


Habitat differences in seed-dispersing vertebrates indicate dispersal limitation in tropical bracken-dominated deforested areas

Silvia C. Gallegos^{1,2,3}  | Cesar Mayta^{1,2,3}  | Mariana Villegas^{3,4}  | Guido M. Ayala^{5,6}  | Kazuya Naoki^{4,7}  | Josef Rechberger⁸ | Valeria Rojas⁷ | María E. Viscarra⁵  | Nuria Bernal-Hoverud^{5,8,9}  | Mauricio Espejo³ | Isabell Hensen^{1,10} 

¹Institute of Biology/Geobotany and Botanical Garden, Martin Luther University Halle-Wittenberg, Halle, Germany

²Herbario Nacional de Bolivia, Instituto de Ecología, Carrera de Biología, Universidad Mayor de San Andrés, La Paz, Bolivia

³Santiago de Chirca Biological Station, La Paz, Bolivia

⁴Instituto de Ecología, Carrera de Biología, Universidad Mayor de San Andrés, La Paz, Bolivia

⁵Greater Madidi-Tambopata Landscape Program, Wildlife Conservation Society, La Paz, Bolivia

⁶Department of Biology & Centre Environmental and Marine Studies (CESAM), University of Aveiro, Aveiro, Portugal

⁷Carrera de Biología, Universidad Mayor de San Andrés, La Paz, Bolivia

⁸Red Boliviana de Mastozoología, La Paz, Bolivia

⁹Department of Biological Sciences, Texas Tech University, Lubbock, Texas, USA

¹⁰German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Leipzig, Germany

Correspondence

Silvia C. Gallegos, Institute of Biology/ Geobotany and Botanical Garden, Martin Luther University Halle-Wittenberg, Grosse Steinstrasse 79/80, Halle D-06108, Germany.
Email: silvia.gallegos.a@gmail.com

Funding information

Deutsche Forschungsgemeinschaft, Grant/Award Number: He 3041/23-1; The Academy of Sciences for the Developing World, Grant/Award Number: 19-107 RG/BIO/LA_I-FR3240310157

Associate Editor: Jennifer Powers

Handling Editor: Kim McConkey

Abstract

Shifting agriculture and anthropogenic fires are among the main causes of deforestation in the tropics. After fire and land abandonment, vast deforested areas are commonly dominated by the bracken fern *Pteridium* for long periods. Although forest regeneration in bracken-dominated areas is mainly hindered by dispersal limitation, little is known about the role of seed-disperser communities in slow forest succession. Our objective was to unravel the differences in the properties of the seed-disperser communities between forests and bracken-dominated areas to assess their role in dispersal limitation to foster ecological restoration. We compared species richness, diversity, abundance, and composition of seed-dispersing birds, bats, and medium and large terrestrial mammals between both habitats in a montane forest of Bolivia. The species richness and diversity were similar for bats and higher for birds in bracken-dominated areas than in the forest, but species composition was different between both habitats and groups. Although species composition was similar between both habitats for terrestrial mammals, the abundance was higher in the forest than in bracken-dominated areas. Differences in species composition of seed-dispersing birds and bats could be one of the main causes of dispersal limitation in forest regeneration in tropical bracken-dominated areas. The few shared species between both

This is an open access article under the terms of the [Creative Commons Attribution](https://creativecommons.org/licenses/by/4.0/) License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

© 2024 The Authors. *Biotropica* published by Wiley Periodicals LLC on behalf of Association for Tropical Biology and Conservation.

habitats could explain the low seed rain of animal-dispersed forest tree species in bracken-dominated areas and the consequent hindered forest regeneration. Future studies relevant to natural forest regeneration should focus on analyzing the effects of animal-attractants such as perches, artificial bat-roosts, and seedling transplants on disperser communities, seed dispersal effectiveness, and forest regeneration.

Abstract in Spanish is available with online material.

KEYWORDS

bats, birds, Bolivia, camera traps, frugivory, *Pteridium*, restoration, terrestrial mammals

1 | INTRODUCTION

Deforestation is one of the main causes of forest loss and biodiversity decline worldwide, negatively affecting species richness, community composition and biotic interactions (Curtis et al., 2018; Haddad et al., 2015; Marjakangas et al., 2020). Deforestation is threatening tropical montane forests, which are biodiversity hotspots of high conservation value (Beck & Richter, 2008; Karger et al., 2021). The main causes of deforestation in tropical montane forests are shifting agriculture, logging and anthropogenic fires (Behling, 2008; FAO, 2020; Karger et al., 2021). After fire or land abandonment, bracken fern, *Pteridium* spp., frequently colonizes deforested areas and dominates the vegetation for long periods, hindering forest regeneration (Carvalho et al., 2022; Hartig & Beck, 2003; Ssali et al., 2017). Since most tropical forest tree species are dispersed by animals (Acosta-Rojas et al., 2023; Howe & Smallwood, 1982; Moles et al., 2007), forest regeneration in the deforested areas is highly dependent on seed-dispersing animals (Catterall, 2018; Costa et al., 2022; Wunderle, 1997). Although the seed rain and seedling recruitment of forest tree species in bracken-dominated areas is low (Gallegos et al., 2016; Saavedra et al., 2015; Ssali et al., 2018), the properties of seed disperser communities in tropical bracken-dominated areas have not been studied (but see Maya-Elizarrarás & Schondube, 2015).

Birds, large mammals, and bats are the most important seed dispersers in tropical forests (Howe & Smallwood, 1982; Medellín & Gaona, 1999). Therefore, these agents are essential to ensure the establishment of animal-dispersed trees in deforested habitats (Catterall, 2018; Howe, 2016; Muscarella & Fleming, 2007; Wunderle, 1997). This is particularly important for large-seeded plant species that are mainly dispersed by large frugivores, which are the first animals to be extirpated from disturbed habitats (Magioli et al., 2021; Markl et al., 2012). Deforestation threatens animal species and their ecological functions with cascading effects (Magioli et al., 2021). Plant-frugivore interactions are affected by deforestation in terms of quantity and diversity of visits, seed removal, and seed dispersal distance (Fontúrbel et al., 2015; Marjakangas et al., 2020; Markl et al., 2012). Furthermore, many seed dispersers avoid most deforested areas due to the lack of perch structures, food resources, hides, roosts, and vegetation complexity (Brady et al., 2011; Wunderle, 1997), consequently reducing the probability

of seed arrival into deforested areas. These negative impacts are detrimental to forest recovery in deforested areas, especially if they are characterized by dispersal limitation.

Bracken occurs in all continents except Antarctica (Marrs & Watt, 2006) and is considered an invasive species in most parts of the world (Amouzgar et al., 2022; Hartig & Beck, 2003; Marrs et al., 2000). It dominates vegetation after fire or post-agricultural land abandonment and is very difficult to control (Alday et al., 2013; Pakeman et al., 2005; Suazo-Ortuño et al., 2015). Despite its dominance for long periods, the role of bracken in tropical forest regeneration is still controversial. Some authors claim that bracken inhibits forest regeneration because the high density of its fronds and litter shade other plants and act as physical barriers for seeds reaching the ground and seedling growth (Carvalho et al., 2022; Levy-Tacher et al., 2015; Marrs et al., 2000; Paz et al., 2022), that is, habitat limitation (sensu Münzbergová & Herben, 2005). Other authors suggest that habitat is hardly limited, as tree seedling survival and growth rates are similar in bracken-dominated areas and forest (Gallegos et al., 2016). Bracken presence reduces photosynthetic and water stress in adult plants (Paz et al., 2022). Tree seedling performance in bracken-dominated areas is higher than after bracken removal, both for naturally regenerating tree seedlings and after seed addition (Gallegos et al., 2015, 2016; López et al., 2023). Similar patterns were found in South America and Africa (Palomeque et al., 2017; Silva Matos & Belinato, 2010; Ssali et al., 2017, 2018). Therefore, Gallegos et al. (2016) suggest that tropical bracken-dominated areas are limited by seed dispersal rather than habitat (sensu Münzbergová & Herben, 2005). This means that tree species cannot establish in bracken-dominated areas because their seeds do not arrive, rather than they cannot grow there. Dispersal limitation was associated with lower species richness and density in seed rain, soil seed bank and tree seedlings in bracken-dominated areas, compared to forests (Gallegos et al., 2016; Günter et al., 2007; Palomeque et al., 2017; Saavedra et al., 2015; Ssali et al., 2017, 2018). Consequently, if the main limiting factor for forest regeneration in bracken-dominated areas is dispersal limitation and the main seed dispersers of most forest tree species are animals, the study of the seed disperser community is essential to understand the main filters of forest regeneration in such widely distributed habitats. This knowledge is essential for proposing restoration strategies to accelerate forest regeneration.

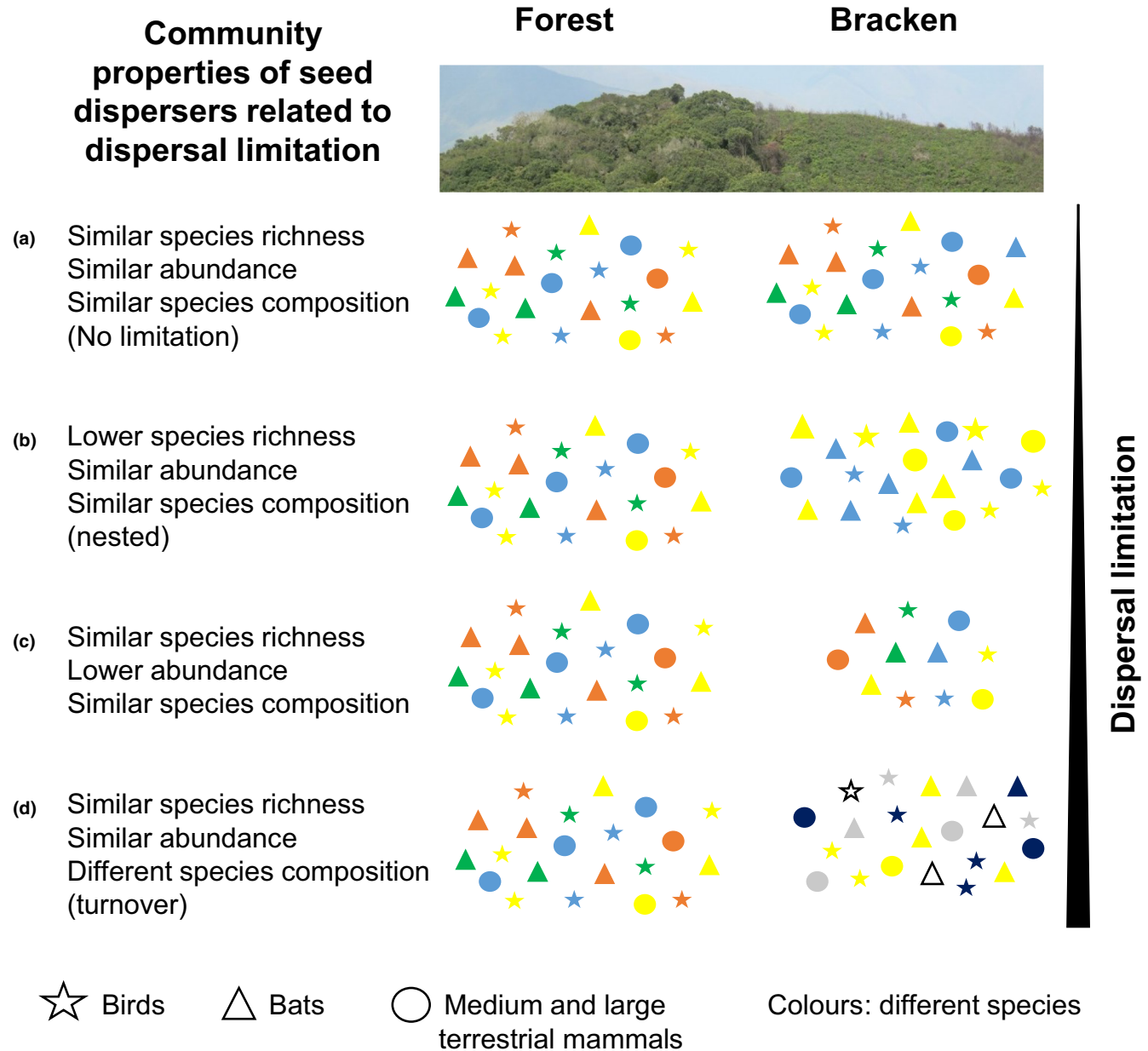


FIGURE 1 Scheme of likely scenarios of differences in the seed disperser community properties between the forest (left) and the bracken-dominated area (right) that could be related to dispersal limitation. The likely scenarios are ordered from lower (a) to higher (d) expected effects on dispersal limitation.

Dispersal limitation could be related to lower species richness or abundance of seed-dispersers in the deforested area compared to the forest (Figure 1b,c), or to differences in species composition of seed dispersers in the two habitats (Figure 1d). Differences in the community properties of seed-dispersers can be detrimental for forest regeneration in tropical disturbed areas, because of cascading effects on seed rain and, consequently, seedling establishment. To date, few studies evaluated seed disperser communities in tropical bracken-dominated areas (Maya-Elizarrarás & Schondube, 2015) and few studies analyzed the whole seed disperser community in deforested areas and adjacent forests at the same spatial and temporal scales (Catterall, 2018; Escribano-Avila et al., 2014; Santos et al., 1999). Therefore, our main

objective is to unravel the differences in the community properties of seed dispersers between forests and bracken-dominated areas to assess their role in dispersal limitation (Figure 1). We aim to answer the following questions: What are the differences in species richness, diversity, and abundance of seed-dispersing birds, bats and terrestrial mammals between a tropical montane forest and the surrounding bracken-dominated areas? Does the species composition of seed dispersers differ between the two habitats? Are the dominant species in the forest also common in deforested areas? To our knowledge, this is the first study to compare seed-dispersing communities from different vertebrate groups between bracken-dominated areas and forests in the tropics.

2 | METHODS

2.1 | Study area

The study was carried out between 2020 and 2022 on the eastern slope of the Andes, in the vicinity of Chulumani village, Sud Yungas, La Paz, Bolivia (16°24' S, 67°31' W). The study area is located in the tropical montane humid forest between 1850 and 2450 m a.s.l. (Figure S1). The mean annual temperature is 20.5°C and the mean annual precipitation is 1400 mm, with a peak between December and February (Molina-Carpio et al., 2019). The landscape is heavily deforested by frequent human-induced fires and the extension of coca (*Erythroxylum coca*) plantations for traditional use (Killeen et al., 2008). Today, there are only two relicts of mature continuous forest (Lippok et al., 2014) of about 1000 and 3500 ha in the area. These relicts are surrounded by fire-degraded areas dominated by the tropical bracken fern *Pteridium esculentum* subsp. *arachnoideum* (Kaulf.) J.A.Thomson (Schwartzburd et al., 2018), successional shrubs, and grasslands (Lippok et al., 2013).

2.2 | Experimental design

2.2.1 | Birds and bats

To capture birds and bats, we installed understory mist nets at the edges of the two forest fragments at eight sites 1–12 km apart (Figure S1). Each site was sampled four times between March 2020 and June 2021, covering all seasons during the sampling period. We placed eight (9 × 2.5 m) mist nets 0.5 m from the ground, at each site, four in the forest and four in the bracken-dominated area, each 20 m inward or outward from the forest border. Mist nets were open for 3 days at each site, from 0630 to 1830 h to capture birds, and from 1830 to 2300 h to capture bats, with a total capture effort of 4067 net-hours for birds and 2576 net-hours for bats. After capture, birds and bats were kept for 20–30 min in cloth bags to collect regurgitates and fecal samples. The captured individuals were then identified, measured, tagged, and released. All species that had intact seeds in their feces were included as seed dispersers in the analyses. Other captured species were classified as seed dispersers only if they frequently disperse seeds according to the literature (Billerman et al., 2022; Herzog et al., 2016; Stotz et al., 1996).

2.2.2 | Terrestrial mammals

To survey terrestrial mammals, we established 100 m-long transects perpendicular to the forest edge at five sites separated by at least 2 km (Figure S1). In the first sampling period from October 2020 to September 2021, we installed two Reconyx Hyperfire2 TM camera traps with infrared sensors at each transect, one in the forest interior, 50 m from the forest edge, and one in the bracken-dominated area, 50 m from the forest edge. In the second sampling period, from

February to June 2022, we installed four camera traps at each transect: two in each habitat, 50 and 20 m inward and outward from the forest border. The cameras were placed near animal paths, without bait, tied to a pole or tree 50–80 cm above the ground. The cameras were programmed to take pictures 24 h a day, with high-sensitivity and 5-s interval between consecutive pictures (10 per trigger). Cameras were checked every 3 months, when batteries and memory cards were replaced. The photographs were handled using NAIRA III free software (Pulido et al., 2018), and the species were classified manually by three experts. We considered independent events when consecutive photographs of individuals of the same species were taken more than 24 h apart at the same camera station to avoid overestimation of unmarked animals (Jax et al., 2015). In the second sampling period, data from cameras at 20 and 50 m inwards and outwards from the forest edge were pooled together before analysis. The total sampling effort was 4558 days. We detected 7255 photographs with terrestrial mammals (including small, medium, and large mammals). We classified as seed dispersers all registered medium and large terrestrial mammals (>800 g, hereafter terrestrial mammals) that had at least 20% of their diet consisting of fruits/seeds (Marjakangas et al., 2020) according to the Elton Traits database (Wilman et al., 2014). We removed all the other mammals from the analyses.

2.3 | Data analysis

We performed separate Generalized Mixed Effects Models to compare species richness and abundance of seed-dispersing birds, bats, and terrestrial mammals in the forest and bracken-dominated areas with the package lme4 (Bates et al., 2015). All models included habitat (forest vs. bracken) as the fixed independent variable and site as the random effect, to control for the study design. For each animal group, we included species richness or abundance as the response variables, considering a Poisson distribution of errors or negative binomial in cases of overdispersion. To analyze diversity, we built Linear Mixed Effects Models (LMM) with a similar structure, including the inverse Simpson's index as the response variable (Magurran, 2004). For terrestrial mammals, we calculated the camera trapping rates or relative abundance index (RAI) per camera trap (to consider the variation among cameras, sites and habitats) as in Mandujano (2022). We built a LMM including the RAI as the response variable. In every case, we calculated *p* values from log-likelihood ratio tests (LRT) comparing each model with a null model containing site as random effect, with the package MuMIn (Barton, 2022). For each model, we also calculated the marginal coefficient of determination R^2 to obtain the variance explained by the habitat. We also quantified the sample completeness of the surveys and compared species richness between habitats with individual-based rarefaction curves with the package iNEXT.4steps (Chao et al., 2020).

To assess the effect of habitat on community composition, we performed permutational multivariate analyses of variance (PERMANOVA) using the *adonis2* function from the *vegan* package

(Oksanen et al., 2022), setting the locality as strata to consider the block design, and the Jaccard dissimilarity method, and 999 permutations to calculate p values. To visualize differences in community composition, we performed nonmetric multidimensional scaling (NMDS) with the Jaccard dissimilarity index for birds and bats, and the Bray-Curtis index for terrestrial mammals, using the metaMDS function from the package vegan (Oksanen et al., 2022). Finally, we plotted rank-abundance curves to visualize the distribution of species abundance in forest and bracken-dominated communities. Due to the high degradation of our study area, we compared the species that were detected during our surveys (Table S1) with those included on a reference list that was built from the findings of previous studies in the area and its surroundings (Tables S2–S4). All analyses were conducted in R version 4.2.1 (R Core Team, 2022).

3 | RESULTS

For seed-dispersing birds, we captured 37 species (173 individuals): 14 species (63 individuals) in the forest, and 32 species (110 individuals) in the bracken-dominated area (Table S1). For bats, we captured 12 species (57 individuals): 8 species (34 individuals) in the forest, and 8 species (23 individuals) in the bracken-dominated area. In the camera traps, we recorded nine species of medium and large terrestrial mammals (370 independent events): nine species (226 individuals) in the forest and eight species (144 individuals) in the bracken-dominated areas.

The richness and diversity of the bird species were significantly higher in the bracken-dominated area than in the forest (Richness: $\chi^2_1=11.164$, $p<.001$, $R^2=0.33$, Figure 2a; Diversity: $\chi^2_1=7.88$, $p=.005$, $R^2=0.44$, Figure 2d), while the abundance of birds was similar between habitats ($\chi^2_1=2.073$, $p=.149$, $R^2=0.15$, Figure 2g). The richness, diversity and abundance of bat species were similar between the forest and the bracken-dominated area (Richness: $\chi^2_1=0.03$, $p=.862$, $R^2=0.002$, Figure 2b; Diversity: $\chi^2_1=0.263$, $p=.608$, $R^2=0.02$, Figure 2e; Abundance: $\chi^2_1=2.136$, $p=.144$, $R^2=0.098$, Figure 2h). The richness and diversity of terrestrial mammal species were similar between the forest and the bracken-dominated area (Richness: $\chi^2_1=0.002$, $p=.96$, $R^2=0.002$, Figure 2c; Diversity: $\chi^2_1=0.69$, $p=.406$, $R^2=0.03$, Figure 2f), while the relative abundance was higher in the forest than in the bracken-dominated area (RAI: $\chi^2_1=6.004$, $p=.014$, $R^2=0.67$, Figures 1c and 2i). We observed the same patterns of species richness for the three groups after rarefaction (Figure S2).

The completeness analysis for seed-dispersing birds revealed that in the forest we sampled 26% of the total species assemblage, with the detected species covering 86% of the assemblage's individuals and 100% of the most abundant species ($q=0, 1, 2$ in Figure S2a). In the bracken-dominated habitat, we sampled 69% of the total bird species assemblage, with the detected species covering 87% of the assemblage's individuals and 99% of the most abundant species. For bats, in the forest, we sampled 51% of the total species assemblage, with the

detected species covering 88% of the assemblage's individuals, and 99% of the most abundant species ($q=0, 1, 2$ in Figure S2c). In the bracken-dominated habitat, we sampled 79% of the total bat species assemblage, with the detected species covering 88% of the assemblage's individuals, and 96% of the most abundant species. For terrestrial mammals, in the forest, we sampled 100% of the species ($q=0, 1, 2$ in Figure S2e) while in the bracken-dominated habitat, we sampled 94% of the total species assemblage, with the detected species comprising 99% of the assemblage's individuals, and 99% of the most abundant species.

We found significant differences in species composition between forest and bracken-dominated areas for birds (PERMANOVA, $R^2=0.23$, $F=3.91$, $p=.008$, Figures 1d and 3a) and bats (PERMANOVA, $R^2=0.18$, $F=2.58$, $p=.03$, Figures 1d and 3b), but not for terrestrial mammals (PERMANOVA, $R^2=0.05$, $F=0.375$, $p=.75$, Figure 3c).

Of the three most common species of birds recorded in the forest, only one was also among the most common birds recorded in the bracken-dominated area (*Mionectes striaticollis*, Figure 4a). Out of the remaining two, one species (*Chiroxiphia boliviana*) was rare in the bracken-dominated area, while the other (*Atlapetes rufinucha*) was only the fifth most common species in the bracken-dominated area. Besides *M. striaticollis*, the other two species of common birds in the bracken-dominated area (*Elaenia albiceps* and *E. obscura*) were absent in the forest.

Two of the three most common bat species detected in the forest were also among the most common bats in the bracken-dominated area (*Carollia perspicillata* and *Sturnira tildae*, Figure 4b), while the other common bat species in the forest (*Carollia brevicauda*) was only the fifth most common species in the bracken-dominated area. The most common bat species in the bracken-dominated area (*Sturnira oporaphilum*) was scarce in the forest.

For terrestrial mammals, two of the three most common species in the forest were also among the three most common species in the bracken-dominated area (*Mazama americana* and *Dasyprocta variegata*, Figure 4c). The second most common species in the forest (*Cuniculus paca*) was scarce in the bracken-dominated area. The third most common species in the bracken-dominated area (*Eira barbara*) was the sixth most common species in the forest.

4 | DISCUSSION

We compared the communities of seed-dispersing birds, bats, and terrestrial mammals in an Andean tropical montane forest and surrounding bracken-dominated areas to assess their contribution to dispersal limitation. We found that species richness, diversity, and abundance were similar for bats and higher for birds in the bracken-dominated areas than in the forest, but species composition was different between habitat types for both groups. Terrestrial mammals had a similar species composition in both habitats, but a higher abundance in the forest than in the bracken-dominated area. The high turnover in the species composition of seed dispersers could be

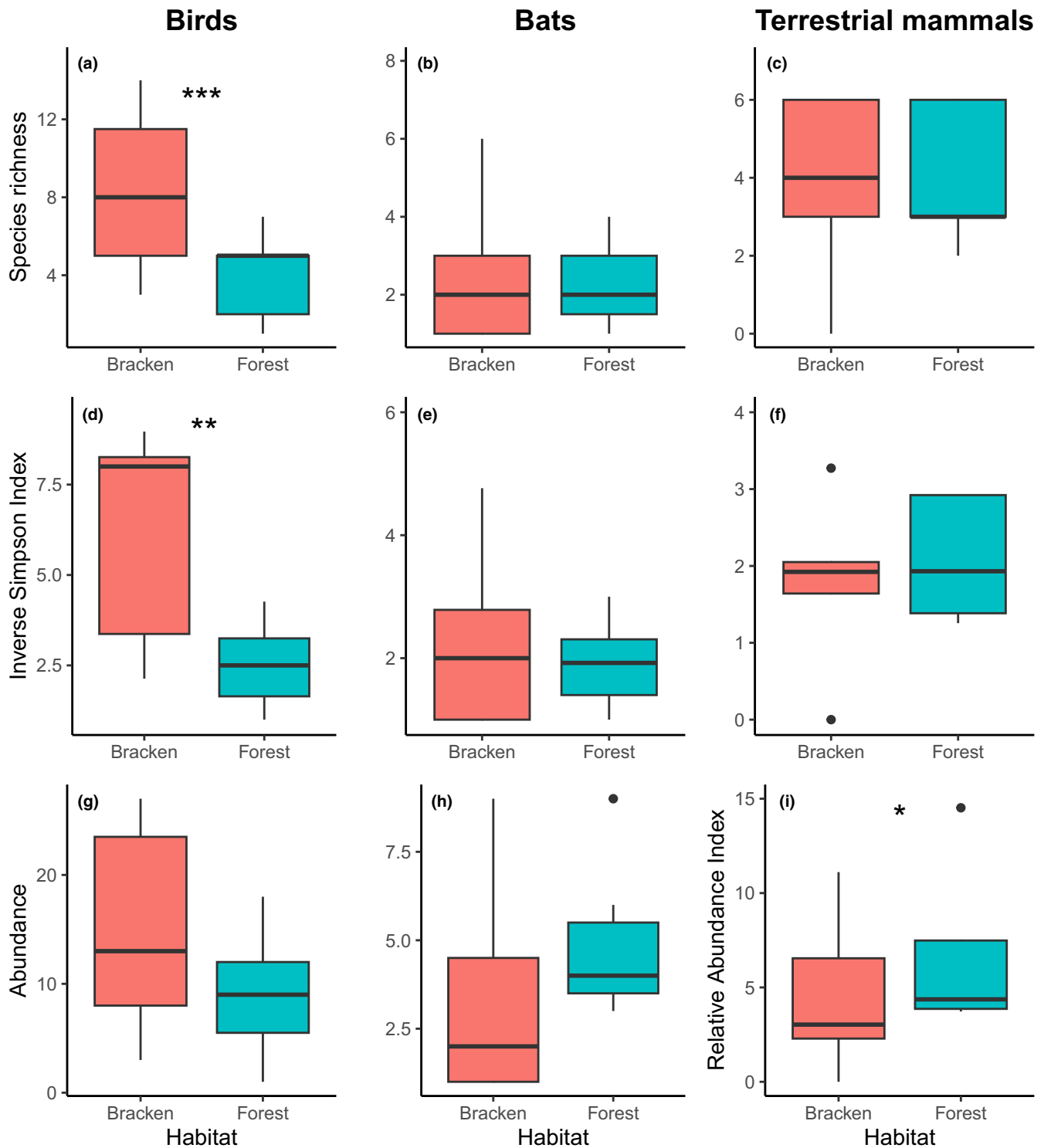


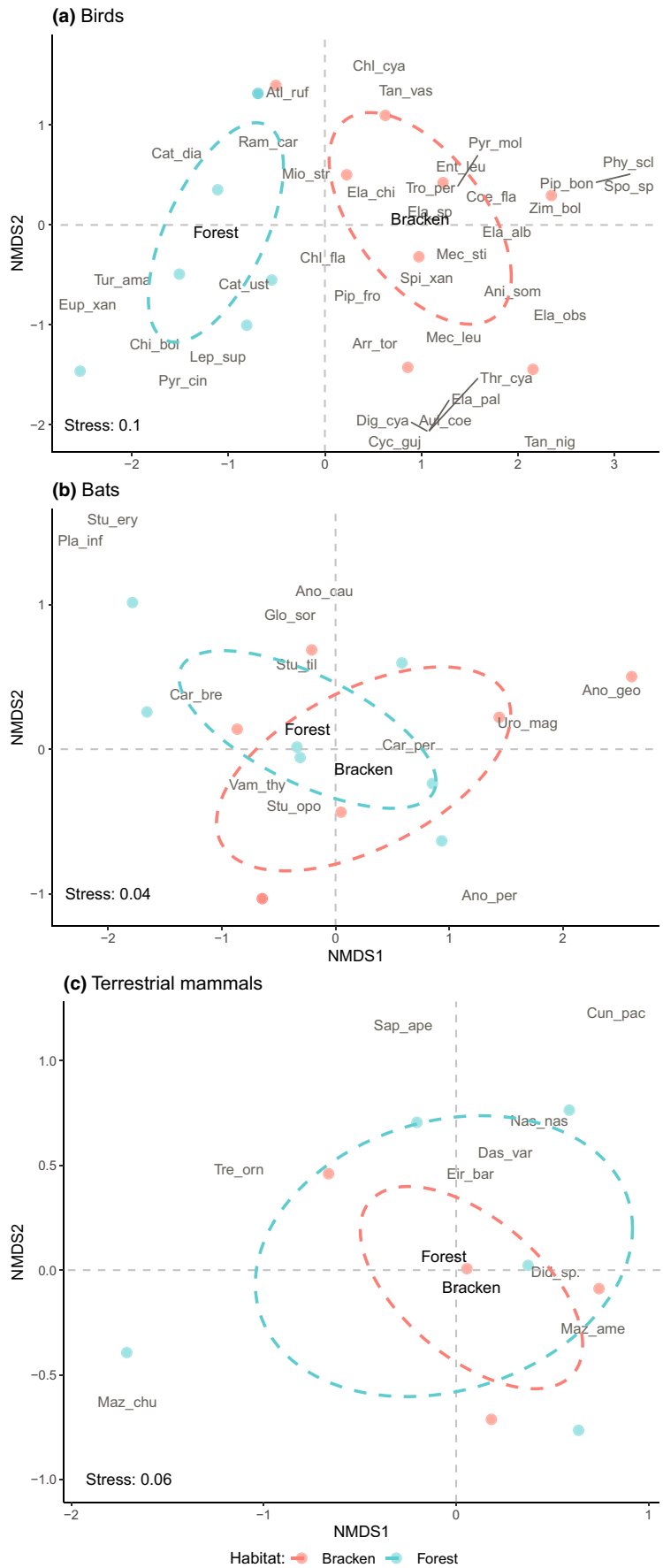
FIGURE 2 Differences in biodiversity between forest and bracken-dominated areas for seed-dispersing birds (left column), bats (medium column) and medium and large terrestrial mammals (right column) in terms of (a–c) species richness, (d–f) inverse Simpson index, (g–h) abundance, and (i) relative abundance index. Asterisks indicate significant differences between both habitats ($p < .05$).

one of the main causes of dispersal limitation in bracken-dominated areas, because few species are shared between both habitats, which reduces the seed rain of animal-dispersed forest tree species in deforested areas, hindering forest regeneration. Therefore, shared species are a keystone for forest recovery.

4.1 | Birds

Species richness and diversity of seed-dispersing birds were higher in the bracken-dominated area than in the forest, and bird abundance showed a similar trend. These results may reflect

FIGURE 3 Comparison of seed disperser communities of (a) birds, (b) bats, and (c) terrestrial mammals, between forest and bracken-dominated areas using non-metric multidimensional scaling ordinations (NMDS). Species are denoted in gray, forest sites in green, and bracken-dominated sites in red. Ellipses differentiate the communities with their names on the centroids. Species abbreviations are shown in Table S1.



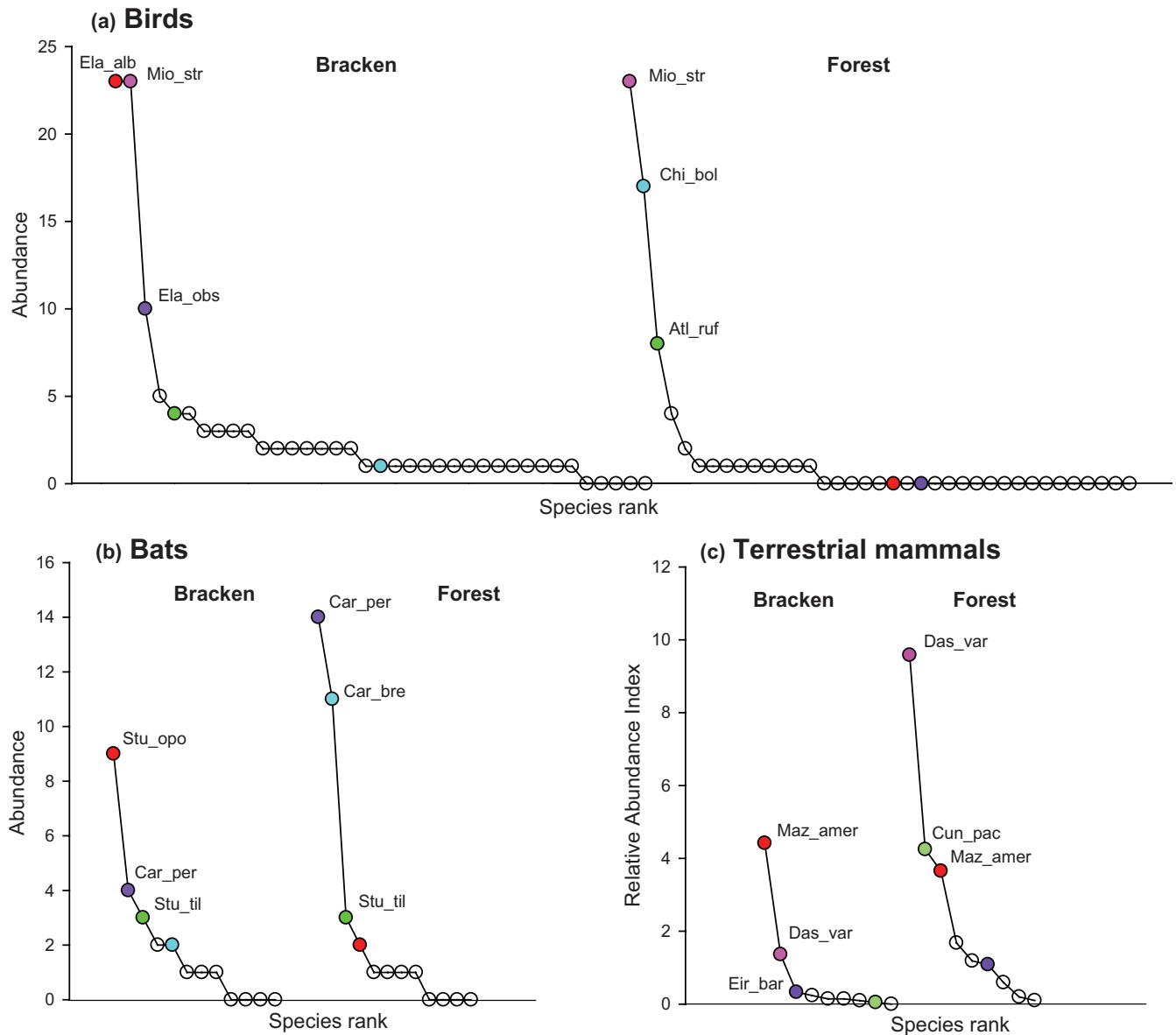


FIGURE 4 Rank-abundance curves for seed disperser communities of (a) birds, (b) bats, and (c) terrestrial mammals between forest and bracken-dominated areas. The species are ranked from highest to lowest abundance. The three most abundant species in each habitat are labeled with their abbreviation (first three letters of the genus and the species) and indicated by different colors. The same colors in both habitats denote the same species. Full species abbreviations are shown in [Table S1](#).

the high diversity of open-land generalist birds in early and mid-successional forests in the tropics (Catterall et al., 2012; Pizo & dos Santos, 2011; Shankar Raman et al., 1998), as well as the ability of several bird species to survive in disturbed habitats, especially generalist frugivores (de Souza Leite et al., 2022; Gomes et al., 2008; O'Dea & Whittaker, 2007). Higher bird diversity has been reported in areas of moderate disturbance, such as forest edges (O'Dea & Whittaker, 2007; Saavedra et al., 2014). This is consistent with the intermediate disturbance hypothesis as a result of the interplay of disturbance and competition/colonization that promote species coexistence (Liao et al., 2022). In contrast to our results, Maya-Elizarrarás and Schondube (2015) found lower species richness but similar abundance of birds in bracken-dominated areas than

in forests in Mexico. We may have obtained different results because our study sites were older (5–10 years old) than theirs (<3-years old), and they used a different method (i.e., point-counts for 2 months). Our lower species richness and abundance of birds in the forest may also be due to a lower survey completeness since the mist-nets only capture a subset of the community, especially small understory birds (Thiel et al., 2021). However, because small birds usually have a higher proportion of interactions in dispersal networks than other species (Béllo Carvalho et al., 2023; Carreira et al., 2020), our results may be representative of seed dispersers involved in interactions between both habitats. Furthermore, although bird species richness is commonly used to assess forest recovery, this indicator is not useful for discerning variations in

community composition, which is important when analyzing the role of seed dispersers for forest recovery (Catterall et al., 2012; Dunn, 2004).

Species composition of seed-dispersing birds was different between the two habitats, consistent with other studies (Maya-Elizarrarás & Schondube, 2015; O'Dea & Whittaker, 2007), which could be the result of species replacement or rewiring (Marjakangas et al., 2020). Differences in species composition in deforested areas may be detrimental for forest recovery because a low number of species using both habitats reduces the likelihood that forest animal-dispersed seeds will arrive in deforested areas. In fact, only nine species from the forest were also registered in the bracken-dominated area, suggesting that forest regeneration in disturbed habitats is highly dependent on these shared species (Rehm et al., 2017). These compositional dissimilarities could be explained by differences in habitat preferences, particularly for forest specialists, which are more sensitive to habitat disturbance (Colles et al., 2009; de Souza Leite et al., 2022; O'Dea & Whittaker, 2007). Future studies should analyze the interaction networks and functional traits from the seed dispersers and plant species to understand how species composition affects seed dispersal dynamics.

In our study, *M. striaticollis* was the only species of seed-dispersing birds common in both habitats. This species tolerates intermediate disturbance (Montaño-Centellas & Garitano-Zavala, 2015) and can feed on fruits and insects (Greeney et al., 2006). Interestingly, this was one of the species with more seed-dispersal interactions at the forest edge (Saavedra et al., 2014) and in bracken-dominated habitats in our study area, where it dispersed the highest number of forest dependent plant species (C. Mayta in progress). Generalists such as *M. striaticollis* can be critical to the dispersal and establishment of woody plants, increasing plant diversity in deforested areas (Carlo & Morales, 2016). Further data suggest that *M. striaticollis* could be a keystone species in our area because it is abundant in both habitats, disperses several forest species, and its seeds have high germination rates (Rojas, 2022). Some bird species registered only in the bracken-dominated area can also disperse seeds from early-successional species. However, since early-successional species are light-demanding and bracken is an important source of shade, early-successional species rarely colonize these areas (López et al., 2023). Therefore, shade-tolerant forest species, which are mainly dispersed by animals will have more chances to establish in bracken-dominated areas and promote forest regeneration. In addition to the understory birds that we captured in mist nets, we observed large frugivorous birds, such as *Penelope montagnii* and *Aulacorrynchus coeruleicinctis* (C. Mayta submitted), in the forest and also sometimes perching in scatter burned trunks in bracken-dominated habitats. Both species move large distances through different habitats and are capable of dispersing several forest tree species (Reid et al., 2021; Saavedra et al., 2014), including large-seeded species with higher probabilities of establishment in bracken-dominated areas (Gallegos et al., 2015; Ssali et al., 2019) because of their higher germination rates and shade-tolerance (Bazzaz & Pickett, 1980; Daws et al., 2007). Depending on perch abundance and frequency of flights, guans and toucans may

play an important role in forest regeneration in bracken-dominated areas.

In this study, we registered 37 bird species, corresponding to only 49% of the frugivorous/omnivorous species previously registered in the study region (Rubey & Hennessey, 2005; Saavedra et al., 2014; M. Villegas unpublished data, Table S2). However, the completeness analysis revealed that we registered more than 86% of the abundant species in both habitats. Abundant species are particularly relevant, because they might collectively disperse more seeds. Since mist-nets only capture understory small birds, we could not capture species like *Tersina viridis*, *Tangara* spp., and *Psarocolius* spp. which commonly move in the canopy, or other large species such as *P. montagnii*, *Ortalis guttata*, *Zentrygon frenata*, and *Patagioenas* spp. Point counts could be more effective to register a larger set of bird species than mist-nets (Mulvaney & Cherry, 2020). Nevertheless, mist-nets were useful for our study to assess birds' diet and to detect the abundant species. We also only captured birds in the bracken-dominated area and the forest edge, and not in the forest interior. Several species from the reference list such as *Lipaugus uropygialis*, *Pharomachus antisanus*, and *Odontophorus balliviani* are typical for the forest interior and avoid forest edges, explaining their absence from our dataset. However, since our aim was to examine the species that could potentially disperse seeds into bracken-dominated areas, those species that avoid the forest edge probably also avoid deforested areas, and will not disperse seeds into bracken-dominated areas. Contrarily, we found some species that were not previously registered in the study area, including *Spinus* spp. which are more common in drier ecosystems, *Elaenia* spp. which have preference for edges and open habitats, and *Cyralis guianensis* and *Leptopogon superciliaris* which are typical for forest edges. Given the high deforestation rates in the study area, leaving only two large forest patches, several species that are more sensitive to forest degradation could be locally extinct, potentially explaining the absence of *Ampelion rufaxilla*, *Myadestes ralloides*, *Creurgops dentata* and *Phylloscartes ophthalmicus*.

4.2 | Bats

We found similar species richness, abundance, and diversity of seed-dispersing bats in forest and bracken-dominated habitats. Other studies also found similar species richness and abundance of frugivorous bats between disturbed and undisturbed areas (de Oliveira et al., 2017; Laurindo et al., 2019). These patterns could be related to their tolerance to habitat disturbance and to the high affinity of many frugivorous bats for early successional plant species, like *Piper*, *Solanum*, and *Cecropia* (Muscarella & Fleming, 2007) that are common close to the forest edge.

The species composition of bats was different between the two habitats, agreeing with other studies (Chambers et al., 2016; de Oliveira et al., 2017; Valle et al., 2021). These patterns could reflect the longer time that species composition takes to recover after disturbance (Dunn, 2004) or species-specific differences related to food resources and home ranges (Chambers et al., 2016).

The most common bat in the forest was *C. perspicillata* and was also present in bracken-dominated areas but in lower abundance. Since *Piper* is the main food resource for this species (Muscarella & Fleming, 2007), this pattern could be related to the lower availability of *Piper* in bracken-dominated areas (Lippok et al., 2013). Since *C. perspicillata* can change its feeding habitat depending on food resources (Trevelin et al., 2013), planting *Piper* in bracken-dominated areas could increase its abundance, and consequently seed dispersal.

In this study, we detected 86% of the frugivore/omnivore bat species previously reported in the study region, in the Cotapata National Park located 35 km from our study area (Montaño-Centellas et al., 2015; Moya et al., 2024; SERNAP, 2005). This high percentage was not reflected in the completeness analyses, which suggested that we sampled only 51% of the total species assemblage in the forest and 79% in the bracken-dominated area. This could be related to the high amount of singletons that we found during sampling, which probably overestimated the species richness of the study region. The high number of species that we registered only once could suggest a low sampling effort, or could be a result of the high proportion of rare bat species in certain tropical areas (Meyer et al., 2015). The completeness analysis also suggests that we sampled at least 88% of the abundant species. In this study, we registered *Anoura caudifer*, *Acinia peruana* and *Uroderma magnirostrum*, which were not detected previously in the region. We did not register *Artibeus planirostris* and *Platyrrhinus umbratus*, which were found in the Cotapata National park. We probably were not able to detect these species because they normally move in the canopy, or because these species are rare at these elevations (Meyer et al., 2010). Their absence from our study site could be also related to their sensitivity to habitat degradation. Longer-term monitoring would be necessary to be able to detect a higher proportion of the bat assemblage (Meyer et al., 2015).

4.3 | Terrestrial mammals

We found similar species richness, diversity, and composition of seed-dispersing terrestrial mammals in both habitats. These patterns could be related to the high vegetation cover in bracken-dominated areas, which is positively related to mammal species richness (Brady et al., 2011), as well as the short distance to the forest remnants, the high mobility of these animals and the presence of different food resources (Estrada et al., 1994). However, we found lower relative abundance of terrestrial mammals in bracken-dominated areas than in the forest, probably because of the higher availability of resources, hides, and roosts in the forest (Brady et al., 2011).

M. americana was the most common species in the bracken-dominated habitat and the third most common in the forest interior. The high abundance of this species could be related to their large body size and greater foraging range, being able to cross the forest edges and exploit other habitats (Lees & Peres, 2009). *D. variegata* was the most common species found in the forest and the second

most common in the areas dominated by bracken. *Dasyprocta* species are important seed dispersers, common in forests and disturbed areas (Jax et al., 2015). Therefore, *D. variegata* could be a keystone species, because it travels relatively long distances, frequently eats fruits, and could disperse forest tree species to bracken-dominated areas. Many of the terrestrial mammal species that we recorded as seed dispersers can also be classified as herbivores, omnivores, or even seed predators, and their disappearance can have cascading effects on forest regeneration (Kurten, 2013). Furthermore, since most tree seeds in the forest of our study areas are smaller than 1 cm, there is little risk that they will be preyed upon by most recorded species (Norconk et al., 1998).

We detected 82% of the species of seed-disperser terrestrial mammals registered in Cotapata National Park located 35 km from the study area. The completeness analysis revealed that we sampled 100% of the species. The absence of the two missing species could be related to the rarity of *Cuniculus taczanowskii*, and to the high gaming pressure for *Tayassu tajacu* in the past decades in our study area. However, as the completeness analysis suggested, we were able to detect the abundant species in both habitats. Furthermore, the presence of *Tremarctos ornatus* and different felids highlight the conservation value of the forest remnants in our study area.

Although several studies analyze seed-dispersal networks (Castaño et al., 2018; Chaves et al., 2022; Saavedra et al., 2014), additional analysis of the seed dispersal community has the advantage of assessing the source of seed limitation. Seed dispersal is thought to be limited in deforested areas because of lower number of animals dispersing seeds. However, in this study, we show that the main cause of seed dispersal limitation is the scarcity of shared species between both habitats. This pattern could explain the low seed rain and the low seedling establishment of forest tree species previously reported in tropical bracken-dominated areas. Bracken-dominated areas are covered by bracken fronds, creating shade and a potential physical barrier, which gives shade-tolerant species advantages to recruit, survive and grow (Gallegos et al., 2016; Ssali et al., 2019). Given that forest shade-tolerant species tend to have larger seeds, and these seeds are mainly dispersed by animals, promoting the arrival of their seed dispersers will probably increase seed rain (Saavedra et al., 2015) and seedling establishment (C. Mayta, submitted).

Based on our findings, we suggest that increasing visitation by seed-dispersing animals capable of moving across both habitat types could help reduce dispersal limitation in bracken-dominated areas. This could be done by installing animal attractants in the form of artificial and natural perch structures that increase species richness and abundance of bird-dispersed seeds (Saavedra et al., 2015) and seedlings in bracken-dominated areas (C. Mayta, submitted). We also suggest installing artificial bat roosts (Kelm et al., 2008), which increased seed rain of bat-dispersed species in bracken-dominated areas in a parallel study (C. Mayta, submitted). In addition, transplanting nursery-raised seedlings of several animal-dispersed species, including *Clusia*, *Miconia*, *Hieronyma*, *Piper*, *Vismia*, *Cecropia*, and

Ficus, into bracken-dominated areas could foster their establishment and rapid growth. These transplants could accelerate the availability of food resources and shelter for seed dispersers in the medium and long term, and increase species richness and abundance of animal-dispersed tree seeds (Camargo et al., 2020; Galindo-González et al., 2000) and seedlings (Martinez-Garza & Howe, 2003; Reid et al., 2021; Rivas-Alonso et al., 2021). Future research should focus on evaluating the effect of these restoration measures on seed disperser communities, seed dispersal effectiveness, and forest regeneration.

Assessing community properties of the entire seed dispersing community is critical to understanding constraints on forest regeneration in deforested areas. Here, we found that while species richness of seed-dispersing bats was similar and that of birds was higher in bracken-dominated areas than in the forest, the species composition of both groups was different in both habitats. These results could explain the low seed rain and seedling establishment of forest tree species previously reported in tropical bracken-dominated areas. Our results highlight the importance of including animal-related aspects in restoration projects.

AUTHOR CONTRIBUTIONS

SCG, IH, JR, GMA conceptualized the research and methodology; CM, MV, VR, ME and SCG conducted the investigation and data curation; SCG, GMA, JR, MEV, NB-H, KN conducted the formal analysis; SCG and IH were involved in project administration, funding acquisition, and wrote the original draft; SCG, IH, CM, MV, NBH and KN wrote, reviewed and edited the manuscript.

ACKNOWLEDGMENTS

We thank Noel Taboada, Jairo Dominguez, Miguel Montenegro, Cristian Vargas and Cecilia L. López for field assistance. We are grateful to the private land owners and local communities for facilitating access to their lands. We thank Diana Bowler for language polishing and two anonymous reviewers for their comments. This study was financed by the German Research Foundation DFG (grant He 3041/23-1) and by TWAS-Sida (grant 19-107 RG/BIO/LA_I-FR3240310157). All captured animals were manipulated according to the Bolivian regulations (permit: CAR/MMAYA/VMABCCGDF/DGBAP/MEG 0012/2020). Open Access funding enabled and organized by Projekt DEAL.

CONFLICT OF INTEREST STATEMENT

The corresponding author confirms on behalf of all authors that there have been no involvements that might raise the question of bias in the work reported or in the conclusions, implications, or opinions stated.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in Dryad Digital Repository at doi:10.5061/dryad.cvdncjt9z (Gallegos et al., 2024).

ORCID

Silvia C. Gallegos  <https://orcid.org/0000-0003-4102-7456>
 Cesar Mayta  <https://orcid.org/0009-0000-3986-2028>
 Mariana Villegas  <https://orcid.org/0000-0001-9944-7272>
 Guido M. Ayala  <https://orcid.org/0000-0002-7968-7460>
 Kazuya Naoki  <https://orcid.org/0000-0002-6656-6950>
 Maria E. Viscarra  <https://orcid.org/0000-0003-4992-504X>
 Nuria Bernal-Hoverud  <https://orcid.org/0000-0002-5688-1201>
 Isabell Hensen  <https://orcid.org/0000-0001-6470-9359>

REFERENCES

- Acosta-Rojas, D. C., Barczyk, M., Espinosa, C. I., Tinoco, B. A., Neuschulz, E. L., & Schleuning, M. (2023). Climate and microhabitat shape the prevalence of endozoochory in the seed rain of tropical montane forests. *Biotropica*, 55(2), 408–417. <https://doi.org/10.1111/btp.13195>
- Alday, J. G., Cox, E. S., Pakeman, R. J., Harris, M. P. K., LeDuc, M. G., & Marrs, R. H. (2013). Overcoming resistance and resilience of an invaded community is necessary for effective restoration: A multi-site bracken control study. *Journal of Applied Ecology*, 50(1), 156–167. <https://doi.org/10.1111/1365-2664.12015>
- Amouzgar, L., Ghorbani, J., Shokri, M., Marrs, R. H., & Alday, J. G. (2022). A regional assessment of the *Pteridium aquilinum* growth and phenology: A case study in Southwestern Asia. *Landscape and Ecological Engineering*, 19, 137–150. <https://doi.org/10.1007/s11355-022-00528-4>
- Barton, K. (2022). *MuMIn: Multi-model inference*. <http://r-forge.r-project.org/projects/mumin/>
- Bates, D., Maechler, M., Bolker, B. M., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, 67(1), 1–48. <https://doi.org/10.18637/jss.v067.i01>
- Bazzaz, F. A., & Pickett, S. T. A. (1980). Physiological ecology of tropical succession: A comparative review. *Annual Review of Ecology and Systematics*, 11(1980), 287–310. <https://doi.org/10.1146/annurev.es.11.110180.001443>
- Beck, E., & Richter, M. (2008). Ecological aspects of a biodiversity hotspot in the Andes of South Ecuador. In S. R. Gradstein, J. Homeier, & D. Gansert (Eds.), *The Tropical Mountain Forest—Patterns and Processes in a Biodiversity Hotspot*. *Biodiversity and Ecology Studies* 2 (pp. 195–217). Göttingen Centre for Biodiversity and Ecology.
- Behling, H. (2008). Tropical mountain forest dynamics in Mata Atlantica and Northern Andean biodiversity hotspots during the late quaternary. In S. R. Gradstein, J. Homeier, & D. Gansert (Eds.), *The Tropical Mountain Forest—Patterns and Processes in a Biodiversity Hotspot*. *Biodiversity and Ecology Series* (pp. 25–33). Göttingen Centre for Biodiversity and Ecology.
- Béllo Carvalho, R., Malhi, Y., & Oliveras Menor, I. (2023). Frugivory and seed dispersal in the Cerrado: Network structure and defaunation effects. *Biotropica*, 55, 1–17. <https://doi.org/10.1111/btp.13234>
- Billerman, S. M., Keeney, B. K., Rodewald, P., & Schulenberg, T. S. (2022). *Birds of the World*. Cornell Laboratory of Ornithology.
- Brady, M. J., McAlpine, C. A., Possingham, H. P., Miller, C. J., & Baxter, G. S. (2011). Matrix is important for mammals in landscapes with small amounts of native forest habitat. *Landscape Ecology*, 26(5), 617–628. <https://doi.org/10.1007/s10980-011-9602-6>
- Camargo, P. H. S. A., Pizo, M. A., Brancalion, P. H. S., & Carlo, T. A. (2020). Fruit traits of pioneer trees structure seed dispersal across distances on tropical deforested landscapes: Implications for restoration. *Journal of Applied Ecology*, 57(12), 2329–2339. <https://doi.org/10.1111/1365-2664.13697>
- Carlo, T. A., & Morales, J. M. (2016). Generalist birds promote tropical forest regeneration and increase plant diversity via rare-biased

- seed dispersal. *Ecology*, 97(7), 1819–1831. <https://doi.org/10.1890/15-2147.1>
- Carreira, D. C., Dáttilo, W., Bruno, D. L., Percequillo, A. R., Ferraz, K. M. P. M. B., & Galetti, M. (2020). Small vertebrates are key elements in the frugivory networks of a hyperdiverse tropical forest. *Scientific Reports*, 10(1), 1–11. <https://doi.org/10.1038/s41598-020-67326-6>
- Carvalho, T. F., Carvalho, A. C., Zanuncio, J. C., de Oliveira, M. L. R., Machado, E. L. M., José, A. C., Santos, J. B., & Pereira, I. M. (2022). Does invasion by *Pteridium aquilinum* (Dennstaedtiaceae) affect the ecological succession in Atlantic forest areas after a fire? *Environmental Science and Pollution Research*, 29(10), 14195–14205. <https://doi.org/10.1007/s11356-021-16761-7>
- Castaño, J. H., Carranza, J. A., & Pérez-Torres, J. (2018). Diet and trophic structure in assemblages of montane frugivorous phyllostomid bats. *Acta Oecologica*, 91, 81–90. <https://doi.org/10.1016/j.actao.2018.06.005>
- Catterall, C. P. (2018). Fauna as passengers and drivers in vegetation restoration: A synthesis of processes and evidence. *Ecological Management and Restoration*, 19, 54–62. <https://doi.org/10.1111/emr.12306>
- Catterall, C. P., Freeman, A. N. D., Kanowski, J., & Freebody, K. (2012). Can active restoration of tropical rainforest rescue biodiversity? A case with bird community indicators. *Biological Conservation*, 146(1), 53–61. <https://doi.org/10.1016/j.biocon.2011.10.033>
- Chambers, C. L., Cushman, S. A., Medina-Fitoria, A., Martínez-Fonseca, J., & Chávez-Velásquez, M. (2016). Influences of scale on bat habitat relationships in a forested landscape in Nicaragua. *Landscape Ecology*, 31(6), 1299–1318. <https://doi.org/10.1007/s10980-016-0343-4>
- Chao, A., Kubota, Y., Zelený, D., Chiu, C. H., Li, C. F., Kusumoto, B., Yasuhara, M., Thorn, S., Wei, C. L., Costello, M. J., & Colwell, R. K. (2020). Quantifying sample completeness and comparing diversities among assemblages. *Ecological Research*, 35(2), 292–314. <https://doi.org/10.1111/1440-1703.12102>
- Chaves, P. P., Timóteo, S., Gomes, S., & Rainho, A. (2022). Response of avian and mammal seed dispersal networks to human-induced forest edges in a sub-humid tropical forest. *Journal of Tropical Ecology*, 38, 199–209. <https://doi.org/10.1017/S0266467422000062>
- Colles, A., Liow, L. H., & Prinzing, A. (2009). Are specialists at risk under environmental change? Neoecological, paleoecological and phylogenetic approaches. *Ecology Letters*, 12(8), 849–863. <https://doi.org/10.1111/j.1461-0248.2009.01336.x>
- Costa, A., Heleno, R., Dufrene, Y., Huckle, E., Gabriel, R., Doudee, D., & Kaiser-Bunbury, C. N. (2022). Seed dispersal by frugivores from forest remnants promotes the regeneration of adjacent invaded forests in an oceanic Island. *Restoration Ecology*, 30(8), 1–9. <https://doi.org/10.1111/rec.13654>
- Curtis, P. G., Slay, C. M., Harris, N. L., Tyukavina, A., & Hansen, M. C. (2018). Classifying drivers of global forest loss. *Science*, 361(6407), 1108–1111. <https://doi.org/10.1126/science.aau3445>
- Daws, M. I., Ballard, C., Mullins, C. E., Garwood, N. C., Murray, B., Pearson, T. R. H., & Burslem, D. F. R. P. (2007). Allometric relationships between seed mass and seedling characteristics reveal trade-offs for Neotropical gap-dependent species. *Oecologia*, 154(3), 445–454. <https://doi.org/10.1007/s00442-007-0848-2>
- de Oliveira, H. F. M., de Camargo, N. F., Gager, Y., & Aguiar, L. M. S. (2017). The response of bats (mammalia: Chiroptera) to habitat modification in a Neotropical savannah. *Tropical Conservation Science*, 10, 1–14. <https://doi.org/10.1177/1940082917697263>
- de Souza Leite, M., Boesing, A. L., Metzger, J. P., & Prado, P. I. (2022). Matrix quality determines the strength of habitat loss filtering on bird communities at the landscape scale. *Journal of Applied Ecology*, 59(11), 2790–2802. <https://doi.org/10.1111/1365-2664.14275>
- Dunn, R. R. (2004). Recovery of faunal communities during tropical forest regeneration. *Conservation Biology*, 18(2), 302–309. <https://doi.org/10.1111/j.1523-1739.2004.00151.x>
- Escribano-Avila, G., Calviño-Cancela, M., Pias, B., Virgós, E., Valladares, F., & Escudero, A. (2014). Diverse guilds provide complementary dispersal services in a woodland expansion process after land abandonment. *Journal of Applied Ecology*, 51(6), 1701–1711. <https://doi.org/10.1111/1365-2664.12340>
- Estrada, A., Coates-Estrada, R., & Meritt, D. (1994). Non flying mammals and landscape changes in the tropical rain forest region of Los Tuxtlas, Mexico. *Ecography*, 17(3), 229–241. <https://doi.org/10.1111/j.1600-0587.1994.tb00098.x>
- FAO. (2020). Global Forest Resources Assessment 2020: Main report. <https://doi.org/10.4324/9781315184487-1>
- Fontúrbel, F. E., Candia, A. B., Malebrán, J., Salazar, D. A., González-Browne, C., & Medel, R. (2015). Meta-analysis of anthropogenic habitat disturbance effects on animal-mediated seed dispersal. *Global Change Biology*, 21(11), 3951–3960. <https://doi.org/10.1111/gcb.13025>
- Galindo-González, J., Guevara, S., & Sosa, V. J. (2000). Bat- and bird-generated seed rains at isolated trees in pastures in a tropical rainforest. *Conservation Biology*, 14(6), 1693–1703. <https://doi.org/10.1111/j.1523-1739.2000.99072.x>
- Gallegos, S. C., Beck, S. G., Hensen, I., Saavedra, F., Lippok, D., & Schleuning, M. (2016). Factors limiting montane forest regeneration in bracken-dominated habitats in the tropics. *Forest Ecology and Management*, 381, 168–176. <https://doi.org/10.1016/j.foreco.2016.09.014>
- Gallegos, S. C., Hensen, I., Saavedra, F., & Schleuning, M. (2015). Bracken fern facilitates tree seedling recruitment in tropical fire-degraded habitats. *Forest Ecology and Management*, 337, 135–143. <https://doi.org/10.1016/j.foreco.2014.11.003>
- Gallegos, S. C., Mayta, C., Villegas, M., Miranda, G. M., Naoki, K., Rechberger, J., Rojas, V., Viscarra, M. E., Bernal-Hoverud, N., Espejo, M., & Hensen, I. (2024). Data from: Habitat differences in seed-dispersing vertebrates indicate dispersal limitation in tropical bracken-dominated deforested areas. *Dryad*. <https://doi.org/10.5061/dryad.cvdncj9z>
- Gomes, L. G. L., Oostra, V., Nijman, V., Cleef, A. M., & Kappelle, M. (2008). Tolerance of frugivorous birds to habitat disturbance in a tropical cloud forest. *Biological Conservation*, 141(3), 860–871. <https://doi.org/10.1016/j.biocon.2008.01.007>
- Greeney, H. F., Dingle, C., Dobbs, R. C., & Martin, P. R. (2006). Natural history of streak-necked flycatcher *Mionectes striaticollis* in north-east Ecuador. *Cotinga*, 25, 59–64.
- Günter, S., Weber, M., Erreis, R., & Aguirre, N. (2007). Influence of distance to forest edges on natural regeneration of abandoned pastures: A case study in the tropical mountain rain forest of Southern Ecuador. *European Journal of Forest Research*, 126(1), 67–75. <https://doi.org/10.1007/s10342-006-0156-0>
- Haddad, N. M., Brudvig, L. A., Clobert, J., Davies, K. F., Gonzalez, A., Holt, R. D., Lovejoy, T. E., Sexton, J. O., Austin, M. P., Collins, C. D., Cook, W. M., Damschen, E. I., Ewers, R. M., Foster, B. L., Jenkins, C. N., King, A. J., Laurance, W. F., Levey, D. J., Margules, C. R., ... Townshend, J. R. (2015). Habitat fragmentation and its lasting impact on Earth's ecosystems. *Science Advances*, 1(2), 1–10. <https://doi.org/10.1126/sciadv.1500052>
- Hartig, K., & Beck, E. (2003). The bracken fern (*Pteridium arachnoideum* (Kaulf.) Maxon) dilemma in the Andes of Southern Ecuador. *Ecotropica*, 9, 3–13.
- Herzog, S. K., Terrill, R. S., Jahn, A. E., Remsen, J. V., Maillard, O., Garcia-Soliz, V. H., MacLeod, R., McCormick, A., & Vidoz, J. Q. (2016). *Birds of Bolivia Field Guide*. Asociación Armonía.
- Howe, H. F. (2016). Making dispersal syndromes and networks useful in tropical conservation and restoration. *Global Ecology and*

- Conservation*, 6, 152–178. <https://doi.org/10.1016/j.gecco.2016.03.002>
- Howe, H. F., & Smallwood, J. (1982). Ecology of seed dispersal. *Annual Review of Ecology and Systematics*, 13(1), 201–228. <https://doi.org/10.1146/annurev.es.13.110182.001221>
- Jax, E., Marin, S., Rodriguez-Ferraro, A., & Isasi-Catala, E. (2015). Habitat use and relative abundance of the spotted Paca *Cuniculus paca* (Linnaeus, 1766) (Rodentia: Cuniculidae) and the red-rumped agouti *Dasyprocta leporina* (Linnaeus, 1758) (Rodentia: Dasyproctidae) in Guatopo National Park, Venezuela. *Journal of Threatened Taxa*, 7(1), 6739–6749. <https://doi.org/10.11609/jott.1783.6739-6749>
- Karger, D. N., Kessler, M., Lehnert, M., & Jetz, W. (2021). Limited protection and ongoing loss of tropical cloud forest biodiversity and ecosystems worldwide. *Nature Ecology & Evolution*, 5(6), 854–862. <https://doi.org/10.1038/s41559-021-01450-y>
- Kelm, D. H., Wiesner, K. R., & von Helversen, O. (2008). Effects of artificial roosts for frugivorous bats on seed dispersal in a Neotropical forest pasture mosaic. *Conservation Biology*, 22(3), 733–741. <https://doi.org/10.1111/j.1523-1739.2008.00925.x>
- Killeen, T. J., Guerra, A., Calzada, M., Correa, L., Calderon, V., Soria, L., Quezada, B., & Steininger, M. (2008). Total historical land-use change in Eastern Bolivia: Who, where, when, and how much? *Ecology and Society*, 13(1), 36.
- Kurten, E. L. (2013). Cascading effects of contemporaneous defaunation on tropical forest communities. *Biological Conservation*, 163, 22–32. <https://doi.org/10.1016/j.biocon.2013.04.025>
- Laurindo, R. S., Novaes, R. L. M., Vizenin-Bugoni, J., & Gregorin, R. (2019). The effects of habitat loss on bat-fruit networks. *Biodiversity and Conservation*, 28(3), 589–601. <https://doi.org/10.1007/s10531-018-1676-x>
- Lees, A. C., & Peres, C. A. (2009). Gap-crossing movements predict species occupancy in Amazonian forest fragments. *Oikos*, 118(2), 280–290. <https://doi.org/10.1111/j.1600-0706.2008.16842.x>
- Levy-Tacher, S. I., Vleut, I., Román-Dañobeytia, F., & Aronson, J. (2015). Natural regeneration after long-term bracken fern control with balsa (*Ochroma pyramidale*) in the neotropics. *Forests*, 6(6), 2163–2177. <https://doi.org/10.3390/f6062163>
- Liao, J., Barabás, G., & Bearup, D. (2022). Competition–colonization dynamics and multimodality in diversity–disturbance relationships. *Ecology*, 103(5), e3672. <https://doi.org/10.1002/ecy.3672>
- Lippok, D., Beck, S. G., Renison, D., Gallegos, S. C., Saavedra, F. V., Hensen, I., & Schleuning, M. (2013). Forest recovery of areas deforested by fire increases with elevation in the tropical Andes. *Forest Ecology and Management*, 295, 69–76. <https://doi.org/10.1016/j.foreco.2013.01.011>
- Lippok, D., Beck, S. G., Renison, D., Hensen, I., Apaza, A. E., & Schleuning, M. (2014). Topography and edge effects are more important than elevation as drivers of vegetation patterns in a Neotropical montane forest. *Journal of Vegetation Science*, 25(3), 724–733. <https://doi.org/10.1111/jvs.12132>
- López, C. L., Mayta, C., Fuentes, A. F., Villegas, M., Jimenez, E., Vasquez, V., Hensen, I., & Gallegos, S. C. (2023). Disentangling the roles of bracken fronds and litter on natural seedling recruitment in fire-deforested tropical montane habitats. <https://doi.org/10.2139/ssrn.4642674>
- Magioli, M., Ferraz, K. M. P. M. d. B., Chiarello, A. G., Galetti, M., Setz, E. Z. F., Paglia, A. P., Abrego, N., Ribeiro, M. C., & Ovaskainen, O. (2021). Land-use changes lead to functional loss of terrestrial mammals in a Neotropical rainforest. *Perspectives in Ecology and Conservation*, 19(2), 161–170. <https://doi.org/10.1016/j.pecon.2021.02.006>
- Magurran, A. E. (2004). *Measuring biological diversity*. Blackwell Science.
- Mandujano, S. (2022). RAI: An R package to calculate relative abundance index from camera-traps (2022-03-28 13:49:45).
- Marjakangas, E. L., Abrego, N., Grøtan, V., de Lima, R. A. F., Bello, C., Bovendorp, R. S., Culot, L., Hasui, É., Lima, F., Muylaert, R. L., Niebuhr, B. B., Oliveira, A. A., Pereira, L. A., Prado, P. I., Stevens, R. D., Vancine, M. H., Ribeiro, M. C., Galetti, M., & Ovaskainen, O. (2020). Fragmented tropical forests lose mutualistic plant–animal interactions. *Diversity and Distributions*, 26(2), 154–168. <https://doi.org/10.1111/ddi.13010>
- Markl, J. S., Schleuning, M., Forget, P. M., Jordano, P., Lambert, J. E., Traveset, A., Wright, S. J., & Böhning-Gaese, K. (2012). Meta-analysis of the effects of human disturbance on seed dispersal by animals. *Conservation Biology*, 26(6), 1072–1081. <https://doi.org/10.1111/j.1523-1739.2012.01927.x>
- Marrs, R. H., Le Duc, M. G., Mitchell, R. J., Goddard, D., Paterson, S., & Pakeman, R. J. (2000). The ecology of bracken: Its role in succession and implications for control. *Annals of Botany*, 85, 3–15. <https://doi.org/10.1006/anbo.1999.1054>
- Marrs, R. H., & Watt, A. S. (2006). Biological flora of the British Isles: *Pteridium aquilinum* (L.) Kuhn. *Journal of Ecology*, 94(6), 1272–1321. <https://doi.org/10.1111/j.1365-2745.2006.01177.x>
- Martinez-Garza, C., & Howe, H. F. (2003). Restoring tropical diversity: Beating the time tax on species loss. *Journal of Applied Ecology*, 40(3), 423–429. <https://doi.org/10.1046/j.1365-2664.2003.00819.x>
- Maya-Elizarrarás, E., & Schondube, J. E. (2015). Birds, cattle, and bracken ferns: Bird community responses to a Neotropical landscape shaped by cattle grazing activities. *Biotropica*, 47(2), 236–245. <https://doi.org/10.1111/btp.12196>
- Medellin, R. A., & Gaona, O. (1999). Seed dispersal by bats and birds in forest and disturbed habitats of Chiapas, Mexico. *Biotropica*, 31(3), 478–485. <https://doi.org/10.1111/j.1744-7429.1999.tb00390.x>
- Meyer, C. F. J., Aguiar, L. M. S., Aguirre, L. F., Baumgarten, J., Clarke, F. M., Cosson, J. F., Estrada Villegas, S., Fahr, J., Faria, D., Furey, N., Henry, M., Jenkins, R. K. B., Kunz, T. H., González, M. C. M., Moya, I., Pons, J. M., Racey, P. A., Rex, K., Sampaio, E. M., ... Kalko, E. K. V. (2015). Species undersampling in tropical bat surveys: Effects on emerging biodiversity patterns. *Journal of Animal Ecology*, 84(1), 113–123. <https://doi.org/10.1111/1365-2656.12261>
- Meyer, C. F. J., Aguiar, L. M. S., Aguirre, L. F., Baumgarten, J., Clarke, F. M., Cosson, J. F., Villegas, S. E., Fahr, J., Faria, D., Furey, N., Henry, M., Hodgkison, R., Jenkins, R. K. B., Jung, K. G., Kingston, T., Kunz, T. H., MacSwiney Gonzalez, M. C., Moya, I., Pons, J. M., ... Kalko, E. K. V. (2010). Long-term monitoring of tropical bats for anthropogenic impact assessment: Gauging the statistical power to detect population change. *Biological Conservation*, 143(11), 2797–2807. <https://doi.org/10.1016/j.biocon.2010.07.029>
- Moles, A. T., Ackerly, D. D., Tweddle, J. C., Dickie, J. B., Smith, R., Leishman, M. R., Mayfield, M. M., Pitman, A., Wood, J. T., & Westoby, M. (2007). Global patterns in seed size. *Global Ecology and Biogeography*, 16, 109–116. <https://doi.org/10.1111/j.1466-822x.2006.00259.x>
- Molina-Carpio, J., Espinoza, D., Coritza, E., Salcedo, F., Farfan, C., Mamani, L., & Mendoza, J. (2019). Clima y variabilidad espacial de la ceja de monte y andino húmedo. *Ecología En Bolivia*, 54(1), 40–56.
- Montaño-Centellas, F. A., & Garitano-Zavala, Á. (2015). Andean bird responses to human disturbances along an elevational gradient. *Acta Oecologica*, 65–66, 51–60. <https://doi.org/10.1016/j.actao.2015.05.003>
- Montaño-Centellas, F. A., Moya, M. I., Aguirre, L. F., Galeón, R., Palabral, O., Hurtado, R., Galarza, I., & Tordoya, J. (2015). Community and species-level responses of phyllostomid bats to a disturbance gradient in the tropical Andes. *Acta Oecologica*, 62, 10–17. <https://doi.org/10.1016/j.actao.2014.11.002>
- Moya, I., Meneses, R. I., Cuba, E., Palabral, A., Rico, A., Thompson, N., Gómez, M. I., Palabral, O., Loayza, E., & Ocampo, M. (2024). *Atlas de biodiversidad para la gestión territorial del Corredor Madidi—Pilón Lajas—Cotapata*. MMAyA-Bolivia.
- Mulvaney, J. M., & Cherry, M. I. (2020). The effectiveness of point counts and mist-netting in surveying Afrotemperate forest bird community

- structure in South Africa. *Emu - Austral Ornithology*, 120(2), 103–113. <https://doi.org/10.1080/01584197.2020.1726186>
- Münzbergová, Z., & Herben, T. (2005). Seed, dispersal, microsite, habitat and recruitment limitation: Identification of terms and concepts in studies of limitations. *Oecologia*, 145(1), 1–8. <https://doi.org/10.1007/s00442-005-0052-1>
- Muscarella, R., & Fleming, T. H. (2007). The role of frugivorous bats in tropical forest succession. *Biological Reviews*, 82(4), 573–590. <https://doi.org/10.1111/j.1469-185X.2007.00026.x>
- Norconk, M. A., Grafton, B. W., & Conklin-Brittain, N. L. (1998). Seed dispersal by Neotropical seed predators. *American Journal of Primatology*, 45(1), 103–126. [https://doi.org/10.1002/\(SICI\)1098-2345\(1998\)45:1<103::AID-AJP8>3.0.CO;2-%23](https://doi.org/10.1002/(SICI)1098-2345(1998)45:1<103::AID-AJP8>3.0.CO;2-%23)
- O'Dea, N., & Whittaker, R. J. (2007). How resilient are Andean montane forest bird communities to habitat degradation? *Biodiversity and Conservation*, 16(4), 1131–1159. <https://doi.org/10.1007/s10531-006-9095-9>
- Oksanen, J., Simpson, G., Blanchet, F., Kindt, R., Legendre, P., Minchin, P., O'Hara, R., Solymos, P., Stevens, M., Szoecs, E., Wagner, H., Barbour, M., Bedward, M., Bolker, B., Borcard, D., Carvalho, G., Chirico, M., De Caceres, M., Durand, S., ... Weedon, J. (2022). *Vegan: Community ecology package* (R package version 2.6-2).
- Pakeman, R. J., Small, J. L., Le Duc, M. G., & Marrs, R. H. (2005). Recovery of moorland vegetation after aerial spraying of bracken (*Pteridium aquilinum* (L.) Kuhn) with asulam. *Restoration Ecology*, 13(4), 718–724. <https://doi.org/10.1111/j.1526-100X.2005.00091.x>
- Palomeque, X., Günter, S., Siddons, D., Hildebrandt, P., Stimm, B., Aguirre, N., Arias, R., & Weber, M. (2017). Natural or assisted succession as approach of forest recovery on abandoned lands with different land use history in the Andes of southern Ecuador. *New Forests*, 48(5), 643–662. <https://doi.org/10.1007/s11056-017-9590-8>
- Paz, H., Ortiz-Alcaraz, A., & Del-Val, E. (2022). The effects of the aggressive species *Pteridium caudatum* on the vegetation of Socorro Island: Restoration challenges and opportunities. *Journal for Nature Conservation*, 67, 126160. <https://doi.org/10.1016/j.jnc.2022.126160>
- Pizo, M. A., & dos Santos, B. T. P. (2011). Frugivory, post-feeding flights of frugivorous birds and the movement of seeds in a Brazilian fragmented landscape. *Biotropica*, 43(3), 335–342. <https://doi.org/10.1111/j.1744-7429.2010.00695.x>
- Pulido, L. F., Isaza, C., & Diaz-Pulido, A. (2018). NAIRA III: Una herramienta para el procesamiento y manejo de imágenes de cámaras trampa. *Mammalogy Notes*, 5, 39–44.
- R Core Team. (2022). *R: A language and environment for statistical computing* (4.2.1). R Foundation for Statistical Computing.
- Rehm, E. M., Chojnacki, J., Rogers, H. S., & Savidge, J. A. (2017). Differences among avian frugivores in seed dispersal to degraded habitats. *Restoration Ecology*, 1–7, 760–766. <https://doi.org/10.1111/rec.12623>
- Reid, J. L., Zahawi, R. A., Zárrate-Chary, D. A., Rosales, J. A., Holl, K. D., & Kormann, U. (2021). Multi-scale habitat selection of key frugivores predicts large-seeded tree recruitment in tropical forest restoration. *Ecosphere*, 12(12), e03868. <https://doi.org/10.1002/ecs2.3868>
- Rivas-Alonso, E., Martínez-Garza, C., De La Peña-Domene, M., & Mendez-Toribio, M. (2021). Large trees in restored tropical rainforest. *Forest Ecology and Management*, 498(1), 119563. <https://doi.org/10.1016/j.foreco.2004.06.007>
- Rojas, V. D. (2022). Efecto del paso de semillas por el tracto digestivo de aves y murciélagos sobre el tiempo germinación y la emergencia de plántulas en áreas deforestadas de los Yungas. Licenciature Thesis. Universidad Mayor de San Andres, La Paz, Bolivia.
- Rubey, L., & Hennessey, A. B. (2005). *Birder's guide to Bolivia. Part I: The Bolivian highlands*. <http://birdbolivia.com/Apa%20Apa%20Reserve-Bird%20List.htm>
- Saavedra, F., Hensen, I., Beck, S. G., Böhning-Gaese, K., Lippok, D., Töpfer, T., & Schleuning, M. (2014). Functional importance of avian seed dispersers changes in response to human-induced forest edges in tropical seed-dispersal networks. *Oecologia*, 176(3), 837–848. <https://doi.org/10.1007/s00442-014-3056-x>
- Saavedra, F., Hensen, I., & Schleuning, M. (2015). Deforested habitats lack seeds of late-successional and large-seeded plant species in tropical montane forests. *Applied Vegetation Science*, 18(4), 603–612. <https://doi.org/10.1111/avsc.12184>
- Santos, T., Telleria, J. L., & Virgos, E. (1999). Dispersal of Spanish juniper *Juniperus thurifera* by birds and mammals in a fragmented landscape. *Ecography*, 2, 193–204. <https://doi.org/10.1111/j.1600-0587.1999.tb00468.x>
- Schwartzburd, P. B., Yañez, A., & Prado, J. (2018). Formal recognition of six subordinate taxa within the South American bracken fern, *Pteridium esculentum* (P. *esculentum* subsp. *arachnoideum* s.l.—Dennstaedtiaceae), based on morphology and geography. *Phytotaxa*, 333(1), 22–40. <https://doi.org/10.11646/phytotaxa.333.1.2>
- SERNAP. (2005). *Plan de Manejo del Parque Nacional y Área Natural de Manejo Intergrado Cotapata*. SERNAP-Bolivia.
- Shankar Raman, T. R., Rawat, G. S., & Johnsingh, A. J. T. (1998). Recovery of tropical rainforest avifauna in relation to vegetation succession following shifting cultivation in Mizoram, north-east India. *Journal of Applied Ecology*, 35(2), 214–231. <https://doi.org/10.1046/j.1365-2664.1998.00297.x>
- Silva Matos, D. M., & Belinato, T. A. (2010). Interference of *Pteridium arachnoideum* (Kaulf.) Maxon. (Dennstaedtiaceae) on the establishment of rainforest trees. *Brazilian Journal of Biology*, 70(2), 311–316. <https://doi.org/10.1590/S1519-69842010000200012>
- Ssali, F., Moe, S. R., & Sheil, D. (2017). A first look at the impediments to forest recovery in bracken-dominated clearings in the African highlands. *Forest Ecology and Management*, 402(March), 166–176. <https://doi.org/10.1016/j.foreco.2017.07.050>
- Ssali, F., Moe, S. R., & Sheil, D. (2018). Tree seed rain and seed removal, but not the seed bank, impede forest recovery in bracken (*Pteridium aquilinum* (L.) Kuhn)-dominated clearings in the African highlands. *Ecology and Evolution*, 8(8), 4224–4236. <https://doi.org/10.1002/ece3.3944>
- Ssali, F., Moe, S. R., & Sheil, D. (2019). The differential effects of bracken (*Pteridium aquilinum* (L.) Kuhn) on germination and seedling performance of tree species in the African tropics. *Plant Ecology*, 220(1), 41–55. <https://doi.org/10.1007/s11258-018-0901-8>
- Stotz, D. F., Fitzpatrick, J. W., Parker, T. A., III, & Moskovits, D. K. (1996). *Neotropical Birds: Ecology and Conservation*. The University of Chicago Press.
- Suazo-Ortuño, I., Lopez-Toledo, L., Alvarado-Díaz, J., & Martínez-Ramos, M. (2015). Land-use change dynamics, soil type and species forming mono-dominant patches: The case of *Pteridium aquilinum* in a Neotropical Rain Forest Region. *Biotropica*, 47(1), 18–26. <https://doi.org/10.1111/btp.12181>
- Thiel, S., Tschapka, M., Heymann, E. W., & Heer, K. (2021). Vertical stratification of seed-dispersing vertebrate communities and their interactions with plants in tropical forests. *Biological Reviews*, 96(2), 454–469. <https://doi.org/10.1111/brv.12664>
- Trevelin, L. C., Silveira, M., Port-Carvalho, M., Homem, D. H., & Cruz-Neto, A. P. (2013). Use of space by frugivorous bats (Chiroptera: Phyllostomidae) in a restored Atlantic forest fragment in Brazil. *Forest Ecology and Management*, 291, 136–143. <https://doi.org/10.1016/j.foreco.2012.11.013>
- Valle, D., Griffith, D. M., Jara-Guerrero, A., Armijos-Ojeda, D., & Espinosa, C. I. (2021). A multifaceted approach to understanding bat community response to disturbance in a seasonally dry tropical forest. *Scientific Reports*, 11(1), 1–13. <https://doi.org/10.1038/s41598-021-85066-z>

- Wilman, H., Belmaker, J., Simpson, J., de La Rosa, C., Rivadeneira, M. M., & Jetz, W. (2014). EltonTraits 1.0: Species-level foraging attributes of the world's birds and mammals. *Ecology*, 95(7), 2027. <https://doi.org/10.1890/13-1917.1>
- Wunderle, J. M. J. (1997). The role of animal seed dispersal in accelerating native forest regeneration on degraded tropical lands. *Forest Ecology and Management*, 99, 223–235. [https://doi.org/10.1016/S0378-1127\(97\)00208-9](https://doi.org/10.1016/S0378-1127(97)00208-9)

How to cite this article: Gallegos, S. C., Mayta, C., Villegas, M., Ayala, G. M., Naoki, K., Rechberger, J., Rojas, V., Viscarra, M. E., Bernal-Hoverud, N., Espejo, M., & Hensen, I. (2024). Habitat differences in seed-dispersing vertebrates indicate dispersal limitation in tropical bracken-dominated deforested areas. *Biotropica*, 56, e13317. <https://doi.org/10.1111/btp.13317>

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.