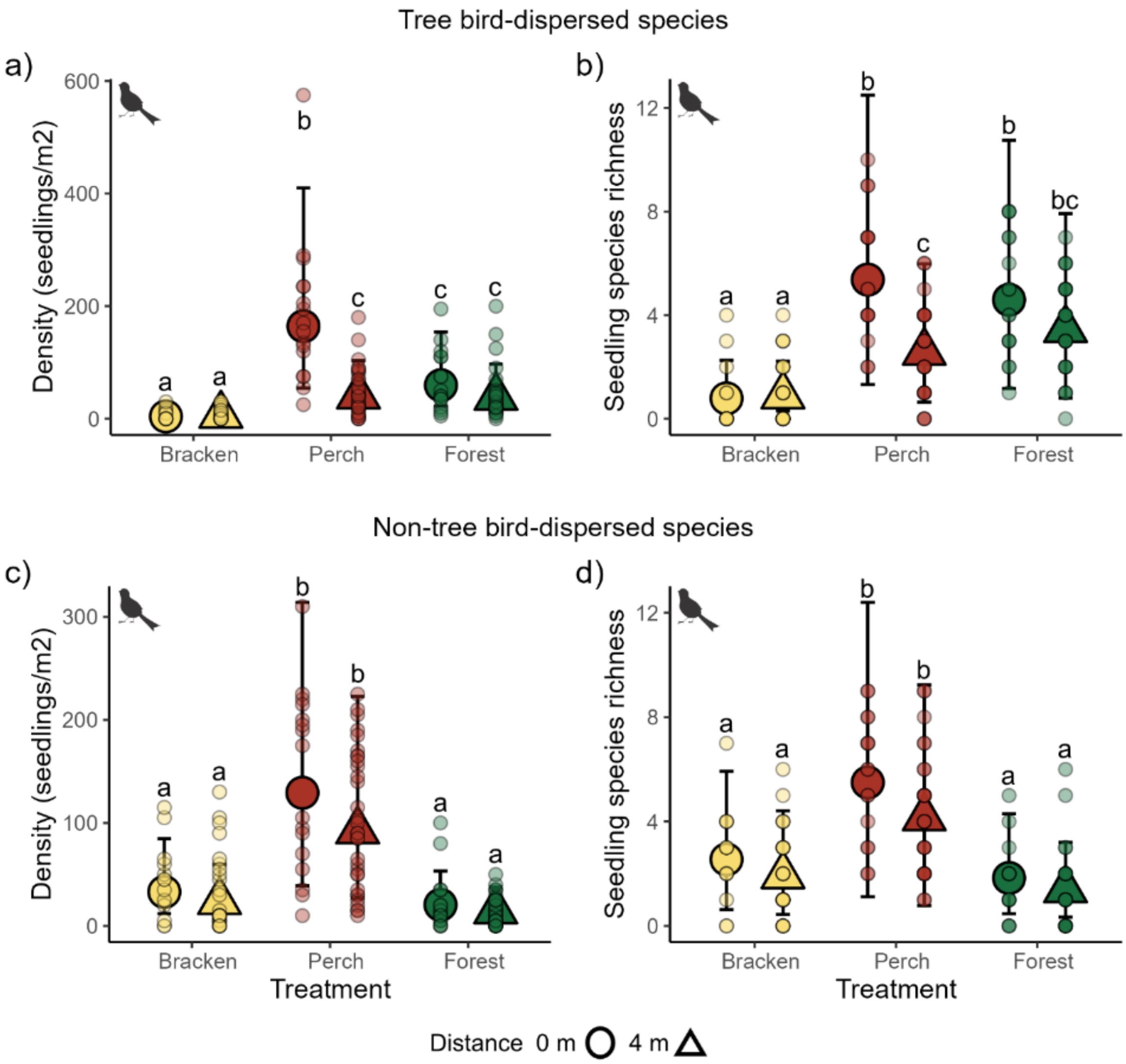
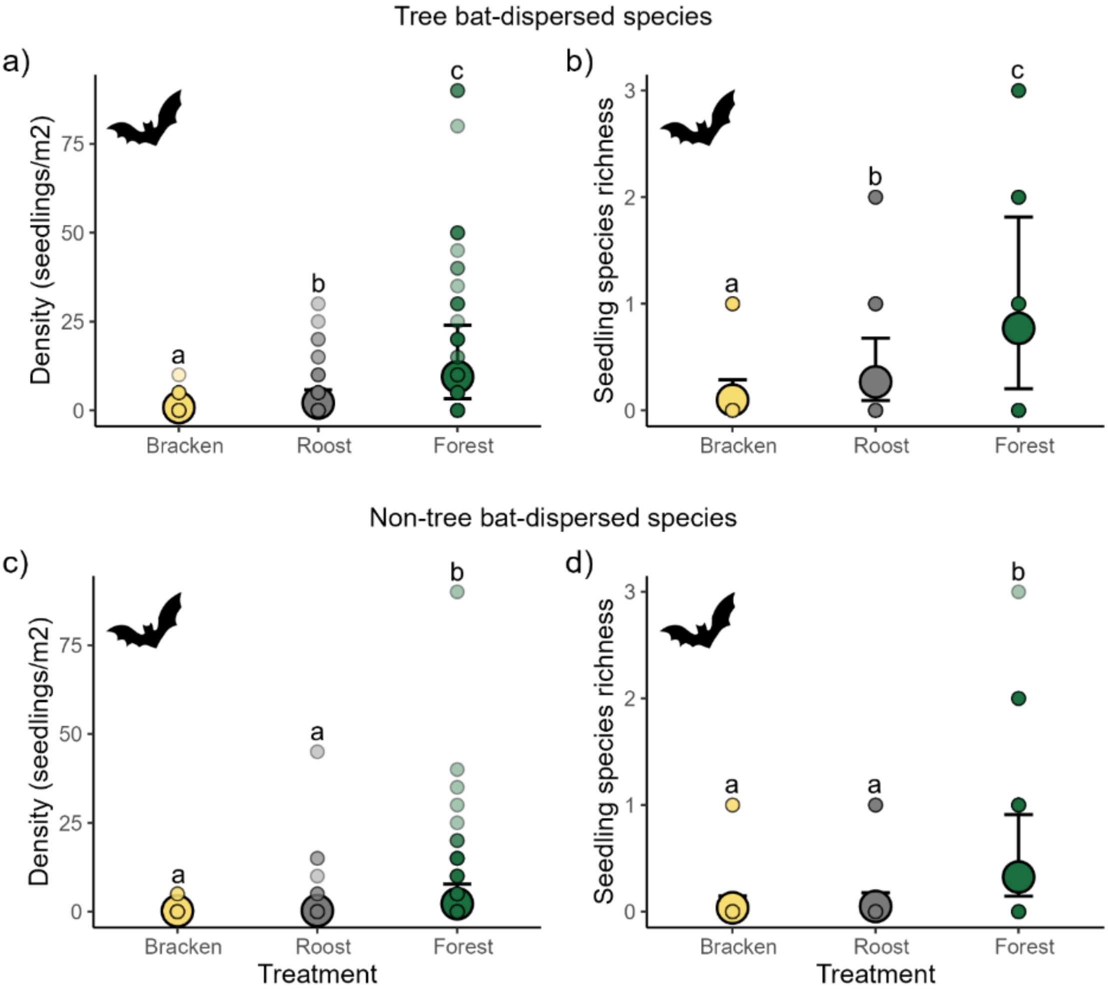


Figure 8. Seedling density and species richness of bird-dispersed species per recruitment plot in bracken, at perch and in forest. a) density and b) species richness of non-tree seedlings, c) density and d) species richness of tree seedlings. The colors represent the different treatments, and the symbols represent the distance category of the recruitment plots: circle = under the perch (distance 0 m), triangle= 4m 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.

The best model for density and species richness of bat-dispersed seedlings included only the treatment (Table S12, Figure S6), while the distance was not important. Seedling density and richness of tree and non-tree species were significantly higher in the forest compared to bracken and roost (X^2 = 44.04, p < 0.001 tree seedling density, X^2 = 39.84, p < 0.001 tree seedling richness, X^2 = 15.59, p < 0.001 non-tree seedling density, X^2 = 25.41, p < 0.001 non-tree seedling richness, Figure 9a-d). Seedling density and richness of tree species were 3.7 and 3.1 times higher in roost compared to bracken (Figure 9a-b, Table S13). Seedling density and species richness were 72.9 and 27.5 times higher in perch than in roost, respectively (X^2

= 166.21, p < 0.001 seedling density, $X^2 = 198.32$, p < 0.001 seedling density, Figure S5, Table S9).

Figure 9. Seedling density and species richness of bat-dispersed species per recruitment plot



in bracken, at roost 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 ± 95% CI estimated by the GLMMs of seed density (figures a and c) and species richness (figures b and d), small circles denote observed values.

3.2.3 The effect of animal attractants on dispersal limitation and establishment limitation

I 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 S14).

3.2.3.1 Dispersal limitation

On average, I 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 ($X^2 = 17.68$, $p < 0.001$), being 23% lower in the forest compared to bracken (Fig. 10a, Table S15). At perch, dispersal limitation was about 24% lower than in bracken (Fig. 10a, Table S15). I did not find differences between bracken and roost, and perch had a similar dispersal limitation as forest (Fig. 10a, Table S15). In terms of life strategy, I found significant differences on dispersal limitation of pioneer and non-pioneer species between forest, perch and bracken ($X^2 = 17.45$, $p < 0.001$), being 23% lower for both categories in forest compared to bracken (Fig 10b, Table S15). At perch, there was a reduction in dispersal limitation of 26% for pioneer species and 22% for non-pioneer species, compared to bracken (Fig 10b, Table S15). At roost, there was a reduction in dispersal limitation for both life strategy categories compared to bracken, although the reduction was not significant. (Fig 10b, Table S15). I did not find differences between perch and forest for pioneer and non-pioneer species. Regarding seed size, I found significant differences between forest, perch and bracken ($X^2 = 19.22$, $p < 0.001$). Dispersal limitation was 21% and 23% lower in forest than in bracken for large and small seeds, respectively. (Fig. 10c, Table S15). I found a similar pattern as for life strategy. No differences were observed between bracken and roost for small and large seeds (Fig 10c, Table S15). Perch had significantly lower dispersal limitation of small and large seeds than bracken, and similar dispersal limitation compared to forest for both size categories (Fig. 10c, Table S15)

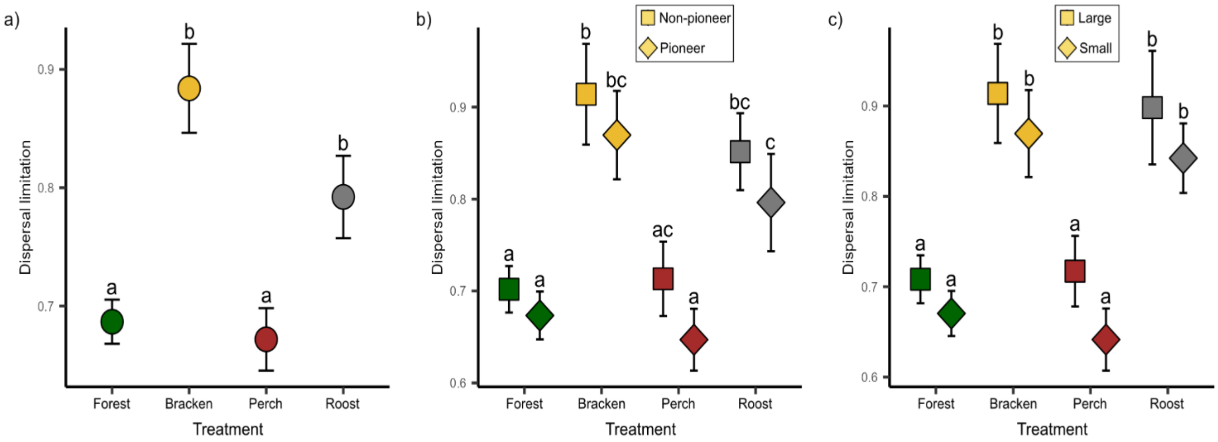


Figure 10. Indices of dispersal limitation for a) forest, bracken, perch and roost, and for the same treatments considering b) life strategy, and c) seed size. The colors represent the different treatments, and the symbols represent characteristics of life strategy (non-pioneer or pioneer) and seed size 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.

3.2.3.2 Establishment limitation

In general, most species had a high establishment limitation (higher than 70%), only *Myrcia* sp. had an establishment limitation lower than 70%. Establishment limitation was significantly different between forest, bracken and perch ($X^2 = 32.21$, $p < 0.001$), 26% lower in forest than in bracken (Fig. 11a, Table S16). Establishment limitation in perch was approximately 25% lower than in bracken (Fig. 11a, Table S16). I did not find differences between bracken and roost, and between perch and forest (Fig. 11a, Table S16). In terms of life strategy, there were significant differences among forest, perch and bracken ($X^2 = 37.26$, $p < 0.001$). Establishment limitation of pioneer and non-pioneer species were 16% and 25% lower, respectively, in forest than in bracken (Fig. 11b, Table S16). The presence of perch structures reduced the establishment limitation of pioneer and non-pioneer species by about 25% and 23%, respectively, compared to bracken (Fig. 11b, Table S16). For non-pioneer species, establishment limitation was similar between bracken and roost, and I found lower establishment limitation in roost compared to bracken; however, this difference was not significant (Fig. 11b, Table S16). The establishment limitation of non-pioneer species was similar between perch and forest, while perch had a significantly lower establishment limitation of pioneer species compared to forest (Fig. 11b, Table S16). Regarding seed size, establishment limitation of small and large-seeded species was 16% and 25% lower, respectively, in forest than in bracken (Fig. 11c, Table S16). At perch, the reduction in establishment limitation was 23% for small seeds and 24% for large seeds, compared to bracken (Fig. 11c, Table S16). I did not find differences for both size categories between roost and bracken, and for large-seeded species, there were no differences between perch and forest (Fig. 11c).

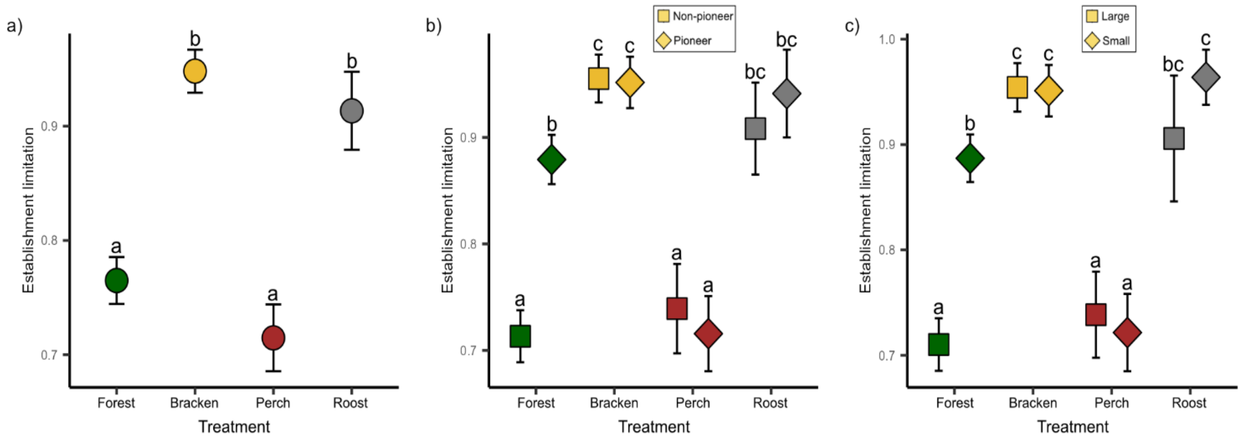


Figure 11. Indices of establishment limitation for a) forest, bracken, perch and roost, and for the same treatments considering b) life strategy, and c) seed size. The colors represent the different treatments, and the symbols represent characteristics of life strategy (non-pioneer or pioneer), and seed 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.

Chapter 4 Discussion

Animal-mediated seed dispersal is a critical process in tropical forest regeneration (Sekercioglu, 2006), because most woody species rely on animals, especially birds and bats, to disperse their seeds (Howe and Smallwood, 1982). In this study, I found that the functional traits related to seed dispersal of birds and bats were similar between forest and bracken-dominated areas, showing that the functional composition of the seed-disperser community in both habitats is conserved. However, birds had higher abundance and richness of interactions in bracken areas compared to forest, while bats had higher interaction richness in forest compared to bracken areas. The birds and bats captured in bracken had more seeds from pioneer than non-pioneer species in their droppings, which could be related to the slow forest regeneration in bracken-dominated areas, because pioneer species have low establishment probabilities in bracken-dominated areas. After installing animal attractants, I found that bird perches and artificial bat roosts increased the abundance and richness of seeds and seedlings in bracken areas. I found that bird perches helped to reduce dispersal and establishment limitations. In contrast, although artificial bat roosts increased seed rain and seedling establishment of bat-dispersed species, this increase did not correspond to a reduction in dispersal and establishment limitations.

4.1 Functional trait composition of birds and bats

Deforested environments can favor the dominance of a subset of functional traits in birds and bats (Bovo et al., 2018; Frank et al., 2017). I expected that birds in forest would have a higher body mass and gape width than birds in bracken, because birds in highly disturbed habitats tend to be smaller than birds in less disturbed habitats (Bovo et al., 2018; Pavlacky et al., 2015). Moreover, studies in the same sites found that the species composition of seed-dispersing birds and bats are different between bracken and forest (Gallegos et al., 2024). However, I did not find differences in body mass and gape width of birds in the two habitats. The majority of birds captured in bracken and forest habitats corresponded to omnivorous and small frugivorous birds; both guilds are dominant in forest edges and deforested areas (Menezes Pinto et al., 2021) and have similar morphological characteristics.

I found that birds captured in bracken had higher hand-wing index (HWI) compared to those captured in forest. Birds with high HWI can fly long distances and cross open areas and are less sensitive to habitat fragmentation than birds with low HWI that tend to avoid deforested areas (Falconí-López et al., 2024; Jones et al., 2023; Weeks et al., 2023). In birds, differences in dispersal ability are not necessarily guild-specific. For example, species within the same guild—such as frugivorous—may have varying dispersal abilities, which means some species may be more sensitive to deforestation than others (Weeks et al., 2023). Possibly, the birds captured in the bracken, which had greater flight capacity, were able to move between forest patches and cross open areas. It is also possible that changes in trait composition would have been more pronounced if the comparison had been made between bracken habitats and the interior of forest fragments. Previous work in the study area showed that large-bodied and large-gaped bird species increase in importance towards the forest interior (Saavedra et al., 2014). I did not find differences in the trait composition of bats. Frugivorous bats are known to tolerate habitat disturbance (Farneda et al., 2020) and these bats can move between forested and open areas, possibly in search of fruit resources from pioneer species (Muscarella and Fleming, 2007). Accordingly, in the study area, there are species of *Piper, Vismia* and *Solanum* in deforested areas (Lippok et al., 2014, 2013a) that are preferentially consumed by frugivorous bats, but in low densities. Another reason for the weak differences in bird and bat communities could be the sampling method (mist netting) that tends to favor the capture of small seed dispersers, while especially large birds are more likely to escape from mist nets (Jenni et al., 1996). Although most bird and bat traits were similar between bracken and forest habitats, it appears that dispersal ability in birds is a key factor determining which species are likely to be present in bracken areas.

4.2 Seed-dispersal interactions

The loss of forested areas affects the communities of seed-dispersing animals, plants and their interactions (Emer et al., 2020; Menezes Pinto et al., 2021). Some studies found less interactions in disturbed habitats due to the reduced abundance of seed-dispersing animals (Li et al., 2022; Marjakangas et al., 2020; Menezes Pinto et al., 2021). Contrary, I found that bracken had more bird interactions richness and abundance than forest. This could be related to the fact that in the study sites, the species richness and abundance of small omnivorous/frugivorous birds are higher in bracken than in the forest (Gallegos et al., 2024). On the other hand, in bracken areas there are small-seeded/fruited plants of the families Melastomataceae and Ericaceae (Lippok et al., 2013a) that bear fruits most of the year and are attractive to birds. For bats, I found higher interaction abundance in forest than in bracken. In the study sites, the abundance of frugivorous bats tends to be higher in forest compared to bracken (Gallegos et al., 2024), and there are more species and more individuals of plants of the families Piperaceae and Solanaceae in forest than in bracken (Lippok et al., 2014, 2013a). Thus, the results for bats could be related to higher abundance of food resources in forest compared to bracken.

4.3 Life strategies of animal-dispersed species

I found that birds and bats present in bracken carried significantly more seeds of pioneer species than birds and bats captured in the forest. This could be related to the fact that the majority of birds and bats that disperse seeds in bracken were small frugivorous and omnivorous species that mostly consume fruits with small seeds (Arteaga et al., 2006; Emer et al., 2018; Snow, 1981), a characteristic of pioneer plants (Swaine and Whitmore, 1988; Valio and Scarpa, 2001). Most of the seeds of pioneer species found in bracken were typical of deforested areas, and are rare in the forest. On the other hand, non-pioneer, shade-tolerant plant species that usually have large seeds (Khurana and Singh, 2006; Thompson and Rabinowitz, 1989) are mostly dispersed by large specialist frugivorous birds (Carlo et al., 2022; Snow, 1981) and large mammals (Cramer et al., 2007), which were rare in bracken. For instance, Saavedra et al. (2015) found a lack of non-pioneer and large-seeded plants in the seed rain in bracken of the study area, suggesting that there was very little dispersal of such species from the forest. In the forest interior and forest edge of the study area there are several species of Lauraceae, and species such as *Symplocos arechea* that have large seeds (>10 mm) and are non-pioneer species (Lippok et al., 2014; López et al., 2024; Saavedra et al., 2015). Due to the shade it produces, bracken fosters the establishment of non-pioneer species, but not of pioneer species (Gallegos et al., 2015; López et al., 2024; Ssali et al., 2019). Although pioneer species arrive into bracken, the recruitment of these species is hindered by the low light conditions under bracken, that are detrimental to light demanding pioneer species (Gallegos et al., 2016, 2015; López et al., 2024). In this study, I did not analyze the actual seed deposition by birds and bats. There is a possibility that animals captured in bracken from both groups are moving from one forest patch to another. However, there is also the possibility that birds perch in the plants that remain/resprout in the deforested area. Also, since bats can defecate in flight (Muscarella and Fleming, 2007), they could drop seeds while they are moving from one forest patch to another.

To gain a deeper understanding of the seed-dispersal process in the bracken area, future studies could combine different techniques to study seed-dispersal interactions. For example, the use of mist nets combined with focal observations could help to have more complete and representative data of the interactions between plants and birds (Quintero et al., 2022). I acknowledge that direct observations of plant-animal interactions in bracken areas and nearby forests could be very effective. However, one of the best methods to know which seeds are actually delivered by birds and bats to deforested sites is mist netting which allowed me to estimate the actual seed-dispersal functions by both groups of seed dispersers. It is important to recognize that this method primarily captures small frugivores in the understory and may underestimate the role of large and other frugivorous animal groups from the canopy.

4.4 The effect of bird perches on seed rain and seedling establishment

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 and Guilherme 2020). I 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 areas compared to pastures, and pastures with shrubs, as those found by Maya-Elizarrarás and Schondube (2015) in an evergreen tropical rainforest in Mexico.

Independently of seed density, I found that perch also increased the density and species richness of bird-dispersed seedlings compared to bracken and forest, highlighting their potential for forest restoration. The results of this thesis 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 and Wolfe 1993), where bird perches increased seedling establishment.

After classifying bird-dispersed seeds in the seed rain, I found the highest seed density of non-tree species under perch, while non-tree species richness was similar under perch and in forest. Saavedra et al. (2015) reached a similar conclusion regarding the density and richness of non-tree species. Regarding seedling establishment, I recorded the highest density and richness of non-tree seedlings under perch. The most abundant species belonged to *Miconia* and *Gaultheria*. The highest density of non-tree seeds and seedlings under perch 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 I 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 perch corresponded to *Cecropia* sp1, *Morella pubescens* and *Myrsine* sp. These species had small and intermediate seeds (<10 mm length), while I found few species with large seeds (≥ 10 mm length) under perch. However, the density of seeds and seedlings of large-seeded species were still higher under perch than in bracken. Large seeds require large birds to be dispersed, and large birds are usually rare in tropical deforested areas (Sodhi and Smith, 2007; Thiollay, 1992), but can be important seed dispersers of species with large seeds in tropical forests under high disturbance (Moreira et al., 2017). Accordingly, in a parallel study with camera traps (Mayta unpublished), I registered large bird species such as *Aulacorhynchus coeruleicinctis* (Ramphastidae, ~208 g) and *Penelope montagnii* (Cracidae, ~706 g) using the bird 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 perch, while the seed traps 4 m away received fewer seeds. This pattern is related to the behavior of birds 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, I 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, for example, 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 perch 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 the study area (Saavedra et al., 2014) and these species have high germination and establishment rates in bracken-dominated areas (Gallegos et al., 2015).

4.5 The effect of artificial bat roosts on seed rain and seedling establishment

My results showed that roost 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 this study, I 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. I confirmed bat visitation to roosts from camera traps and signs such as droppings and fruit remains in seven of the eight roosts installed. Although none of the roosts were permanently colonized, they were frequently used as foraging sites.

Seeds of tree and non-tree bat-dispersed species had higher densities and species richness near roost than in bracken. The most abundant bat-dispersed genera found in the seed rain around the roost 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 in forest slopes and landslides in a montane rainforest in Ecuador (Lindner and 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 roost 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. I found that seed density and species richness were not limited by distance to roost. 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 roost compared to bracken areas. For example, *Vismia crassa, V. pozuzoensis* and *V. rusbyi* had higher densities near roost than in bracken-dominated areas without the roost. Density and species richness of non-tree seedlings were similar between roost and bracken, which is possibly associated to 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., 2002a). 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 this study I 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., 2013b; Ssali et al., 2018).

Comparing both techniques, I observed that perch had a higher density and species richness of seeds and seedlings than roost. This result could be related to the fact that in the study site there are more plants that are dispersed by birds (Lippok et al. 2013a; 2014), and that birds frequently disperse seeds from shade-tolerant species, which are better adapted to grow under bracken (López et al., 2024, Gallegos et al., 2016). In this study, perches and artificial bat roosts were placed at 50 m from the forest margin, which may be too close to the forest. However, in the 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 (Gallegos et al., 2016; Saavedra et al., 2015). Other studies in the tropics have shown that seed dispersal decreases between 8 m (Cubiña and Aide, 2001) and 30 m from the forest edge (Teegalapalli et al., 2010). Therefore, the results of this study reflect how bird 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.

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

In this study, the installation of bird perches significantly reduced dispersal limitation to a level comparable to that observed in forested areas. This result is linked to the considerable increase in the density of bird-dispersed seeds with the installation of perches, a finding observed in this thesis and also by (Saavedra et al., 2015) in the same study area. Moreover, the abundance and richness of generalist frugivorous birds, which cope well with the loss of forested areas (Gomes et al., 2008), are higher in bracken areas than at forest edges (Gallegos et al., 2024).

I 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), especially, shade-tolerant. The similar levels of establishment limitation observed in both, forest and perch, indicate that seed arrival is a primary filter for plant species in these deforested areas. Furthermore, they highlight the potential of the inclusion of perch structures to overcome both limitations in bracken-dominated areas.

In tropical forests, bats are important seed dispersers that contribute to forest regeneration by dispersing pioneer species. However, in this study, the presence of artificial bat roosts did not reduce the dispersal limitation of bat-dispersed species, despite a recorded increase in the density of bat-dispersed seeds around the roosts, which could be due to the low density of bat-dispersed seeds. This result may be related to the scarcity of food resources for bats in bracken areas (Lippok et al., 2013a). The presence of roosts did not reduce the establishment limitation either. Besides the characteristics of bat food resources in bracken, 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. 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, I 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. These results show that this technique has limited effectiveness to assist forest regeneration in bracken areas. However, the use of roosts could have some advantages in comparison to the use of bird perches in other environments. For example, if the stake used as a perch do not have the capacity of resprouting, the perch may decompose within a few years (Holl et al., 2024). The materials used in the construction of the roosts could last much longer than a stake of wood. Nevertheless, the construction of artificial bat roosts is more expensive than the installation of perches.

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

Regarding life strategy, perches allowed the reduction of dispersal limitation of non-pioneer and pioneer species. I expected to find higher dispersal limitation of non-pioneer species, even with the presence of perches, because these types of seeds are generally more limited in deforested areas (de Almeida et al., 2016; de la Peña-Domene et al., 2018). Furthermore, non-pioneer species 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). However, I did not find differences between both life strategies. This may be due to the ability of some birds to move between forest and open areas, carrying non-pioneer species from the forest. 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. I 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., 2002b). However, López et al. (2024) found that the presence of bracken did not reduce the density of early and late-successional trees and shrubs, and that these species established under bracken taking advantage of the ameliorated conditions of temperature and soil humidity in comparison to open areas. Our results highlight the importance of bird perches to overcome both dispersal and establishment limitations for pioneer and non-pioneer bird-dispersed species in bracken dominated areas, and they should be studied in other tropical disturbed forests.

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 the 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., 2014, 2013a). Also, bats defecate while flying (Muscarella and Fleming, 2007) and although I 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 I did not find all the seeds and seedlings dispersed by bats. However, since bats disperse mainly pioneer species which need high light conditions, their contribution to forest regeneration in bracken-dominated areas is probably low in general.

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

Concerning seed size, I expected that large-seeded species will have higher dispersal limitation than small-seeded species in perch. I did not find significant differences between both size categories; however large seeds tended to be more limited than small seeds in all the treatments. Large frugivorous birds are scarce in deforested areas (Markl et al., 2012), but I observed that the bird 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). I also did not find differences in establishment limitation between small and large-seeded species, both being reduced by the presence of bird perches. For example, under perches I found seedlings of species such as *Nectandra cuspidata, Hedyosmum racemosum* and *H. angustifolium* that are common in forest and have medium to large seeds, highlighting the potential of perches to reduce dispersal and establishment limitations of large and small-seeded species. Roosts were unable to reduce dispersal and establishment limitation of small and large-seeded species. As already mentioned, this is related to the characteristics of the bat communities in our study area and the characteristics of their food resources.

It is important to evaluate the techniques that aim the recovery of forest in sufficient periods of time (Holl et al., 2024). The study had a short duration (15 months), and it is possible that some seeds needed more time to germinate. It is also worth mentioning that in the 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 the 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.

My results reinforce the idea that dispersal limitation is one of the most important filters that plant species must overcome in tropical 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 all the ecological processes that contribute to the slow regeneration of these deforested areas. Understanding the traits of plants that promote both establishment and growth is crucial. 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.

Chapter 5 Summary

Tropical montane forests harbor a vast diversity and provide numerous ecosystem services. However, these forests are threatened by human activities. The expansion of agricultural land through logging and burning practices generate large deforested areas, which in many cases are dominated by ferns of the genus *Pteridium* (hereafter bracken). Forest succession in bracken-dominated areas is often arrested. The presence of bracken and its negative effects on forest regeneration have been linked to the microclimatic conditions created by its fronds and litter, which could prevent the establishment of tree species, a process known as establishment limitation. On the other hand, evidence suggests that the main filter in forest regeneration in these deforested areas is seed dispersal limitation, related to the high proportion of animal-dispersed species in tropical humid forests. Although some plant species dispersed by animals can establish in bracken-dominated areas, the arrival of their seeds is limited by the lack of attractants for seed-dispersing animals (i.e., food, perches and shelters). Bird perches and artificial bat roosts can be installed to attract birds and bats to bracken-dominated areas. In order to understand the role of the main seed dispersers on forest regeneration, it is important to study the traits related to seed dispersal in the communities of seed-dispersing animals, the seed rain generated by these animals, and the success of the dispersed seeds in their establishment. At the same time, it is important to evaluate the contribution of the main seed-dispersers and animal attractants to reduce seed dispersal and establishment limitations.

This thesis aims to contribute to a better understanding of the role of seed-dispersing animals in the regeneration of bracken-dominated areas. It is based on field experiments that I performed in tropical montane forests of Bolivia. At eight study sites, in bracken areas and forest edges, I captured birds and bats with mist-nets, measured their traits, and analyzed the characteristics of the seeds they dispersed. Additionally, I installed bird perches and artificial bat roosts to attract seed-dispersing animals, to assess their impact on seed rain and seedling establishment, and their contribution to reduce the dispersal and establishment limitations.

I found that birds and bats captured in bracken and forests had similar traits, with the exception of the hand-wing index, which was higher in birds captured in bracken-dominated areas compared to those captured in forests, showing their higher mobility. Bats and birds dispersed a higher number of seeds from pioneer species in comparison to non-pioneer species in bracken-dominated areas. The installation of bird perches and artificial bat roosts was successful in increasing the density and species richness of seeds and seedlings established in bracken-dominated areas. However, I found that the increase in seed rain and seedling establishment due to the presence of roosts was not sufficient to reduce the dispersal and establishment limitations of bat-dispersed species. On the other hand, the installation of bird perches led to the reduction of dispersal and establishment limitations of bird-dispersed species, reaching values similar to those found in forests.

The fact that birds and bats carried higher quantities of pioneer seeds in bracken-dominated areas compared to non-pioneer species is an important finding for forest regeneration in these deforested areas. Pioneer species are negatively affected in their germination and establishment in the presence of bracken due to its shade. This finding shows that, although

the seed dispersal function persists in deforested areas, the types of seeds dispersed have a low chance of germination and establishment, contributing poorly to forest regeneration. Regarding the use of animal attractants as a restoration technique, the installation of perches increased the density of bird-dispersed seeds and seedlings, helping to overcome both dispersal and establishment limitations. The effect of perches was consistent for pioneer and non-pioneer species and for small and large-seeded species. On the other hand, the presence of artificial bat roosts did not reduce either limitation, probably because bats mainly disperse light demanding species which rarely establish in bracken. These results demonstrate that bird perches are more effective than artificial bat roosts in fostering forest regeneration in bracken-dominated areas.

This thesis gives important cues about the seed-dispersal related drivers of slow forest regeneration in bracken-dominated areas. My results support the hypothesis that dispersal limitation of animal-dispersed species acts as a major filter for forest regeneration in bracken-dominated areas. To overcome this limitation, restoration strategies should consider installing bird perches and complement them with other restoration practices, such as seed addition and planting seedlings of non-pioneer animal-dispersed species to assist forest regeneration of these widely distributed deforested areas in tropical regions.

Zusammenfassung

Tropische Bergwälder beherbergen eine enorme Vielfalt und leisten zahlreiche Ökosystemdienstleistungen. Dennoch sind diese Wälder durch menschliche Aktivitäten bedroht. Der Zuwachs landwirtschaftlicher Flächen durch Abholzung und Brandrodung führt zu großen entwaldeten Gebieten, die in vielen Fällen von Farnen der Gattung *Pteridium* (im Folgenden als Adlerfarne bezeichnet) dominiert werden. Die Waldsukzession in diesen Adlerfarn-dominierten Gebieten ist oft gehemmt. Das Vorkommen von Adlerfarn und seine negativen Auswirkungen auf die Waldregeneration werden mit den mikroklimatischen

Bedingungen in Verbindung gebracht, die durch seine Wedel und sein Laub geschaffen werden, und die Ansiedlung von Baumarten verhindern können – ein Prozess, der als Etablierungslimitierung bezeichnet wird. Weiterhin deutet vieles darauf hin, dass der Hauptfaktor für die Waldregeneration in diesen entwaldeten Gebieten eine Limitierung der Samenausbreitung ist, die mit dem hohen Anteil an zoochoren Arten in tropischen Feuchtwäldern zusammenhängt. Obwohl sich einige der durch Tiere ausgebreiteten Pflanzenarten in Adlerfarn-dominierten Gebieten ansiedeln können, wird der Sameneintrag durch das Fehlen von Attraktoren für samenausbreitende Tiere (bpsw. Nahrung, Sitzwarten und Quartiere) begrenzt. Vogelsitzwarten und künstliche Fledermausquartiere können installiert werden, um Vögel und Fledermäuse in Adlerfarn-dominierte Gebiete zu locken. Um die Rolle der wichtigsten Samenverbreiter bei der Waldregeneration zu verstehen, ist es wichtig, die Merkmale der Samenverbreitung in den Gemeinschaften der Samenverbreiter, den Samenregen, der durch diese Tiere erzeugt wird, und den Erfolg der verbreiteten Samen bei ihrer Etablierung zu untersuchen. Gleichzeitig ist es wichtig, den Beitrag der wichtigsten Samenverbreiter und tierischen Anziehungspunkte zu bewerten, um die Begrenzungen der Samenverbreitung und Etablierung zu verringern.

Diese Dissertation zielt darauf ab, ein besseres Verständnis der Rolle von samenverbreitenden Tieren bei der Regeneration von Adlerfarn-dominierten Gebieten zu entwickeln. Sie basiert auf Feldexperimenten, die ich in den tropischen Bergwäldern Boliviens durchgeführt habe. An acht Untersuchungsstandorten, in Adlerfarn-Gebieten und Waldrändern, fing ich Vögel und Fledermäuse mit Netzen, maß ihre Merkmale und analysierte die Eigenschaften der Samen, die sie verbreiteten. Zusätzlich installierte ich Vogel-Sitzstangen und künstliche Fledermausquartiere, um samenverbreitende Tiere anzulocken, ihren Einfluss auf den Samenregen und die Etablierung von Sämlingen zu bewerten und ihren Beitrag zur Verringerung der Begrenzungen der Verbreitung und Etablierung zu untersuchen.

Ich fand heraus, dass Vögel und Fledermäuse, die in Adlerfarn und Wäldern gefangen wurden, ähnliche Merkmale aufwiesen, mit Ausnahme des Hand-Flügel-Index, der bei gefangenen Vögeln in Adlerfarn-dominierten Gebieten höher war als bei denen, die in Wäldern gefangen wurden, was ihre höhere Mobilität zeigte. Fledermäuse und Vögel verbreiteten in Adlerfarn-dominierten Gebieten mehr Samen von Pionierarten im Vergleich zu Nicht-Pionierarten. Die Installation von Vogel-Sitzstangen und künstlichen Fledermausquartieren war erfolgreich, da sie die Dichte und Artenvielfalt der Samen und Sämlinge in Adlerfarn-dominierten Gebieten erhöhte. Allerdings fand ich, dass der Anstieg des Samenregens und der Etablierung von Sämlingen aufgrund der Anwesenheit von Quartieren nicht ausreichte, um die Begrenzungen der Samenverbreitung und Etablierung, bei von Fledermäusen verbreiteten Arten, zu verringern. Andererseits führte die Installation von Vogel-Sitzstangen zur Reduzierung der

Begrenzungen der Verbreitung und Etablierung bei von Vögeln verbreiteten Arten, wobei Werte erreicht wurden, die denen in Wäldern ähnlich waren.

Die Tatsache, dass Vögel und Fledermäuse in Adlerfarn-dominierten Gebieten höhere Mengen an Pionier-Samen verbreiteten als an Nicht-Pionierarten, ist ein wichtiges Ergebnis für die Waldregeneration in diesen abgeholzten Gebieten. Pionierarten sind in ihrer Keimung und Etablierung in Anwesenheit von Adlerfarnen und deren Schattenbildung negativ betroffen. Dieses Ergebnis zeigt, dass, obwohl die Funktion der Samenverbreitung in abgeholzten Gebieten erhalten bleibt, die verbreiteten Samenarten eine geringe Chance auf Keimung und Etablierung haben, was nur wenig zur Waldregeneration beiträgt. Hinsichtlich der Nutzung von tierischen Anziehungspunkten als Restaurierungstechnik erhöhte die Installation von Sitzstangen die Dichte der von Vögeln verbreiteten Samen und Sämlinge und half, sowohl die Begrenzungen der Verbreitung als auch der Etablierung zu überwinden. Der Effekt der Sitzstangen war sowohl bei Pionier- als auch Nicht-Pionierarten und bei kleinen und großen Samenarten konstant. Andererseits verringerten die künstlichen Fledermausquartiere keine der Begrenzungen, vermutlich weil Fledermäuse hauptsächlich lichtbedürftige Arten verbreiten, die sich selten in Adlerfarn-dominierten Gebieten etablieren. Diese Ergebnisse zeigen, dass Vogel-Sitzstangen effektiver sind als künstliche Fledermausquartiere bei der Förderung der Waldregeneration in Adlerfarn-dominierten Gebieten.

Diese Dissertation liefert wichtige Hinweise auf die samenverbreitungsbedingten Treiber der langsamen Waldregeneration in Adlerfarn-dominierten Gebieten. Meine Ergebnisse unterstützen die Hypothese, dass die Begrenzung der Samenverbreitung bei von Tieren verbreiteten Arten als wichtiger Filter für die Waldregeneration in Adlerfarn-dominierten Gebieten wirkt. Um diese Begrenzung zu überwinden, sollten Restaurierungsstrategien die Installation von Vogel-Sitzstangen in Betracht ziehen und diese mit anderen Restaurierungspraktiken wie Samenaddition und das Pflanzen von Sämlingen nicht-pionierartiger, zoochorer Arten kombinieren, um die Waldregeneration dieser weit verbreiteten abgeholzten Gebiete in tropischen Regionen zu unterstützen.

Chapter 6 References

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List of figures

Appendices

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Supplementary figures and tables

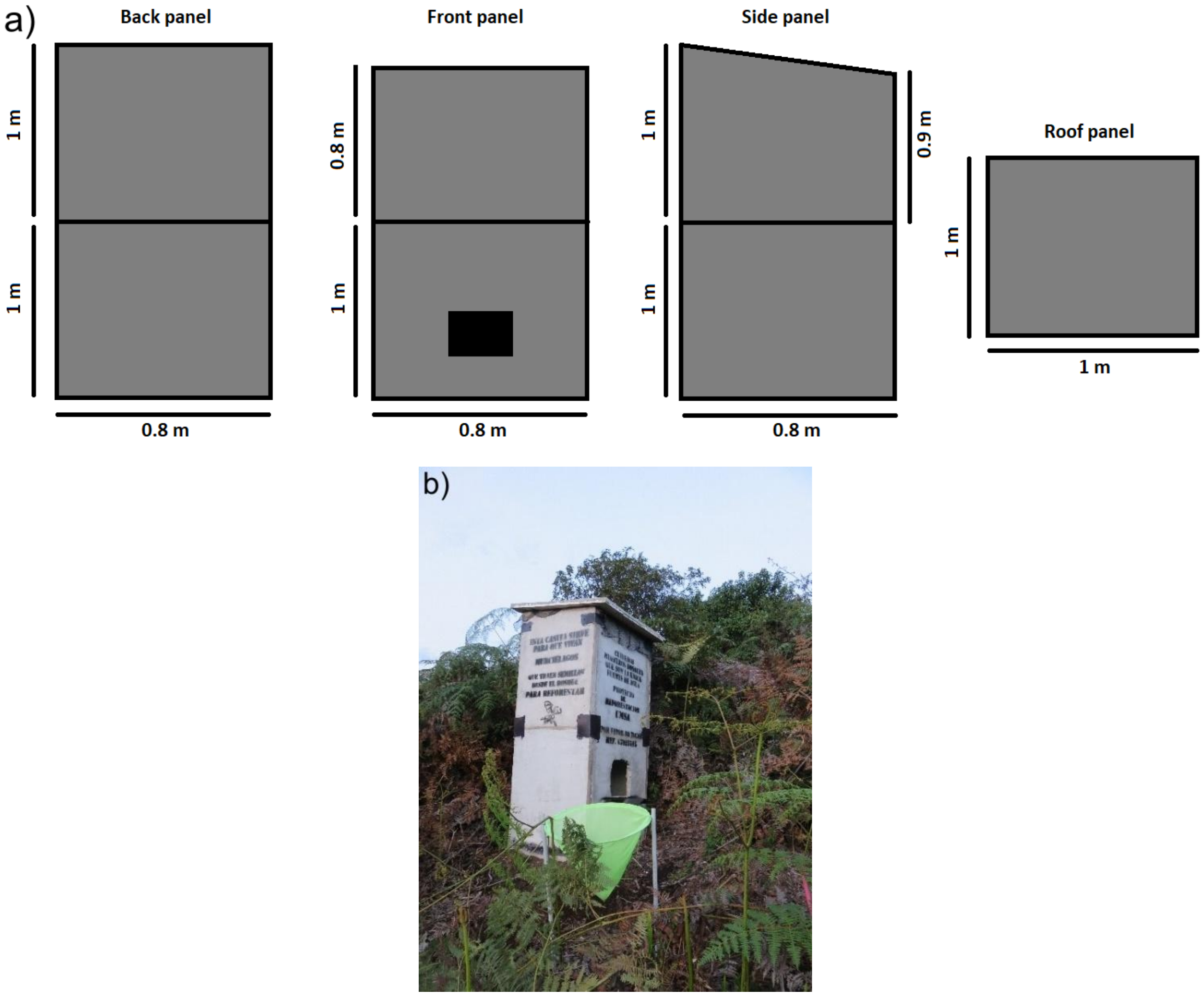

Figure S1. Details of the construction of the artificial bat roosts. The artificial bat roosts were modified from Kelm et al. (2008), to make them lighter and to have better thermal insulation. The roosts were built with panels of expanded polystyrene (2 cm thick), covered by wire mesh, a layer of cement and a layer of plaster. a) Scheme of the parts that were used to build the roosts. Each roost consisted of one back panel, one front panel, two side panels and one roof panel, each panel consisted of two parts to facilitate mobility. A cloth mesh was placed on the roof panel interior to allow bats to hang from the top. All the panels were joined with adhesive cement and bent metal plates secured with bolts. The entrance was at the bottom of the front panel and measured 30 x 30 cm. We added and additional bent metal plate to the bottom of the entrance to avoid serpents entering to the roost. We oriented the roost entrance to the southeast to minimize solar radiation inside the roost b) Image of the roost and a seed trap set in bracken-dominated area.

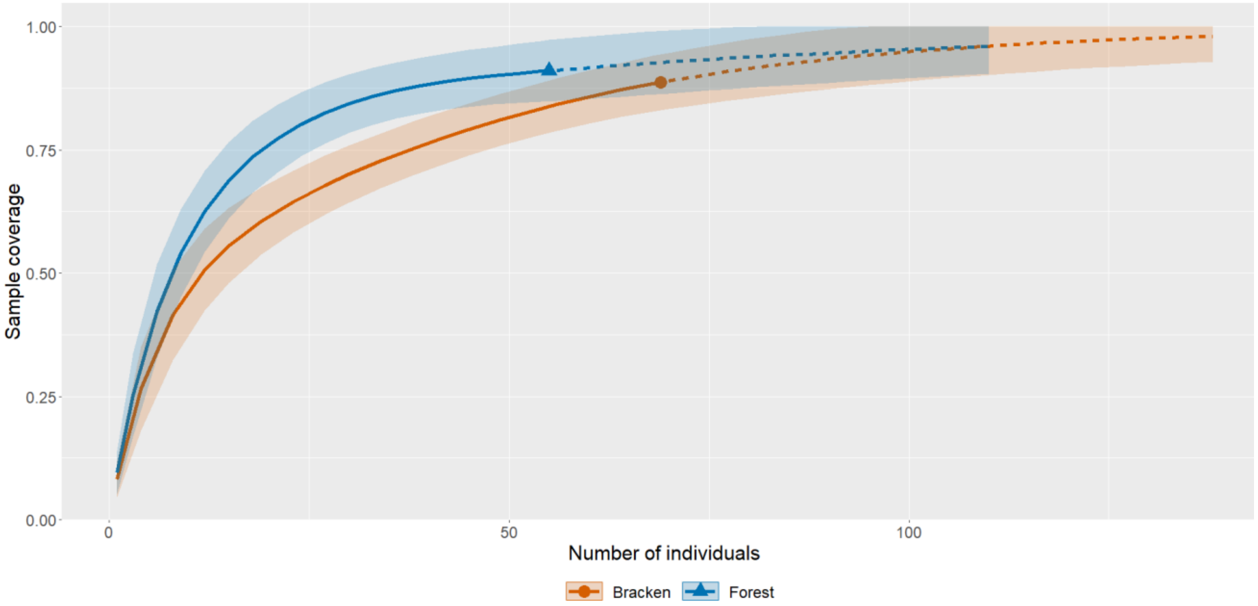

Figure S2. Sampling completeness of seed dispersal interactions using interpolation/extrapolation method. We performed this analysis using the iNEXT function in the R package 'iNEXT' v3.0.0.

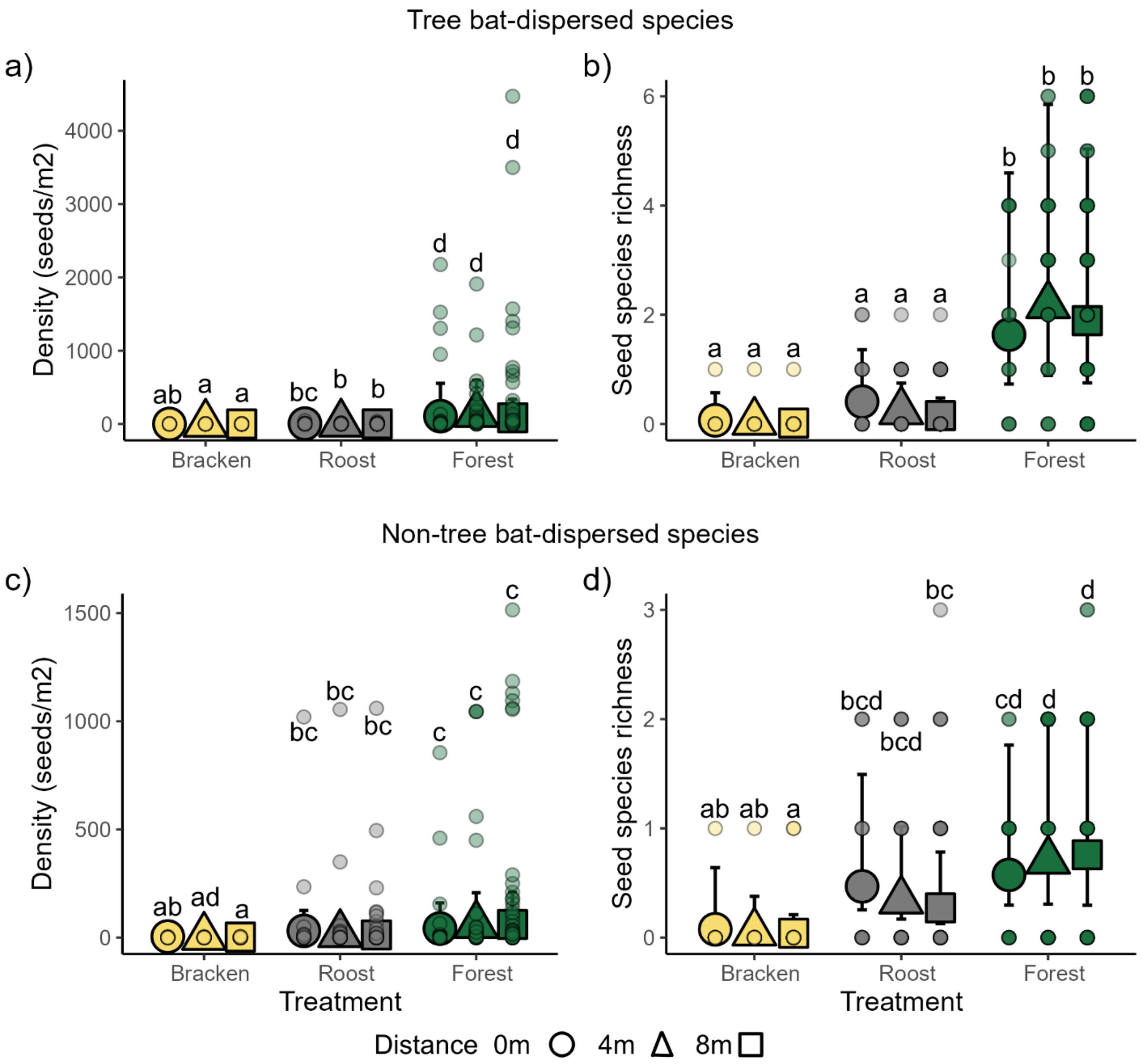

Figure S3. Seed density and species richness of bat-dispersed species per seed traps in bracken, at roosts and in forest. a) density and b) species richness of tree seeds, c) density and d) species richness of non-tree seeds. The colors represent the different treatments, and the symbols represent the distance category of the seed traps: circle = at the entrance of the roost (distance 0 m), triangle= 4m away from the roost (distance 4 m), square = 8m away from the roost (distance 8 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.

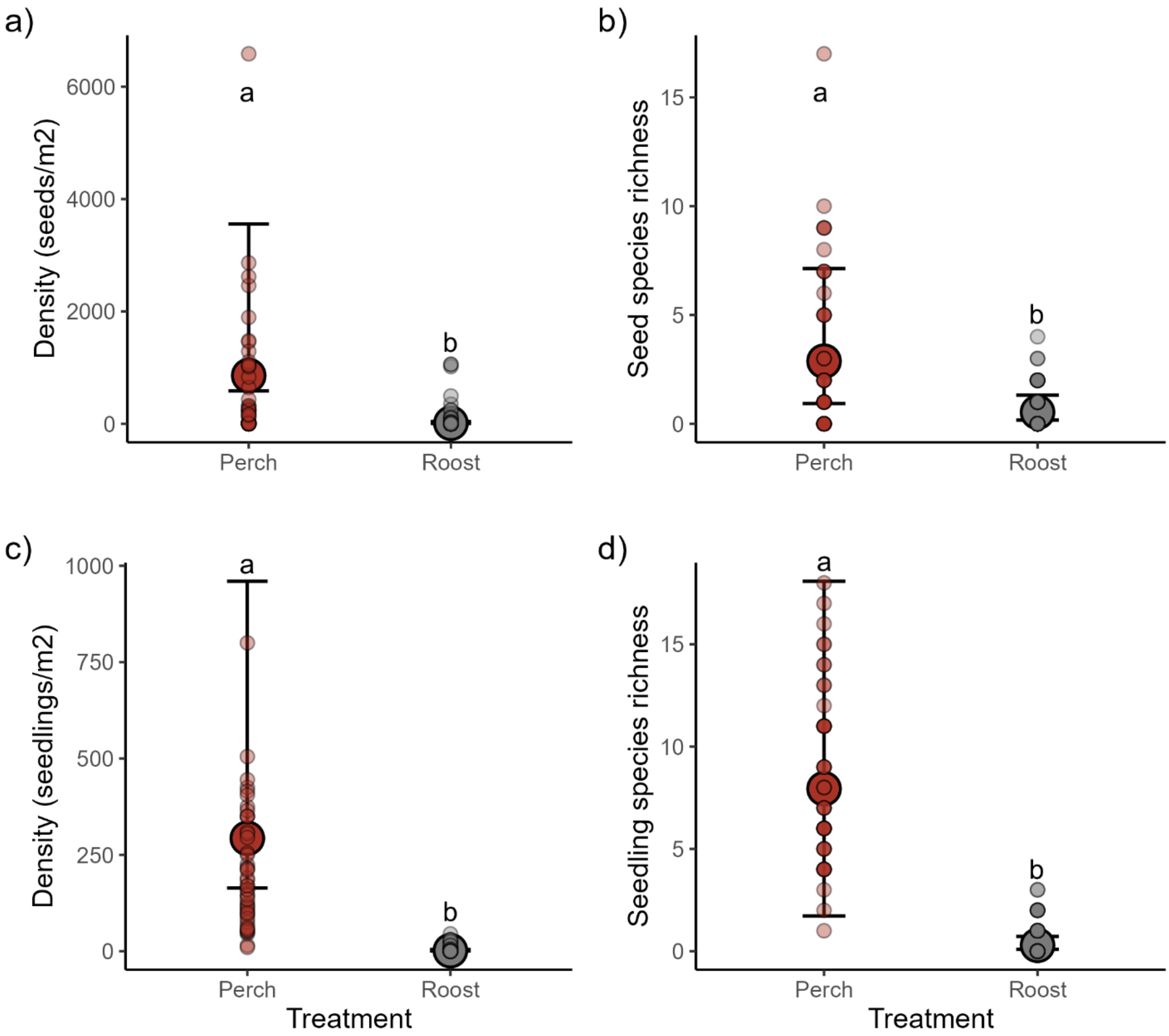

Figure S4. Comparison of a) density, b) richness of animal-dispersed seeds, and c) density, d) richness of animal-dispersed seedlings between perches and artificial bat roosts. The colors represent the different treatments. Large circles with error bars denote means ± 95% CI estimated by the GLMMs, small circles denote observed values.

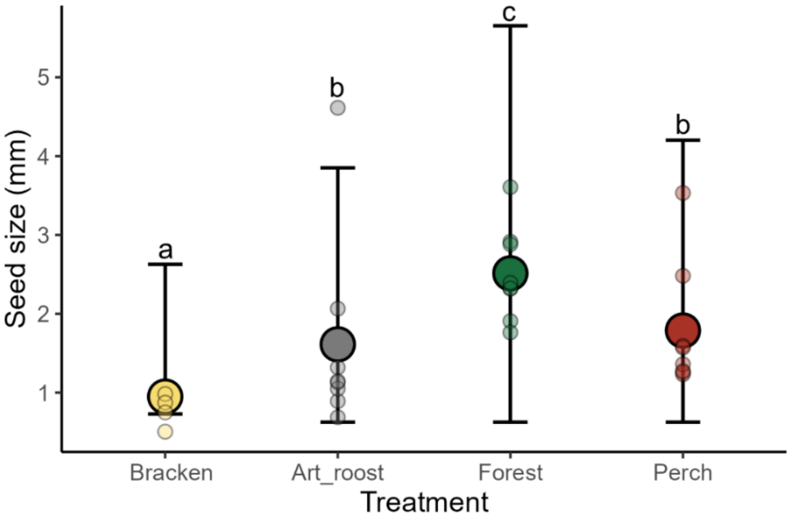

Figure S5. Comparison of seed sizes from animal-dispersed seeds among treatments. Large circles with error bars denote means ± 95% CI estimated by the LMMs, small circles denote observed values.

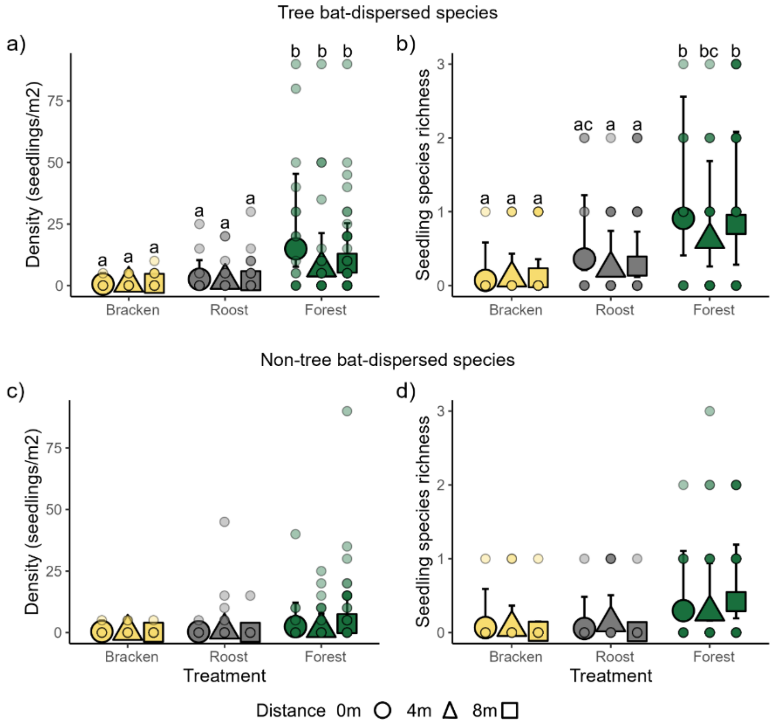

Figure S6. Seedling density and species richness of bat-dispersed species per recruitment plot in bracken, at roosts and in forest. a) density and b) species richness of tree seedlings, c) density and d) species richness of non-tree seedlings. The colors represent the different treatments, and the symbols represent the distance category of the recruitment plots: circle = at the entrance of the roost (distance 0 m), triangle= 4m away from the roost (distance 4 m), square = 8m away from the roost (distance 8 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.

Table S1. Species list and abundance of omnivorous and frugivorous birds, and bats. Shared species between bracken and forests are denoted in bold.

Taxa	Abbreviation	Species	Bracken	Forest
Birds	Ani_som	*Anisognathus somptuosus*	2	0
	Arr_tor	***Arremon torquatus***	**2**	**1**
	Atl_ruf	***Atlapetes rufinucha***	**4**	**8**
	Aul_coe	*Aulacorynchus coeruleicinctis*	2	0
	Cat_ust	***Catharus ustulatus***	**1**	**2**
	Chi_bol	***Chiroxiphia boliviana***	**1**	**17**
	Chl_cya	*Chlorophonia cyanea*	1	0
	Chl_fla	***Chlorospingus flavopectus***	**2**	**4**
	Dig_cya	*Diglossa cyanea*	1	0
	Dys_men	*Dysithamnus mentalis*	0	4
	Ela_alb	*Elaenia albiceps*	23	0
	Ela_chi	*Elaenia chilensis*	3	0
	Ela_obs	*Elaenia obscura*	10	0
	Ela_pal	*Elaenia pallatangae*	1	0
	Ela_sp	***Elaenia* sp.**	**3**	**1**
	Ent_leu	*Entomodestes leucotis*	1	0
	Eup_xan	*Euphonia xanthogaster*	0	1
	Lep_sup	*Leptopogon superciliaris*	0	1
	Mec_leu	*Mecocerculus leucophrys*	3	0
	Mec_sti	*Mecocerculus stictopterus*	1	0
	Mio_str	***Mionectes striaticollis***	**23**	**23**
	Pip_bon	*Pipraeidea bonariensis*	1	0
	Pip_fro	***Pipreola frontalis***	**1**	**1**
	Pyr_mol	*Pyrrhura molinae*	1	0
	Ram_car	*Ramphocelus carbo*	2	1
	Tan_nig	*Tangara nigroviridis*	2	0
	Tan_vas	*Tangara vassorii*	4	0
	Thr_cya	*Thraupis cyanocephala*	1	0

	Tro_per	*Trogon personatus*	1	0
	Tur_ama	*Turdus amaurochalinus*	0	1
	Zim_bol	*Zimmerius bolivianus*	2	0
Bats	Ano_cau	*Anoura caudifer*	1	0
	Ano_geo	*Anoura geoffroyi*	2	0
	Ano_per	*Anoura peruana*	0	1
	Car_bre	***Carollia brevicauda***	**2**	**11**
	Car_per	***Carollia perspicillata***	**4**	**14**
	Glo_sor	*Glossophaga soricine*	1	0
	Pla_inf	*Platyrrhinus infuscus*	0	1
	Stu_ery	*Sturnira erythromos*	1	0
	Stu_opo	***Sturnira oporaphilum***	**9**	**2**
	Stu_til	***Sturnira tildae***	**3**	**3**
	Uro_mag	*Uroderma magnirostrum*	1	0
	Vam_sp	*Vampyressa thyone*	0	1

Table S2. Results of the generalized linear mixed models for bill height, bill width, bill length, bird body mass, bat body mass and bat frugivory degree. P-values ≤ 0.05 are denoted in bold.

		Estimate	Std error	Z value	P-value	LRT test p-value	R2 marginal
Bird body mass	(Intercept)	23.57	2.29	10.31	**<0.001**	0.18	0.11
	Forest	-4.55	3.35	-1.36	0.17		
Bird gape width	(Intercept)	5.46	0.19	27.72	**<0.001**	0.46	0.04
	Forest	-0.21	0.28	-0.73	0.46		
Bird hand-wing index	(Intercept)	19.94	0.83	21.01	**<0.001**	**<0.001**	0.56
	Forest	-5.14	1.21	-4.23	**<0.001**		
Bat body mass	(Intercept)	18.51	0.99	18.52	**<0.001**	0.63	0.02
	Forest	-0.64	1.36	-0.47	0.63		
Bat frugivory degree	(Intercept)	1.04	0.03	29.63	**<0.001**	0.58	0.04
	Forest	0.02	0.04	0.55	0.17		

Table S3. Results of the generalized linear mixed model for number bird interaction richness, bird interaction abundance, bat interaction richness and bat interaction abundance.

		Estimate	Std error	Z value	P-value	LRT test p-value	R2 marginal
Bird interaction richness	(Intercept)	1.22	0.21	5.68	**<0.001**	**0.001**	0.35
	Non-pioneer	-0.62	0.32	-1.95	**0.04**		
	Forest	-0.76	0.33	-2.29	**0.02**		
	Forest:Non-pioneer	-0.14	0.59	-0.25	0.80		
Bird interaction abundance	(Intercept)	4.35	0.39	11.02	**<0.001**	**0.001**	0.31
	Non-pioneer	-1.62	0.45	-3.57	**<0.001**		
	Forest	-1.23	0.43	-2.88	**0.003**		
	Forest:Non-pioneer	0.51	0.67	0.76	0.45		
	(Intercept)	0.28	0.5	0.57	0.56	0.93	0.02

Bat interaction richness	Non-pioneer	0.22	0.67	0.33	0.73		
	Forest	0.11	0.60	0.19	0.84		
	Forest:Non-pioneer	-0.47	0.84	-0.56	0.57		
Bat interaction abundance	(Intercept)	4.31	0.46	9.22	**<0.001**	**0.003**	0.16
	Non-pioneer	-1.54	0.75	-2.02	**0.04**		
	Forest	-1.22	0.57	-2.14	**0.03**		
	Forest:Non-pioneer	1.64	0.94	1.74	0.08		

Table S4. Results of the generalized linear mixed models for abundance and species richness of seeds classified according to their life strategy. P-values ≤ 0.05 are denoted in bold.

		Estimate	**Std error**	**Z value**	**P-value**	**LRT test p-value**	**R2 marginal**
Abundance of bird-dispersed seeds	(Intercept)	4.35	0.39	11.02	**<0.001**	**0.001**	0.30
	Non-pioneer	-1.62	0.45	-3.57	**<0.001**		
	Forest	-1.23	0.43	-2.88	**0.003**		
	Non-pioneer:Forest	0.51	0.67	0.76	0.44		
Richness of bird-dispersed seeds	(Intercept)	1.22	0.22	5.68	**<0.001**	**0.001**	0.35
	Non-pioneer	-0.62	0.32	-1.95	**0.04**		
	Forest	-0.76	0.33	-2.28	**0.02**		
	Non-pioneer:Forest	-0.14	0.58	-0.25	0.8		
Abundance of bat-dispersed seeds	(Intercept)	4.31	0.46	9.22	**<0.001**	**<0.001**	0.16
	Non-pioneer	-1.54	0.76	-2.03	**0.04**		
	Forest	-1.22	0.57	-2.14	**0.03**		
	Non-pioneer:Forest	1.64	0.94	1.74	0.08		
Richness of bat-dispersed seeds	(Intercept)	0.28	0.50	0.57	0.56	0.93	0.03
	Non-pioneer	0.22	0.67	0.33	0.73		
	Forest	0.12	0.60	0.19	0.84		

Non-pioneer:Forest	-0.47	0.84	-0.56	0.57

Table S5. Species list, abundance and successional classification of seeds retrieved from droppings and regurgitates of birds and bats.

Family	Species	No. of seeds	Successional status
Actinidiaceae	*Sarauia* sp.	1	Non-pioneer
Alstroemeriaceae	*Bomarea* sp.	3	Pioneer
Aquifoliaceae	*Ilex* sp.	3	Non-pioneer
Chloranthaceae	*Hedyosmum racemosum*	34	Non-pioneer
Clusiaceae	*Clusia trochiformis*	5	Non-pioneer
Ericaceae	Ericaceae	52	Pioneer
Ericaceae	*Gaultheria buxifolia*	100	Pioneer
Ericaceae	*Gaultheria erecta*	728	Pioneer
Ericaceae	*Gaultheria eriophylla*	270	Pioneer
Ericaceae	*Gaultheria reticulata*	202	Pioneer
Ericaceae	*Gaultheria* sp.	1	Pioneer
Hypericaceae	*Vismia crassa*	17	Pioneer
Hypericaceae	*Vismia glaziovii*	176	Non-pioneer
Lauraceae	*Nectandra* sp.	1	Non-pioneer
Melastomataceae	*Leandra carassana*	30	Pioneer
Melastomataceae	*Miconia uvifera*	11	Pioneer
Melastomataceae	*Miconia cyanocarpa*	20	Pioneer
Melastomataceae	*Miconia elongata*	7	Pioneer
Melastomataceae	*Miconia hygrophila*	109	Pioneer
Melastomataceae	*Miconia minutiflora*	16	Pioneer
Melastomataceae	*Miconia* sp.	24	Pioneer
Melastomataceae	*Miconia theaezans*	21	Pioneer
Moraceae	*Ficus* sp.	5	Non-pioneer
Myriaceae	*Morella pubescens*	14	Pioneer
Pentaphylacaceae	*Freziera* sp.	20	Non-pioneer

Piperaceae	*Piper elongatum*	281	Pioneer
Piperaceae	*Piper* sp.	17	Pioneer
Piperaceae	*Piper trigoniastrifolium*	18	Non-pioneer
Primulaceae	*Myrsine coriaceae*	7	Non-pioneer
Rubiaceae	*Palicourea* sp.	18	Non-pioneer
Rubiaceae	*Palicourea tristis*	27	Non-pioneer
Solanaceae	*Solanum albidum*	21	Pioneer
Solanaceae	*Solanum velutissimum*	73	Pioneer
Urticaceae	*Cecropia* sp1.	68	Pioneer
Urticaceae	*Cecropia* sp2.	152	Pioneer
Viburnaceae	*Viburnum ayavacense*	3	Pioneer
-	Indet	2	-

Table S6. List of animal-dispersed seed species captured in seed traps. Each species includes information of disperser agent (bat, bird or both), life form (tree or non-tree), the number of seeds found in the seed traps and the mean seed length ± SD.

Family	**Species**	**Disperser type**	**Life form**	**No. of seeds**	**Mean seed length ± SD (mm)**
Actinidaceae	*Saurauia peruviana*	Bird	tree	1	0.87 ± 0.11
Cannabaceae	*Trema micrantha*	Bird	tree	63	1.92 ± 0.36
Chloranthaceae	*Hedyosmum angustifolium*	Bat/bird	tree	31	4.08 ± 0.14
Chloranthaceae	*Hedyosmum racemosum*	Bat/bird	tree	229	3.34 ± 0.48
Clusiaceae	*Clusia* sp.	Bird	tree	381	5.12 ± 0.39
Ericaceae	*Gaultheria erecta*	Bird	non-tree	1292	0.52 ± 0.07
Ericaceae	*Gaultheria* sp.	Bird	non-tree	1211	0.49 ± 0.07
Euphorbiaceae	*Alchornea glandulosa*	Bird	tree	11	5.84 ± 0.51
Euphorbiaceae	*Alchornea* sp.	Bird	tree	14	4.98 ± 0.23

Euphorbiaceae	*Alchornea triplinervia*	Bird	tree	25	3.34 ± 0.21
Euphorbiaceae	*Croton pilulifer*	Bird	tree	1	7.17 ± 0.14
Hypericaceae	*Vismia crassa*	Bat	tree	28	1.62 ± 0.02
Hypericaceae	*Vismia glaziovii*	Bat	tree	4	1.76 ± 0.31
Hypericaceae	*Vismia* sp.	Bat	tree	147	1.79 ± 0.25
Lauraceae	*Beilschmiedia* sp.	Bird	tree	2	17.6 ± 1.58
Lauraceae	*Beilschmiedia tovarensis*	Bird	tree	12	25.5 ± 3.12
Lauraceae	*Nectandra cuspidata*	Bird	tree	106	11.52 ± 0.63
Lauraceae	*Ocotea solomonii*	Bird	tree	22	8.15 ± 1.23
Melastomataceae	*Miconia brittonii*	Bird	tree	293	0.72 ± 0.12
Melastomataceae	*Miconia calvescens*	Bird	non-tree	52	0.53 ± 0.12
Melastomataceae	*Miconia cordata*	Bird	non-tree	13	0.92 ± 0.06
Melastomataceae	*Miconia cyanocarpa*	Bird	non-tree	373	0.61 ± 0.09
Melastomataceae	*Miconia elongata*	Bird	non-tree	269	0.57 ± 0.04
Melastomataceae	*Miconia hygrophila*	Bird	tree	2279	0.86 ± 0.04
Melastomataceae	*Miconia leacrenata*	Bird	non-tree	456	0.97 ± 0.21
Melastomataceae	*Miconia micropetala*	Bird	non-tree	49	0.88 ± 0.16
Melastomataceae	*Miconia minutiflora*	Bird	non-tree	106	0.9 ± 0.04
Melastomataceae	*Miconia plumifera*	Bird	non-tree	679	1.01 ±0.13
Melastomataceae	*Miconia* sp nov.	Bird	non-tree	60	0.68 ± 0.09
Melastomataceae	*Miconia* sp.	Bird	non-tree	36	0.72 ± 0.12
Melastomataceae	*Miconia staphidioides*	Bird	non-tree	205	0.67 ± 0.1
Melastomataceae	*Miconia theaezans*	Bird	tree	21	0.72 ± 0.09
Melastomataceae	*Miconia uvifera*	Bird	non-tree	43	0.72 ± 0.12

Moraceae	*Ficus cuatrecasasiana*	Bat/bird	tree	238	1.12 ± 0.09
Moraceae	*Ficus* sp.	Bat/bird	tree	1243	0.98 ± 0.1
Moraceae	Moraceae	Bat/bird	tree	1310	0.66 ± 0.09
Myriaceae	*Morella pubescens*	Bird	tree	410	3.35 ± 0.18
Myrtaceae	*Myrcia* sp.	Bird	tree	54	5.12 ± 0.41
Passifloraceae	*Passiflora* sp.	Bird	non-tree	60	5.3 ± 0.24
Pentaphylacaceae	*Freziera* sp.	Bird	tree	200	1.11 ± 0.49
Phyllanthaceae	*Hieronyma* sp nov.	Bird	tree	1	5.41 ± 0.36
Phyllanthaceae	*Hieronyma fendleri*	Bird	tree	731	3.45 ± 0.19
Piperaceae	*Piper elongatum*	Bat/bird	tree	10	0.88 ± 0.06
Piperaceae	*Piper* sp.	Bat/bird	non-tree	3	0.77 ± 0.12
Piperaceae	*Piper* sp1.	Bat/bird	non-tree	4373	0.75 ± 0.11
Piperaceae	*Piper trigoniastrifolium*	Bat/bird	non-tree	237	1.67 ± 0.04
Primulaceae	*Myrsine* sp.	Bird	tree	936	3.04 ± 0.04
Primulaceae	*Stylogyne ambigua*	Bird	tree	1	8.23 ± 0.32
Rosaceae	*Rubus sp.*	Bird	non-tree	175	1.67 ± 0.25
Rubiaceae	*Faramea candelabrum*	Bird	tree	25	11.42 ± 0.99
Rubiaceae	*Palicourea attenuata*	Bird	non-tree	15	3.21 ± 0.25
Rubiaceae	*Palicourea reticulata*	Bird	tree	8	3.79 ± 0.42
Rubiaceae	*Palicourea* sp.	Bird	non-tree	3	3.3 ± 0.26
Rubiaceae	*Palicourea subtomentosa*	Bird	non-tree	1	2.74 ± 0.33
Rubiaceae	*Palicourea tristis*	Bird	tree	9	4.45 ± 0.21
Rubiaceae	*Psychotria carthagenensis*	Bird	non-tree	9	3.88 ± 0.43
Siparunaceae	*Siparuna tomentosa*	Bird	tree	3	4.34 ± 0.23
Smilacaceae	*Smilax* sp.	Bird	non-tree	3	5.38 ± 0.27

Solanaceae	*Solanum albidum*	Bat	tree	463	2.03 ± 0.21
Solanaceae	*Solanum betaceum*	Bat	non-tree	11	4.07 ± 0.28
Solanaceae	*Solanum iltisii*	Bat	tree	201	3.61 ± 0.13
Solanaceae	*Solanum* sp.	Bat	non-tree	4	3.38 ± 0.2
Solanaceae	*Solanum velutissimum*	Bat	tree	69	2.08 ± 0.58
Symplocaceae	*Symplocos arechea*	Bird	tree	54	14.09 ± 3.8
Urticaceae	*Cecropia* sp1.	Bat/bird	tree	3301	1.94 ± 0.03
Urticaceae	*Cecropia* sp2.	Bat/bird	tree	265	1.87 ± 0.09
Verbenaceae	*Lantana* sp.	Bird	non-tree	2	4.16 ± 0.21
Viburnaceae	*Viburnum ayavacense*	Bird	non-tree	13	6.73 ± 0.51
Viburnaceae	*Viburnum* sp.	Bird	non-tree	6	7.07 ± 0.54
Vitaceae	*Cissus trianae*	Bird	non-tree	36	4.21 ± 0.55

Table S7. Model selection table ordered by the Akaike information criterion (AIC), showing ∆AIC between models and weight, obtained from generalized linear mixed-effects models (GLMMs) including a) density and richness of tree and non-tree bird-dispersed seeds and b) density and richness of tree and non-tree bat-dispersed seeds, as the response variables in separate models. The independent variables, that were initially included in all the models, are: treatment (Treat), distance (dist) and their interaction (Treat:Dist)

	Model	**AICc**	**Delta AICc**	**Weight**
a) Bird-dispersed seeds				
Density of tree seeds	Treat+Dist+Treat:Dist	1023.3	0	1
	Treat+Dist	1046	22.77	0
	Treat	1058.2	34.95	0
	Dist	1084.5	61.23	0
	Null	1089.5	66.21	0
Richness of tree seeds	Treat+Dist+Treat:Dist	338.3	0	1
	Treat+Dist	420.6	82.26	0
	Treat	432.5	94.2	0

	Dist	706.1	367.77	0
	Null	716.1	377.8	0
Density of non-tree seeds	Treat+Dist+Treat:Dist	1128.9	0	0.98
	Treat+Dist	1137.6	8.72	0.01
	Treat	1144.1	15.21	0
	Dist	1191.1	62.22	0
	Null	1192	63.09	0
Richness of non-tree seeds	Treat+Dist+Treat:Dist	336.1	0	0.99
	Treat+Dist	351	14.96	0.001
	Treat	353.8	17.78	0
	Null	417.9	81.87	0
	Dist	418	81.9	0
b) Bat-dispersed seeds				
Density of tree seeds	Treat	1603.4	0	0.77
	Treat+Dist	1606.1	2.68	0.2
	Treat+Dist+Treat:Dist	1609.8	6.41	0.03
	Null	1777.7	174.31	0
	Dist	1781.2	177.85	0
Richness of tree seeds	Treat	544.1	0	0.74
	Treat+Dist	546.6	2.48	0.21
	Treat+Dist+Treat:Dist	549.5	5.36	0.05
	Null	641.9	97.8	0
	Dist	645.4	101.21	0
Density of non-tree seeds	Treat	1449.4	0	0.8
	Treat+Dist	1452.4	2.92	0.18
	Treat+Dist+Treat:Dist	1460.3	10.89	0
	Null	1488.7	39.28	0
	Dist	1491.2	41.81	0
Richness of non-tree seeds	Treat	459.8	0	0.88
	Treat+Dist	463.9	4.14	0.11
	Treat+Dist+Treat:Dist	469.7	9.91	0.006

	Null	499.7	39.88	0
	Dist	503.6	43.84	0

Table S8. Variables included in the best GLMM models for a) bird- and b) bat-dispersed seeds. For bird-dispersed species, bracken and distance 0m are in the intercept, and for bat-dispersed species, bracken is in the intercept. P-values ≤ 0.05 are denoted in bold. Likelihood-Ratio Tests' p-values and R2 marginal are reported for each model.

		Estimate	Std. Error	Z value	P-value	LRT test p-value	R2 marginal
a) Bird-dispersed species							
Density of tree seeds	(Intercept)	1.872	0.822	2.277	**0.02**	**<0.001**	0.83
	Perch	4.284	0.835	5.128	**<0.001**		
	Forest	3.902	0.834	4.675	**<0.001**		
	Distance 4	-1.405	1.294	-1.086	0.277		
	Perch:Distance 4	-3.139	1.453	-2.161	**0.03**		
	Forest:Distance 4	1.267	1.357	0.934	0.35		
Richness of tree seeds	(Intercept)	-1.946	0.707	-2.752	**0.005**	**<0.001**	0.90
	Perch	3.284	0.719	4.57	**<0.001**		
	Forest	3.464	0.717	4.833	**<0.001**		
	Distance 4	-1.273	1.225	-1.039	0.298		
	Perch:Distance 4	-1.739	1.297	-1.341	0.181		
	Forest:Distance 4	1.419	1.237	1.151	0.249		
Density of non-tree seeds	(Intercept)	3.563	0.279	12.756	**<0.001**	**<0.001**	0.96
	Perch	1.283	0.289	4.44	**<0.001**		
	Forest	-0.576	0.357	-1.614	0.106		
	Distance 4	-0.447	0.309	-1.445	0.149		
	Perch:Distance 4	0.134	0.368	0.364	0.716		
	Forest:Distance 4	0.164	0.455	0.36	0.719		
	(Intercept)	0.957	0.185	5.17	**<0.001**	**<0.001**	0.98
	Perch	0.761	0.203	3.742	**<0.001**		

Richness of non-tree seeds	Forest	-0.416	0.257	-1.621	0.105		
	Distance 4	-0.318	0.218	-1.46	0.144		
	Perch:Distance 4	0.012	0.259	0.047	0.962		
	Forest:Distance 4	0.143	0.325	0.441	0.659		
b) Bat-dispersed species							
Density of tree seeds	(Intercept)	0.474	0.746	0.636	0.525	**<0.001**	0.43
	Roost	1.817	0.665	2.732	**0.006**		
	Forest	4.435	0.638	6.949	**<0.001**		
Richness of tree seeds	(Intercept)	-3.489	0.627	-5.562	**<0.001**	**<0.001**	0.68
	Roost	1.938	0.607	3.19	**0.002**		
	Forest	4.15	0.581	7.136	**<0.001**		
Density of non-tree seeds	(Intercept)	1.066	0.678	1.573	0.115	**<0.001**	0.31
	Roost	1.678	0.567	2.96	**0.003**		
	Forest	2.949	0.544	5.416	**<0.001**		
Richness of non-tree seeds	(Intercept)	-3.061	0.544	-5.628	**<0.001**	**<0.001**	0.34
	Roost	1.919	0.528	3.634	**<0.001**		
	Forest	2.725	0.515	5.29	**<0.001**		

Table S9. Results from the generalized linear mixed-effects models (GLMM) comparing the effects of perches and artificial bat roosts on seed density, seed species richness, seedling density and seedling species richness, as the response variables, included in separate models. Perches are in the intercept. P-values ≤ 0.05 are denoted in bold. Likelihood-Ratio Tests' p-values and R2 marginal are reported for each model.

		Estimate	**Std. Error**	**Z value**	**P-value**	**LRT test p-value**	**R^2 marginal**
Seed density	(Intercept)	6.755	0.584	11.562	**<0.001**	**<0.001**	0.35
	Roost	-4.355	0.5361	-8.125	**<0.001**		
Seed species richness	(Intercept)	1.056	0.200	5.273	**<0.001**	**<0.001**	0.27
	Roost	-1.687	0.227	-7.413	**<0.001**		

Seedling density	(Intercept)	5.680	0.419	13.54	**<0.001**	**<.001**	0.61
	Roost	-5.274	0.409	-12.89	**<0.001**		
Seedling richness	(Intercept)	2.072	0.124	16.62	**<0.001**	**<0.001**	0.82
	Roost	-3.314	0.185	-17.91	**<0.001**		

Table S10. Results from a generalized linear mixed-effects models (GLMM) comparing seed size between treatments (bracken, roosts, forest and perches). Bracken is in the intercept. P-values ≤ 0.05 are denoted in bold. The Likelihood-Ratio Tests' p-value and R2 marginal are reported for the model.

		Estimate	**Std. Error**	**Z value**	**P-value**	**LRT test p-value**	**R^2 conditional**
Seed size	(Intercept)	0.949	0.352	2.701	**0.006**	**<0.001**	0.30
	Roosts	0.663	0.287	2.306	**0.02**		
	Forest	1.563	0.287	5.438	**<0.001**		
	Perches	0.838	0.286	2.916	**0.003**		

Table S11. List of seedling species registered in the recruitment plots. For each species, disperser agent (bat, bird or both), life form (tree or non-tree species) and the number of seedlings found.

Family	**Morphospecies**	**Disperser agent**	**Life form**	**No. of seedlings**
Actinidiaceae	*Saurauia peruviana*	Bird	tree	3
Anacardiaceae	*Mauria heterophylla*	Bird	tree	4
Annonaceae	*Guatteria glauca*	Bird	tree	1
Annonaceae	*Guatteria oblongifolia*	Bird	tree	4
Aquifoliaceae	*Ilex boliviana*	Bird	non-tree	1
Aquifoliaceae	*Ilex goudotii*	Bird	tree	3
Aquifoliaceae	*Ilex* sp.	Bird	tree	1

Araceae	*Anthurium acebeyae*	Bat/bird	non-tree	3
Araceae	*Anthurium grande*	Bat/bird	non-tree	1
Araceae	*Anthurium ottobuchtienii*	Bat/bird	non-tree	2
Araceae	*Anthurium* sp.	Bat/bird	non-tree	2
Araceae	*Anthurium weberbaueri*	Bat/bird	non-tree	1
Araceae	Araceae	Bat/bird	non-tree	2
Araceae	*Stenospermation rusbyi*	Bat/bird	non-tree	1
Araliaceae	*Dendropanax sp.*	Bird	tree	20
Araliaceae	*Oreopanax membranaceus*	Bird	tree	2
Araliaceae	*Oreopanax trollii*	Bird	tree	7
Arecaceae	*Geonoma* sp.	Bird	tree	8
Chloranthaceae	*Hedyosmum angustifolium*	Bat/bird	tree	24
Chloranthaceae	*Hedyosmum racemosum*	Bat/bird	tree	150
Clusiaceae	*Clusia elongata*	Bird	tree	189
Clusiaceae	*Clusia lechleri*	Bird	tree	94
Clusiaceae	*Clusia trochiformis*	Bird	tree	33
Ericaceae	Ericaceae	Bird	non-tree	8
Ericaceae	*Gaultheria buxifolia*	Bird	non-tree	5
Ericaceae	*Gaultheria erecta*	Bird	non-tree	438
Ericaceae	*Gaultheria eriophylla*	Bird	non-tree	65
Ericaceae	*Gaultheria reticulata*	Bird	non-tree	144
Ericaceae	*Gaultheria vaccinioides*	Bird	non-tree	56
Ericaceae	*Vaccinium floribundum*	Bird	non-tree	9
Euphorbiaceae	*Alchornea brittonii*	Bird	tree	16

Euphorbiaceae	*Alchornea glandulosa*	Bird	tree	1
Euphorbiaceae	*Alchornea grandiflora*	Bird	tree	13
Euphorbiaceae	*Alchornea* sp.	Bird	tree	1
Euphorbiaceae	*Alchornea triplinervia*	Bird	tree	13
Euphorbiaceae	*Tetrorchidium andinum*	Bird	tree	1
Euphorbiaceae	*Tetrorchidium macrophyllum*	Bird	tree	2
Hypericaceae	*Vismia crassa*	Bat	tree	23
Hypericaceae	*Vismia pozuzoensis*	Bat	tree	8
Hypericaceae	*Vismia rusbyi*	Bat	tree	14
Hypericaceae	*Vismia* sp.	Bat	tree	4
Lauraceae	*Aiouea montana*	Bird	tree	10
Lauraceae	*Aniba* sp.	Bird	tree	3
Lauraceae	*Beilschmiedia latifolia*	Bird	tree	8
Lauraceae	*Beilschmiedia tovarensis*	Bird	tree	4
Lauraceae	*Nectandra acutifolia*	Bird	tree	10
Lauraceae	*Nectandra cuspidata*	Bird	tree	61
Lauraceae	*Ocotea caesifolia*	Bird	tree	2
Lauraceae	*Ocotea comata*	Bird	tree	1
Lauraceae	*Persea bilocularis*	Bird	tree	1
Lauraceae	*Persea* sp.	Bird	tree	1
Melastomataceae	*Leandra carassana*	Bird	non-tree	70
Melastomataceae	*Leandra* sp.	Bird	non-tree	35
Melastomataceae	Melastomataceae	Bird	non-tree	21
Melastomataceae	*Miconia brittonii*	Bird	tree	7
Melastomataceae	*Miconia cordata*	Bird	non-tree	15
Melastomataceae	*Miconia cyanocarpa*	Bird	non-tree	8
Melastomataceae	*Miconia cyanocarpa var. dendritica*	Bird	non-tree	74

Melastomataceae	*Miconia cyanocarpa var. hirsuta*	Bird	tree	34
Melastomataceae	*Miconia cyanocarpa var. parvifolia*	Bird	tree	364
Melastomataceae	*Miconia cyanocarpa var. rotundifolia*	Bird	non-tree	4
Melastomataceae	*Miconia elongata*	Bird	non-tree	18
Melastomataceae	*Miconia hookeriana*	Bird	non-tree	1
Melastomataceae	*Miconia hygrophila*	Bird	tree	151
Melastomataceae	*Miconia leacrenata*	Bird	non-tree	936
Melastomataceae	*Miconia micrantha*	Bird	non-tree	14
Melastomataceae	*Miconia minutiflora*	Bird	non-tree	1
Melastomataceae	*Miconia plumifera*	Bird	non-tree	37
Melastomataceae	*Miconia rugosa*	Bird	non-tree	5
Melastomataceae	*Miconia ruizii*	Bird	non-tree	15
Melastomataceae	*Miconia* sp nov.	Bird	non-tree	4
Melastomataceae	*Miconia* sp.	Bird	non-tree	49
Melastomataceae	*Miconia sublanata*	Bird	non-tree	1
Melastomataceae	*Miconia theaezans*	Bird	tree	12
Melastomataceae	*Miconia uvifera*	Bird	non-tree	4
Monimiaceae	*Mollinedia repanda*	Bird	tree	1
Monimiaceae	*Mollinedia steinbachiana*	Bird	tree	10
Moraceae	*Ficus* sp.	Bat/bird	tree	3
Moraceae	*Pseudolmedia boliviana*	Bat/bird	tree	1
Myricaceae	*Morella pubescens*	Bird	tree	6
Myrtaceae	*Myrcia fallax*	Bird	tree	7

Myrtaceae	*Myrcia fenzliana*	Bird	tree	8
Myrtaceae	*Myrcia lochonphylla*	Bird	tree	1
Myrtaceae	*Myrcia paivae*	Bird	tree	263
Myrtaceae	*Myrcia* sp.	Bird	tree	5
Myrtaceae	*Myrcia splendens*	Bird	tree	15
Myrtaceae	*Myrcia subglabra*	Bird	tree	5
Myrtaceae	*Siphoneugena occidentalis*	Bird	tree	1
Myrtaceae	*Siphoneugena sp.*	Bird	tree	3
Nyctaginaceae	*Neea hermaphrodita*	Bird	tree	1
Nyctaginaceae	*Neea* sp.	Bird	tree	3
Pentaphylacaceae	*Ternstroemia polyandra*	Bird	tree	2
Phyllanthaceae	*Hieronyma fendleri*	Bird	tree	30
Piperaceae	*Peperomia buchtienii*	Bat/bird	non-tree	20
Piperaceae	*Peperomia* sp.	Bat/bird	non-tree	45
Piperaceae	*Peperomia trinervis*	Bat/bird	non-tree	18
Piperaceae	*Piper bangii*	Bat/bird	tree	1
Piperaceae	*Piper crassinervium*	Bat/bird	non-tree	4
Piperaceae	*Piper elongatum*	Bat/bird	tree	12
Piperaceae	*Piper formosum*	Bat/bird	non-tree	9
Piperaceae	*Piper oxyphyllum*	Bat/bird	non-tree	29
Piperaceae	*Piper pilirameum*	Bat/bird	non-tree	1
Piperaceae	*Piper puberulinerve*	Bat/bird	non-tree	3
Piperaceae	*Piper pubiovarium*	Bat/bird	non-tree	48
Piperaceae	*Piper* sp.	Bat/bird	tree	33
Piperaceae	*Piper trichorhachis*	Bat/bird	non-tree	6

Piperaceae	*Piper trigoniastrifolium*	Bat/bird	non-tree	20
Primulaceae	*Myrsine coriaceae*	Bird	tree	834
Primulaceae	*Myrsine latifolia*	Bird	tree	2
Primulaceae	*Myrsine pellucida*	Bird	tree	157
Primulaceae	*Stylogyne ambigua*	Bird	tree	2
Rhamnaceae	*Rhamnus sphaerosperma*	Bird	tree	8
Rosaceae	*Prunus pearcei*	Bird	tree	1
Rosaceae	*Prunus* sp.	Bird	tree	1
Rosaceae	*Rubus boliviensis*	Bird	non-tree	74
Rubiaceae	*Coccocypselum lanceolatum*	Bird	non-tree	197
Rubiaceae	*Coussarea boliviensis*	Bird	tree	10
Rubiaceae	*Faramea candelabrum*	Bird	tree	8
Rubiaceae	*Faramea* sp.	Bird	tree	4
Rubiaceae	*Galium hypocarpium*	Bird	non-tree	53
Rubiaceae	*Galium noxium*	Bird	non-tree	125
Rubiaceae	*Galium* sp.	Bird	non-tree	4
Rubiaceae	*Hoffmannia* sp.	Bird	non-tree	1
Rubiaceae	*Notopleura plagiantha*	Bird	non-tree	1
Rubiaceae	*Palicourea attenuata*	Bird	non-tree	78
Rubiaceae	*Palicourea buchtienii*	Bird	non-tree	73
Rubiaceae	*Palicourea crocea*	Bird	non-tree	4
Rubiaceae	*Palicourea falcata*	Bird	non-tree	1
Rubiaceae	*Palicourea microcarpa*	Bird	tree	10
Rubiaceae	*Palicourea reticulata*	Bird	tree	117

Rubiaceae	*Palicourea* sp.	Bird	non-tree	8
Rubiaceae	*Palicourea subtomentosa*	Bird	non-tree	8
Rubiaceae	*Palicourea tristis*	Bird	tree	65
Rubiaceae	*Psychotria carthagenensis*	Bird	non-tree	5
Rubiaceae	*Psychotria falcata*	Bird	non-tree	1
Rubiaceae	*Randia* sp nov.	Bird	non-tree	8
Rubiaceae	*Randia* sp.	Bird	non-tree	1
Rubiaceae	Rubiaceae	Bird	non-tree	61
Siparunaceae	*Siparuna aspera*	Bird	tree	1
Smilacaceae	*Smilax cognata*	Bird	non-tree	11
Smilacaceae	*Smilax kunthii*	Bird	non-tree	5
Smilacaceae	*Smilax quinquenervia*	Bird	non-tree	1
Smilacaceae	*Smilax* sp.	Bird	non-tree	5
Smilacaceae	*Smilax tomentosa*	Bird	non-tree	8
Solanaceae	*Cestrum racemosum*	Bat/bird	non-tree	1
Solanaceae	*Solanum abutilifolium*	Bat	non-tree	7
Solanaceae	*Solanum clandestinum*	Bat	non-tree	7
Solanaceae	*Solanum mapiriense*	Bat	non-tree	4
Solanaceae	*Solanum maturecalvans*	Bat	non-tree	1
Solanaceae	*Solanum* sp.	Bat	non-tree	2
Solanaceae	*Solanum tenuispinum*	Bat	non-tree	2

Solanaceae	*Solanum velutissimum*	Bat	tree	2
Symplocaceae	*Symplocos arechea*	Bird	tree	5
Symplocaceae	*Symplocos colorata*	Bird	tree	13
Verbenaceae	*Lantana* sp.	Bird	non-tree	8
Viburnaceae	*Viburnum ayavacense*	Bird	non-tree	101
Viburnaceae	*Viburnum incarum*	Bird	non-tree	38
Viburnaceae	*Viburnum seemenii*	Bird	non-tree	24
Viburnaceae	*Viburnum* sp.	Bird	non-tree	17
Vitaceae	*Cissus trianae*	Bird	non-tree	5

Table S12. Model selection table ordered by the Akaike information criterion (AIC), showing ∆AIC between models and weight, obtained from generalized linear mixed-effects models (GLMMs) including a) density and richness of seedlings from tree and non-tree bird-dispersed species and b) density and richness of seedlings from tree and non-tree bat-dispersed species, as the response variables in separate models. The independent variables, that were initially included in all the models, are: treatment (Treat), distance (dist) and their interaction (Treat:Dist).

	Model	**AICc**	**Delta AICc**	**Weight**
a) Bird-dispersed seedlings				
Density of tree seedlings	Treat+Dist+Treat:Dist	1189.3	0	0.99
	Treat+Dist	1198.7	9.43	0.009
	Treat	1209.6	20.29	0
	Dist	1246.8	57.52	0
	Null	1249.8	60.5	0
Richness of tree seedlings	Treat+Dist+Treat:Dist	508.9	0	0.76
	Treat+Dist	511.3	2.42	0.22
	Treat	520.6	11.65	0
	Dist	557.5	48.59	0

	Null	559.4	50.48	0
Density of non-tree seedlings	Treat+Dist	1271.6	0	0.69
	Treat	1273.8	2.2	0.23
	Treat+Dist+Treat:Dist	1276	4.38	0.07
	Null	1313.8	42.22	0
	Dist	1314.7	43.13	0
Richness of non-tree seedlings	Treat+Dist	525.3	0	0.78
	Treat	529.1	3.73	0.12
	Treat+Dist+Treat:Dist	529.5	4.22	0.09
	Dist	560	34.64	0
	Null	560	34.71	0
b) Bat-dispersed seedlings				
Density of tree seedlings	Treat	1118.9	0	0.79
	Treat+Dist	1121.6	2.68	0.21
	Treat+Dist+Treat:Dist	1129.1	10.17	0.005
	Null	1154.1	35.22	0
	Dist	1157.5	35.56	0
Richness of tree seedlings	Treat	484	0	0.82
	Treat+Dist	487	3	0.18
	Treat+Dist+Treat:Dist	494.9	10.94	0.003
	Null	515.3	31.3	0
	Dist	518.6	34.59	0
Density of non-tree seedlings	Treat	589.9	0	0.83
	Treat+Dist	593.6	3.78	0.12
	Treat+Dist+Treat:Dist	595.7	5.85	0.04
	Null	600.9	11.07	0.003
	Dist	605	15.16	0
Richness of non-tree seedlings	Treat	280.5	0	0.8
	Treat+Dist	284.3	3.79	0.12
	Treat+Dist+Treat:Dist	285.1	4.57	0.08
	Null	297.5	16.96	0

Dist	301.6	21.04	0

Table S13. Variables included in the best GLMM models for a) bird- and b) bat-dispersed seedlings. For bird-dispersed species, bracken and distance 0m are in the intercept, and for bat-dispersed species, bracken is in the intercept. P-values ≤ 0.05 are denoted in bold. Likelihood-Ratio Tests' p-values and R2 marginal are reported for each model.

		Estimate	**Std. Error**	**Z value**	**P-value**	**LRT test p-value**	**R2 conditional**
a) Bird-dispersed species							
Density of tree seedlings	(Intercept)	1.418	0.491	2.881	**0.003**	**<0.001**	0.66
	Perch	3.685	0.481	7.673	**<0.001**		
	Forest	2.669	0.493	5.417	**<0.001**		
	Distance 4	0.406	0.524	0.776	0.437		
	Perch:Distance 4	-1.809	0.561	-3.225	**0.001**		
	Forest:Distance 4	-0.856	0.575	-1.49	0.136		
Richness of tree seedlings	(Intercept)	-0.239	0.318	-0.754	0.451	**<0.001**	0.56
	Perch	1.921	0.321	5.981	**<0.001**		
	Forest	1.764	0.324	5.442	**<0.001**		
	Distance 4	0.114	0.357	0.319	0.749		
	Perch:Distance 4	-0.853	0.388	-2.196	**0.02**		
	Forest:Distance 4	-0.401	0.387	-1.037	0.299		
Density of non-tree seedlings	(Intercept)	3.496	0.228	15.3	**<0.001**	**<0.001**	0.47
	Perch	1.365	0.188	7.244	**<0.001**		
	Forest	-0.475	0.225	-2.108	**0.03**		
	Distance 4	-0.338	0.151	-2.239	**0.02**		
	(Intercept)	0.936	0.144	6.514	**<0.001**	**<0.001**	0.4

Richness of non-tree seedlings	Perch	0.769	0.128	5.991	**<0.001**		
	Forest	-0.328	0.159	-2.064	**0.03**		
	Distance 4	-0.283	0.106	-2.666	**0.007**		
b) Bat-dispersed species							
Density of tree seedlings	(Intercept)	-0.226	0.41	-0.552	0.581	**<0.001**	0.22
	Roost	0.959	0.447	2.147	**0.03**		
	Forest	2.473	0.421	5.881	**<0.001**		
Richness of tree seedlings	(Intercept)	-2.333	0.346	-6.75	**<0.001**	**<0.001**	0.23
	Roost	1.016	0.398	2.555	**0.01**		
	Forest	2.072	0.369	5.602	**<0.001**		
Density of non-tree seedlings	(Intercept)	-1.666	0.791	-2.108	**0.03**	**<0.001**	0.22
	Roost	0.402	0.852	0.472	0.636		
	Forest	2.466	0.766	3.218	**0.001**		
Richness of non-tree seedlings	(Intercept)	-3.331	0.582	-5.719	**<0.001**	**<0.001**	0.29
	Roost	0.322	0.686	0.471	0.638		
	Forest	2.205	0.584	3.773	**<0.001**		

Table S14. Family, life strategy, seed length, dispersal and establishment limitation of species registered in the seed rain and recruitment plots in bracken, forest, perches and roosts.

Family	**Species**	**Life strategy**	**Seed length**	**Dispersal limitation**	**Establishment limitation**
		Bracken			
Chloranthaceae	*Hedyosmum racemosum*	Non-pioneer	3.34 ± 0.48	0.93	1
Melastomataceae	*Gaultheria erecta*	Pioneer	0.59 ± 0.06	0.89	0.93
Melastomataceae	*Miconia brittonii*	Pioneer	0.72 ± 0.12	0.93	1
Melastomataceae	*Miconia hygrophila*	Pioneer	0.86 ± 0.04	0.93	0.93
Melastomataceae	*Miconia plumifera*	Pioneer	1.01 ±0.13	0.93	1

Forest					
Actinidiaceae	*Saurauia peruviana*	Non-pioneer	0.87 ± 0.11	0.93	1
Chloranthaceae	*Hedyosmum angustifolium*	Non-pioneer	4.08 ± 0.14	0.79	0.88
Chloranthaceae	*Hedyosmum racemosum*	Non-pioneer	3.34 ± 0.48	0.56	0.71
Euphorbiaceae	*Alchornea glandulosa*	Non-pioneer	5.84 ± 0.51	0.79	1
Euphorbiaceae	*Alchornea triplinervia*	Non-pioneer	3.34 ± 0.21	0.79	0.86
Lauraceae	*Beilschmiedia tovarensis*	Non-pioneer	25.5 ± 3.12	0.86	0.93
Lauraceae	*Nectandra cuspidata*	Non-pioneer	11.52 ± 0.63	0.6	0.79
Melastomataceae	*Leandra carassana*	Pioneer	0.99 ± 0.06	0.57	0.98
Melastomataceae	*Miconia brittonii*	Pioneer	0.72 ± 0.12	0.78	1
Melastomataceae	*Miconia elongata*	Pioneer	0.57 ± 0.04	0.73	0.98
Melastomataceae	*Miconia hygrophila*	Pioneer	0.86 ± 0.04	0.25	0.99
Melastomataceae	*Miconia leacrenata*	Pioneer	0.97 ± 0.21	0.6	0.99
Melastomataceae	*Miconia plumifera*	Pioneer	1.01 ±0.13	0.73	0.92
Melastomataceae	*Miconia theaezans*	Pioneer	0.72 ± 0.09	0.86	1
Melastomataceae	*Miconia uvifera*	Pioneer	0.72 ± 0.12	0.71	1
Myrtaceae	*Myrcia* sp.	Non-pioneer	5.12 ± 0.41	0.79	0.64
Phyllanthaceae	*Hieronyma fendleri*	Non-pioneer	3.45 ± 0.19	0.47	0.91
Piperaceae	*Piper elongatum*	Pioneer	0.88 ± 0.06	0.38	0.99
Piperaceae	*Piper trigoniastrifolium*	Non-pioneer	1.67 ± 0.04	0.66	0.93
Primulaceae	*Stylogyne ambigua*	Non-pioneer	8.23 ± 0.32	0.93	1
Rosaceae	*Rubus boliviensis*	Pioneer	1.67 ± 0.25	0.78	0.99
Rubiaceae	*Faramea candelabrum*	Non-pioneer	11.42 ± 0.99	0.86	0.93

Rubiaceae	*Palicourea attenuata*	Non-pioneer	3.21 ± 0.25	0.82	0.79
Rubiaceae	*Palicourea reticulata*	Non-pioneer	3.79 ± 0.42	0.93	0.93
Rubiaceae	*Palicourea subtomentosa*	Non-pioneer	2.74 ± 0.33	0.93	1
Rubiaceae	*Palicourea tristis*	Non-pioneer	4.45 ± 0.21	0.83	0.86
Rubiaceae	*Psychotria carthagenensis*	Non-pioneer	3.88 ± 0.43	0.82	1
Siparunaceae	*Siparuna tomentosa*	Non-pioneer	4.34 ± 0.23	0.9	1
Smilacaceae	*Smilax* sp.	Pioneer	5.38 ± 0.27	0.93	1
Viburnaceae	*Viburnum ayavacense*	Pioneer	6.73 ± 0.51	0.79	0.82
		Perches			
Chloranthaceae	*Hedyosmum angustifolium*	Non-pioneer	4.08 ± 0.14	0.83	1
Chloranthaceae	*Hedyosmum racemosum*	Non-pioneer	3.34 ± 0.48	0.83	0.83
Ericaceae	*Gaultheria erecta*	Pioneer	0.59 ± 0.06	0.5	0.92
Lauraceae	*Nectandra cuspidata*	Non-pioneer	11.52 ± 0.63	0.83	1
Melastomataceae	*Leandra carassana*	Pioneer	0.99 ± 0.06	0.83	1
Melastomataceae	*Miconia hygrophila*	Pioneer	0.86 ± 0.04	0.38	0.75
Melastomataceae	*Miconia leacrenata*	Pioneer	0.97 ± 0.21	0.72	0.78
Melastomataceae	*Miconia minutiflora*	Pioneer	0.9 ± 0.04	0.55	1
Melastomataceae	*Miconia plumifera*	Pioneer	1.01 ±0.13	0.78	1
Myriaceae	*Morella pubescens*	Pioneer	3.35 ± 0.18	0.67	1
Myrtaceae	*Myrcia* sp.	Non-pioneer	5.12 ± 0.41	0.67	0.67
Phyllanthaceae	*Hieronyma fendleri*	Non-pioneer	3.45 ± 0.19	0.67	1
Piperaceae	*Piper elongatum*	Pioneer	0.88 ± 0.06	0.39	0.89
Rosaceae	*Rubus boliviensis*	Pioneer	1.67 ± 0.25	0.55	0.69

Rubiaceae	*Palicourea attenuata*	Non-pioneer	3.21 ± 0.25	0.83	0.83
Rubiaceae	*Palicourea reticulata*	Non-pioneer	3.79 ± 0.42	0.67	0.83
Solanaceae	*Solanum velutissimum*	Pioneer	2.08 ± 0.58	0.67	1
Symplocaceae	*Symplocos arechea*	Non-pioneer	14.09 ± 3.8	0.83	1
Verbenaceae	*Lantana* sp.	Pioneer	4.16 ± 0.21	0.83	1
Viburnaceae	*Viburnum ayavacense*	Pioneer	6.73 ± 0.51	0.83	0.83
		Roosts			
Hypericaceae	*Vismia crassa*	Non-pioneer	1.62 ± 0.02	0.74	1
Piperaceae	*Piper elongatum*	Pioneer	0.88 ± 0.06	0.74	0.99
Piperaceae	*Piper trigoniastrifolium*	Non-pioneer	1.67 ± 0.04	0.87	1

Table S15. Results of the generalized linear mixed models for dispersal limitation in general and according to their life 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 strategy	(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 strategy	(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		

Table S16. Results of the generalized linear mixed models for establishment limitation in general and according to their life 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 strategy	(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		

Curriculum Vitae

Mario Cesar Mayta Rocabado

Curriculum Vitae March 2025

RESEARCH AND PROFESSIONAL EXPERIENCE

- 2019. **Researcher.** Project: Fortification of generation and transfer of interdisciplinary scientific knowledge of CEAZA, based on the link with the territories and ecosystems of the Coquimbo region. Centro de Estudios Avanzados en Zonas Áridas, Chile.
- 2017. **Researcher.** Project: Evaluation of the effect of the establishment of a pilot stable for the breeding of dairy cattle, as a strategy of adaptive management to climate change, in the Ayllu Corpa. Universidad Mayor de San Andrés, Bolivia.
- 2016. **Research Assistant.** Project: Investigation and rescue of promising species of the Flora of the Tacana I culture, Botanical Garden-Prov. Abel Iturralde. Universidad Mayor de San Andrés, Bolivia.

EDUCATION

- **Ph. D. candidate:** since 2019. Thesis: The role of animal-mediated seed dispersal in the forest regeneration of tropical areas dominated by bracken fern. Advisor – Prof. Dr. Isabell Hensen. Martin-Luther University Halle-Wittenberg, Germany.
- **Master of Science:** 2021**.** Thesis: Vegetation-pollen-climate relationship in mountain ecosystems in the semi-arid region of Chile during the last 4000 years. Advisor – Dr. Antonio Maldonado. Department of Biology, Universidad de La Serena, Chile.
- **Bachelor of Science:** 2017. Thesis: Effect of Tola (*Baccharis incarum*) on the production of Aflatoxin B1. Advisor – Dr. Gloria Rodrigo. Universidad Mayor de San Andrés, Bolivia.

PUBLICATIONS

- **Mayta, C.**, López, C. L., Villegas, M., Aguirre, L. F., Hensen, I. & Gallegos, S. C. 2024. Bird perches and artificial bat roosts increase seed rain and seedling establishment in tropical bracken-dominated deforested areas. Restoration ecology, 32(7): 1-13.
- Gallegos, S. C., **Mayta, C.**, Villegas, M., Ayala, G. M., et al. 2024. Habitat differences in seed-dispersing vertebrates indicate dispersal limitation in tropical bracken-dominated deforested areas. Biotropica, 56(3): 1-15.
- López, C. L., **Mayta, C.**, Fuentes, A. F., et al. 2024. Disentangling the roles of bracken fronds and litter on natural seedling recruitment in fire-disturbed tropical montane habitats. Forest Ecology and Management, 556: 1-9.
- Villegas, M., **Mayta, C.**, López, C. L., Hensen, I. & Gallegos, S. C. 2024. Bird communities respond to the seasonal fruit and flower availability in fragmented tropical Andean landscape. Ornitología Neotropical, 35: 38-45.
- **Mayta, C.** & Maldonado, A. 2022. Climatic and Ecological Changes in the Subtropical High Andes During the Last 4,500 Years. Frontiers in earth Science, 10:833219. doi: 10.3389/feart.2022.833219
- López, C. L., **Mayta, C.**, Naoki, K., Quezada, J. A., Hensen, I. & Gallegos, S. C. 2022. Bracken Fern does not diminish arbuscular mycorrhizal fungus inoculum potential in tropical deforested areas. Mycorrhiza, 32(1): 123-131.
- López, C. L., Domic, A. I., **Mayta, C**., García, E., Quezada, J. A., & Gallegos, S. C. 2021. Pollen limitation and reproductive incompatibility system in a critically endangered tree, Polylepis incarum (Bitter) M. Kessler & Schmidt-Leb (Rosaceae). Neotropical Biodiversity, 7(1): 257-265.
- Velásquez-Noriega, P., **Mayta, C**., Cuba, E., García E., Montaño-Centellas, F. & Krömer, T. 2020. Floral ecology and floral visitors of *Puya atra* (Bromeliaceae), a Bolivian endemic plant. Ecología en Bolivia, 55(1): 36-45.
- López, C. L., Domic, A., **Mayta, C**., García, E. & S. Gallegos. 2018. Variaciones fenológicas de la Queñua (Polylepis incarum, Rosaceae) durante un ciclo annual en la puna mesofitica de La Paz, Bolivia. Ecología Austral. 8: 301-309.

SCIENTIFIC PRESENTATIONS:

- European Conference of Tropical Ecology 2025, “Differences in seed-dispersal networks and functions between tropical montane forest edges and bracken-dominated areas”. Oral presentation.

- European Conference of Tropical Ecology 2025, “Bird perches and artificial bat roosts increase seed rain and seedling establishment in tropical bracken-dominated deforested areas”. Poster presentation.
- V Bolivian Congress of Botany 2023, “Bird perches and artificial bat roosts as restoration strategies for burned areas in Yungas”. Oral presentation.
- V Bolivian Congress of Ecology 2022, “Differences in seed rain between forest and burned areas and their relationship with seedling establishment in the Yungas of La Paz”. Oral presentation.
- First Bolivian Congress on Ecological Restoration 2021, " Artificial bat roosts to attract fruit bats and help the regeneration of deforested areas in the Yungas of La Paz". Oral presentation.
- IV Bolivian Congress of Botany 2019, " Vegetation-climate relationship in Cordillera ecosystems in the semi-arid region of Chile during the last 3000 years ". Oral presentation

Eigenständigkeitserklärung

Hiermit erkläre ich, dass ich die vorliegende Doktorarbeit mit dem Titel “The role of animal-mediated seed dispersal in the forest regeneration of tropical areas dominated by bracken fern” eigenständig und ohne fremde Hilfe verfasst sowie keine anderen als die im Text angegebenen Quellen und Hilfsmittel verwendet habe. Textstellen, welche aus verwendeten Werken wörtlich oder inhaltlich übernommen wurden, wurden von mir als solche kenntlich gemacht. Ich erkläre weiterhin, dass ich mich bisher noch nie um einen Doktorgrad beworben habe. Die vorliegende Doktorarbeit wurde bis zu diesem Zeitpunkt weder bei der Naturwissenschaftlichen Fakultät I – Biowissenschaften der Martin-Luther-Universität Halle-Wittenberg noch einer anderen wissenschaftlichen Einrichtung zum Zweck der Promotion vorgelegt.

Mario Cesar Mayta Rocabado, Halle (Saale), 19.03.2025