Differences in bird and bat traits, seed-dispersal interactions and functions between tropical montane forest and bracken-dominated areas

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Most tropical plant species depend on animals to disperse their seeds. Seed dispersal by animals allows plants to colonize new sites in deforested habitats helping to accelerate forest recovery. However, deforestation can affect the interactions between animals and plants that are crucial for forest regeneration. In this study, we analyze the differences on the composition of functional traits and on seed-dispersal interactions and functions by birds and bats between forest and deforested areas dominated by bracken fern. At eight study sites, we captured birds and bats in bracken-dominated areas and at forest in the tropical montane forest of Bolivia and analyzed their droppings. We found a similar composition of functional traits related to animal size, gape width and degree of frugivory of bats in both habitat types. Hand-wing index of birds was significantly higher in bracken compared to forest. Birds had more interaction richness and abundance in bracken than in forest, and bats had more interaction abundance in forest than in bracken. The majority of seeds dispersed by birds and bats in bracken were from pioneer species. We conclude that, although seed dispersal by birds and bats is maintained in the bracken-dominated areas, most of the dispersed seeds belong to pioneer species. Pioneer species are unlikely to establish in bracken-dominated areas, making the natural regeneration process of these deforested areas very slow.

KEYWORDS

forest regeneration, frugivory, mist nets, non-pioneer, pioneer, Pteridium

1 Introduction

More than 90% of tropical plant species depend on animals to disperse their seeds (Jordano, 2000). Birds and bats are considered particularly important seed dispersers, as they play a key role in forest regeneration due to the number and diversity of seeds that they disperse (Jacomassa and Pizo, 2010). Seed dispersal by these animals allows plants to colonize new sites in deforested habitats helping to accelerate forest recovery (De La Peña-Domene et al., 2014). Deforestation affects the diversity and composition of animals and plants (Haddad et al., 2015) and their biotic interactions, including seed dispersal (Laurance, 2005). Given the importance of birds and bats, it is necessary to evaluate the differences in seed dispersal by birds and bats between forested and deforested areas and to analyze the consequences for forest regeneration.

Many tropical deforested regions harbor forest fragments that are surrounded by open areas often composed by bracken fern (*Pteridium* spp.) (Lippok et al., 2013; Curatola Fernández et al., 2015; Matongera et al., 2018). Bracken usually grows after fire (Roos et al., 2010) and can dominate the vegetation for long periods of time (Hartig and Beck, 2003). Bracken produces dense fronds and a deep litter layer that could impede the establishment of other plant species (Marrs et al., 2000), especially of pioneer species. However, bracken generates microenvironmental conditions (high humidity, low temperature, low light) that could favor the establishment of non-pioneer shade-tolerant species (Gallegos et al., 2015; López et al., 2024; Ssali et al., 2019). The dominance of bracken can last several years, hindering the forest regeneration process. The slow forest regeneration is mainly linked to the seed limitation (i.e. low seed arrival) of animal-dispersed, non-pioneer plant species (Saavedra et al., 2015; Gallegos et al., 2016; Ssali et al., 2018). This limitation could be related to the scarcity of food resources, shelters and perches for animal seed dispersers, and to differences in species composition of seed dispersers between forest and bracken-dominated areas (Saavedra et al., 2015; Gallegos et al., 2024; Mayta et al., 2024). Although there are indications of seed limitation of non-pioneer species, it is unclear whether this is due to the functional traits of seed dispersers or other characteristics in the animal-plant interaction in bracken-dominated areas.

Fragmented landscapes are characterized by the presence of different habitats such as the forest interior, the forest edges and the 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 (Menke et al., 2012; Jankowski et al., 2021), 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 (Renjifo, 1999; Markl et al., 2012), while small frugivores and omnivores seem to better tolerate such disturbances (O'Dea and Whittaker, 2007; Gomes et al., 2008). Tropical forest disturbance could also generate differences in the trait composition of bird communities between forested and deforested areas (Newbold et al., 2013; García-Morales et al., 2016). 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; Messina et al., 2021; Falconí-López 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 (Farneda et al., 2020; Díaz-B et al., 2023). It is therefore 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 remains poorly understood. Deforestation not only affects the diversity and traits of animal seed dispersers, but can also have an effect on the interaction between plants and their animal seed dispersers (González-Varo et al., 2023). In some cases, more disturbed habitats could have less pairwise bird-plant interactions (Menezes Pinto et al., 2021), however, other studies detected an opposite pattern (Menke et al., 2012; Saavedra et al., 2014). Thus, the gain or loss of seed-dispersal interactions may related to the composition of animal and plant communities in the different ecosystems.

In this study, we aim to analyze the differences in trait composition related to seed dispersal, interactions, and seed-dispersal functions of birds and bats between bracken-dominated areas and forest. To this end, we addressed the following questions: 1) Is there a difference in the functional trait composition of animal seed dispersers (birds and bats) between forest and bracken-dominated areas? We 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 large distance than birds captured at forest (Camargo et al., 2020; Messina et al., 2021; Falconí-López et al., 2024), whereas we did not expect differences in the trait composition of bats between both habitats [(Farneda et al., 2020). 2] What are the differences in plant-animal interactions between bracken-dominated areas and forest? We expected to find more seed-dispersal interactions in bracken-dominated areas due to their high 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). 3) Is there a difference in the abundance and richness of seeds from plant species with different life histories between bracken-dominated areas and forests? We expected to find more seeds of pioneer species in animals captured in bracken-dominated areas than in animals captured at forests because of the expected changes in trait composition, particularly in birds. Birds with small gape width usually disperse small seeds (Wheelwright, 1985; Bovo et al., 2018), and small seeds are characteristic of pioneer species (Valio and Scarpa, 2001). Seed dispersal in bracken-dominated areas has primarily studied though the analysis of seed rain. The morphological characteristics of animal seed dispersers (birds and bats), and the characteristics and functions of animal-plant interactions in these widely distributed deforested areas remains poorly understood.

2 Materials and methods

2.1 Study area

The study was conducted in a tropical montane forest in the Bolivian Andes between 1,900 and 2,350 m a.s.l. near the town of Chulumani (16°24'37" S, 67°31'37" W). 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 and human induced fires (Killeen et al., 2005). 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 and Melastomataceae (Lippok et al., 2013). 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., 2013). 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).

2.2 Study design

We conducted the study at eight sites located at the borders of remnant forests separated by at least 1 km (Supplementary Figure S1). At each site, we 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, we 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. We closed mist nets when it rained. Total sampling effort was 4861 net-hours for birds, and 2576 net-hours for bats. It should be noted that the use of mist nets favors the capture of birds and bats present in the understory (Whitman et al., 1997).

2.3 Bird, bat and seed sampling

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. For each bird species, we measured body mass, hand-wing index and gape width, while we could only measure body mass for bats. We chose these traits 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, we 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 (Sheard et al., 2020; Falconí-López et al., 2024). 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 we 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. The bats were identified from external morphological characteristics, so it is possible that there was some misidentification in bats of the same genus (e.g. in Carollia). However, Aguirre et al. (2009) and Díaz et al. (2016) provide clear external morphological differences that may help to reduce misidentifications.

We 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. Overall, 321 seed samples (droppings and/or regurgitates) could be 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 our study site (Gallegos et al., 2016; Lippok et al., 2013, 2014; López et al., 2024), expert knowledge, and information at 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.

2.4 Statistical analysis

We used generalized linear mixed-effects models (GLMMs) for all the analyses. The use of mist nets favors the capture of small birds and bats, and capture efficiency may vary across environments with different vegetation structures (Jenni et al., 1996). To address this potential sampling bias, we performed the analysis of functional traits of birds and bats by randomly drawing the same number of individuals from each habitat at each site. A GLMM was fitted to each subsample, and this process was repeated 999 times. We then interpreted the results using the mean of the estimates across all GLMMs. We analyzed the differences of gape width, body mass and HWI for birds and body mass and frugivory degree for bats. Habitat type (forest and bracken) was included as the independent fixed effect, and bird or bat species, nested within site, nested within fragment, were the random effects. The models used a Gaussian distribution of errors, except for bat's frugivory degree that used an betabinomial distribution of errors. We 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 variable, habitat type (forest and bracken) as the independent fixed effect, and site nested in fragment as the random effects. 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 (Jordano, 2016; Chiu et al., 2023). 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, we estimated the interaction richness with the iNEXT.link package (Chiu et al., 2023). We 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, we 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. We performed the analysis of the abundance of seeds by randomly drawing the same number of individuals from each habitat at each site. A GLMM was fitted to each subsample, this process was repeated 999 times and we interpreted the results using the mean of the estimates across all GLMMs. Species richness of pioneer and non-pioneer species was calculated for each study site. In separate models we tested the abundance of seeds, and seed species richness as the response variables for birds and for bats. In the models used to analyze seed abundance, life history (pioneer or non-pioneer), habitat (forest and bracken) and their interaction were the independent fixed effects. Bird or bat species, nested within site, nested within fragment, were the random effects. For seed species richness models, life history (pioneer or non-pioneer), habitat (forest and bracken) and their interaction were the independent fixed effects. Site nested within fragment were the random effects. The four models used a Poisson distribution of errors. All models were performed with the *glmmTMB* package (Brooks et al., 2017). To determine significant differences between habitats, we performed Tukey *post hoc* tests using the *emmeans* package (Russell et al., 2024). For all models, the significance of the fixed factors was determined by Likelihood Ratio Tests (LRT) between models with and without the term of interest. Additionally, we calculated marginal R^2 values to assess the proportion of variance explained by the fixed factor using the r.squaredGLMM function of the *MuMIn* package (Barton, 2023). Overdispersion in model residuals were tested with *DHARMA* package (Hartig, 2024). All statistical analyses were conducted in R 4.2.2 (R Foundation for Statistical Computing, 2022). We assessed the sample completeness of plant-animal interaction using method "abundance" with the *iNEXT* package (Hsieh et al., 2016).

3 Results

3.1 Functional traits of birds and bats

We captured 31 bird species, 27 species (99 individuals) in bracken and 13 species (65 individuals) at forest (Supplementary

Table S1). We caught 12 bat species, eight in bracken (23 individuals) and eight at forest (34 individuals) (Supplementary 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 we recorded nine and four individuals, respectively. At forest, *M. striaticollis* and *Chiroxiphia boliviana* were the most abundant bird species, of which we recorded 23 and 17 individuals, respectively. Among the bats, *Carollia perspicillata* and *Carollia brevicauda* were the most common species with 14 and 11 records, respectively.

We found no differences in body mass ($X^2 = 0.098$, p = 0.75) and gape width ($X^2 = 0.10$, p = 0.75) of birds between bracken and forest (Figures 1A, B; Supplementary Table S2). The hand-wing index (HWI) was significantly higher in bracken compared to forest ($X^2 = 43.65$, p < 0.001, Figure 1C; Supplementary Table S2). For bats, we found no differences in body mass ($X^2 = 0.06$, p = 0.80) and frugivory degree ($X^2 = 1.47$, p = 0.22) between the two habitat types (Figures 1D, E; Supplementary 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.

3.2 Seed-dispersal interactions

After 7,437 net-hours of sampling effort for birds and bats, we 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 the bracken area and 91% at the forest edge (Supplementary Figure S2). For birds we 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; Figures 2A, B; Supplementary Table S3). For bats we did not find differences for interaction richness between bracken and forest ($X^2 = 3.47$, p = 0.07; Figure 2C; Supplementary Table S3). The abundance of interactions was 2.7 times higher in bracken than in forest ($X^2 = 7.19$, p = 0.007; Figure 2D; Supplementary Table S3).

3.3 Successional status of animal-dispersed species

We found that the abundance and species richness of bird-dispersed pioneer seeds in bracken were 3.34 and 2.15 times higher, respectively, compared to forest (Figures 3A, B; Supplementary Table S4). In bracken the abundance of bird-dispersed pioneer species was 9.54 times higher than the abundance of non-pioneer
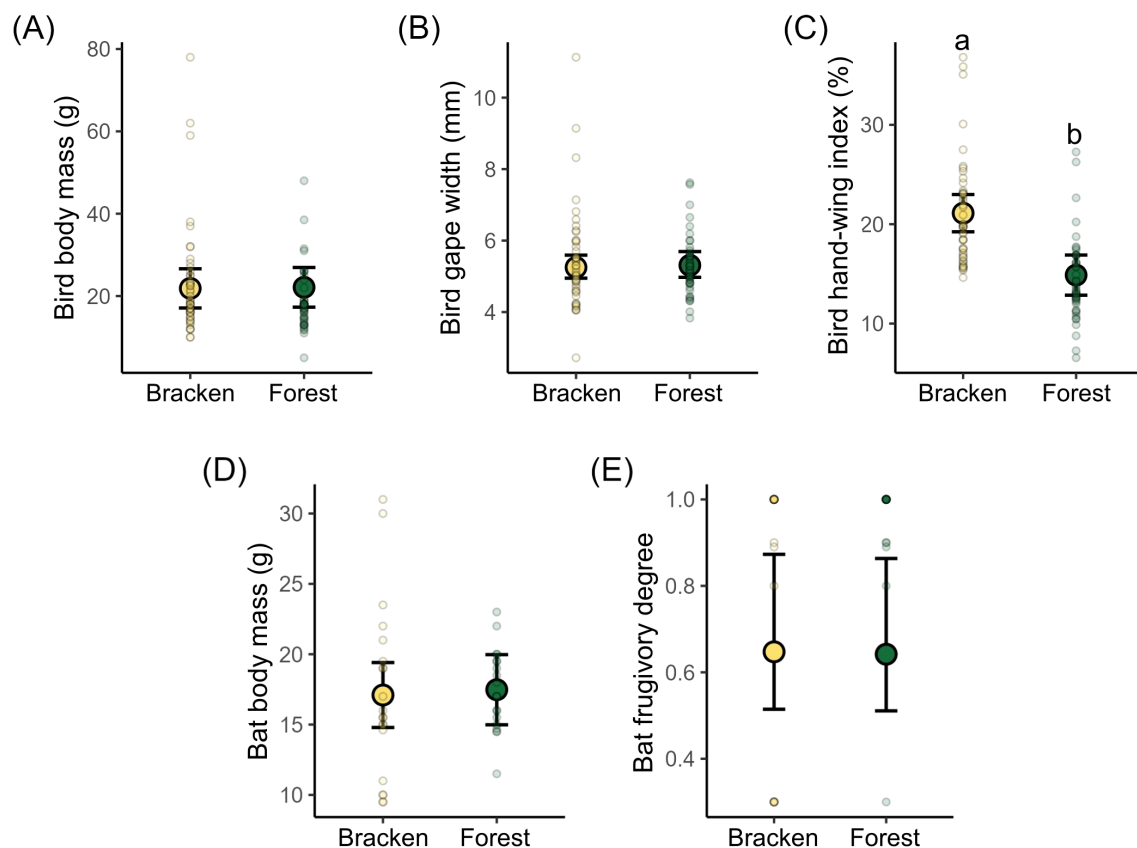
FIGURE 1
Comparison of community-weighted means of **(A)** bird body mass, **(B)** bird gape width and **(C)** bird hand-wing index between bracken and forest habitats of 31 bird species. Comparison of community-weighted means of **(D)** body mass and **(E)** frugivory degree between bracken and forest 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.

species in the same treatment (X^2 = 18.52, p < 0.001; Figure 3A; Supplementary Table S4). Abundance of bat-dispersed pioneer seeds in bracken was 5.12 times higher compared to forest (X^2 = 5.02, p = 0.02; Figure 3C; Supplementary Table S4), and 3.47 times higher compared to non-pioneer seeds in forest (X^2 = 7.80, p = 0.005; Figure 3C; Supplementary Table S4). We did not find differences in bat-dispersed richness between habitats and life history categories (Figure 3D; Supplementary 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) (Supplementary Table S5).

4 Discussion

We found a similar trait composition of birds and bats in bracken and forest, except for the hand-wing index of birds that was higher in bracken compared to forest. We recorded higher interaction richness and abundance for birds in bracken compared to forest, while for bats, interaction abundance was higher in forest than in bracken. Importantly, seed-dispersing animals transported more pioneer than non-pioneer species in bracken. However, pioneer species are unlikely to become established in bracken-dominated areas due to bracken

shade (Gallegos et al., 2015, 2016; Ssali et al., 2019; López et al., 2024). Although previous studies have suggested a limitation of non-pioneer seeds in bracken-dominated areas (Saavedra et al., 2015; Mayta et al., 2024), our work reveals that this limitation is linked to the morphological characteristics of dispersing animals (small animals that disperse small seeds) and the higher quantity of pioneer seeds consumed by these animals.

Deforested environments can favor the dominance of a subset of functional traits in birds and bats (Frank et al., 2017; Bovo et al., 2018). We expected birds in forests to 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 (Pavlacky et al., 2015; Bovo et al., 2018). Moreover, the loss of forested areas could lead to differences in composition of animal-seed disperser communities (Chiarello, 1999; Morante-Filho et al., 2015). For example, Gallegos et al. (2024) found differences in the composition of birds between forest and bracken areas. However, we found no 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. We found that birds captured in bracken had higher hand-wing index (HWI) compared to those
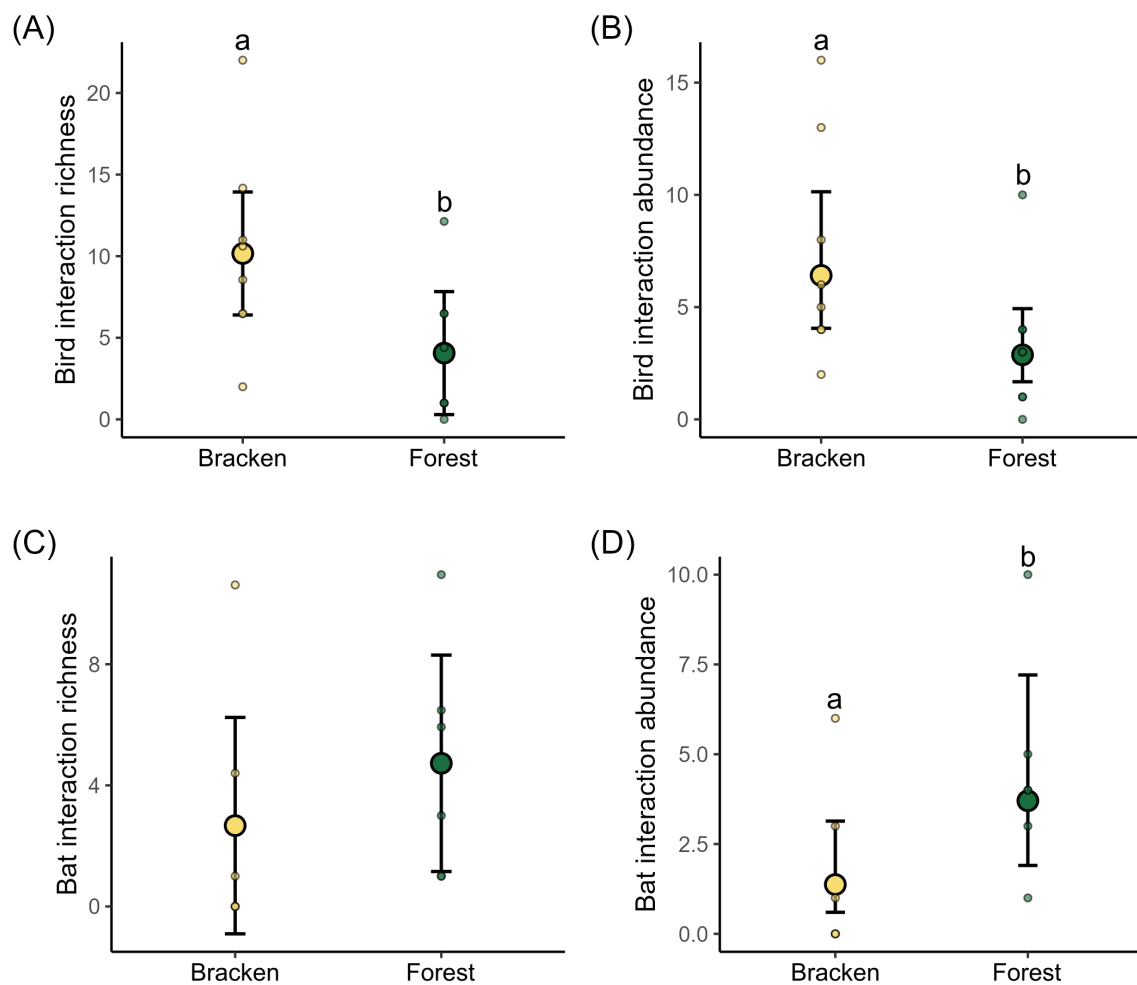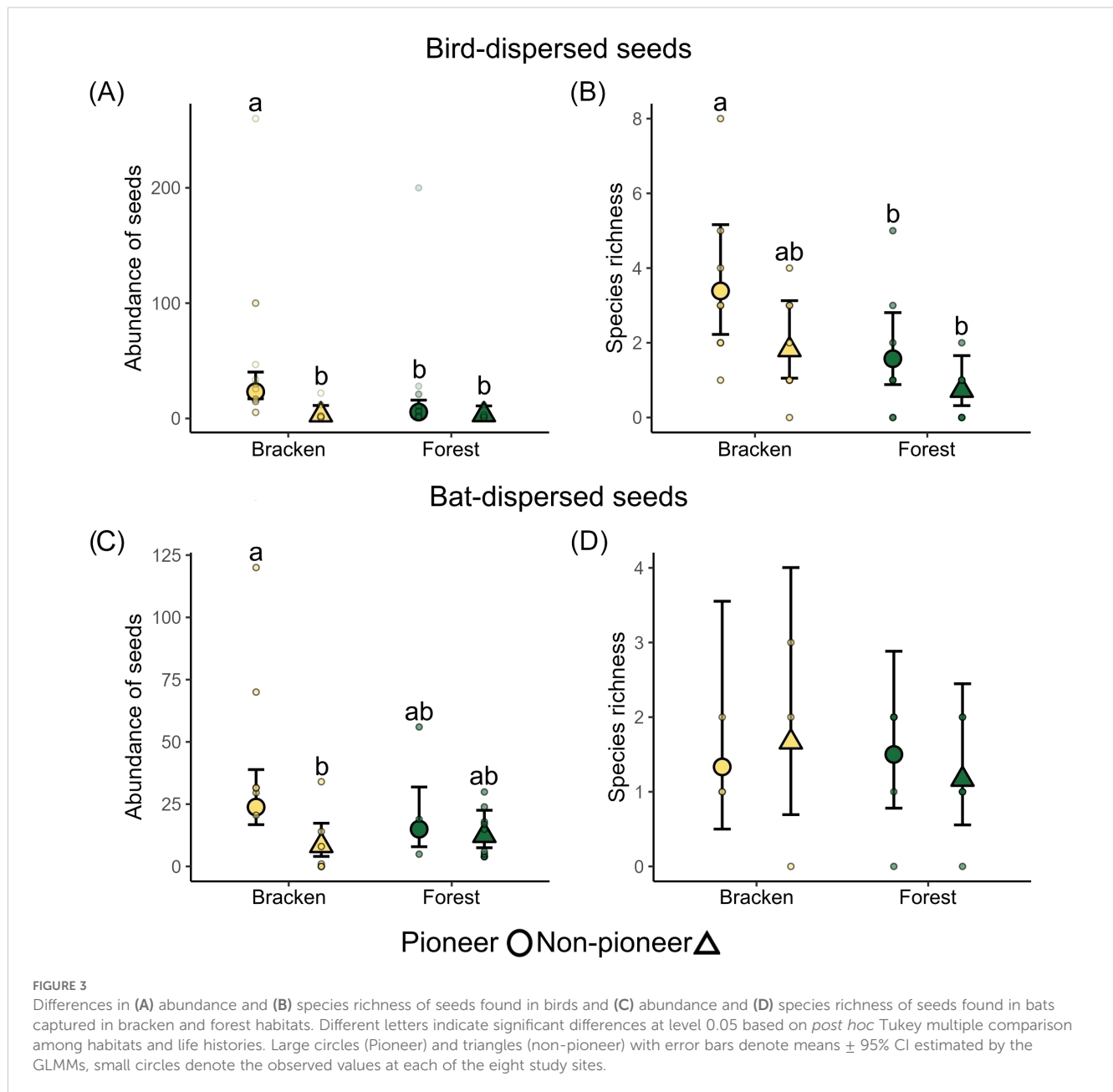
FIGURE 2
Difference in the **(A)** interaction richness and **(B)** abundance of birds and **(C)** interaction richness and **(D)** abundance of bats between bracken and forest habitats. Different letters indicate significant differences at level 0.05 based on *post hoc* Tukey comparison among habitats. 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.

captured in forest. Birds with high HWI could fly long distance and cross open areas and are less sensitive to habitat fragmentation than birds with low HWI (Jones et al., 2023; Falconí-López et al., 2024). It is possible that the changes in trait composition would have been more pronounced if we had compared the bracken habitats with the interior of the forest fragments. Previous studies showed that large-bodied and large-gaped bird species increase in importance towards the most conserved forest interior (Sekercioglu, 2012; Saavedra et al., 2014; Emer et al., 2018). We found no 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 bracken areas, there are species of *Piper, Vismia* and *Solanum* (Lippok et al., 2013, 2014) that are preferentially consumed by frugivorous bats, but in low densities. Another reason for the weak differences in bird and bat communities could be our 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).

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 (Marjakangas et al., 2020; Menezes Pinto et al., 2021; Li et al., 2022). Contrary, we found that bracken had more bird interactions richness and abundance than forest. This could be related to the fact that in our 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 (Huber et al., 1984; Lippok et al., 2013; Martínez-Ramos et al., 2016) that bear fruits most of the year and are attractive to birds. For bats, we found higher interaction abundance in forest than in bracken. The abundance of frugivorous bats is related to the abundance of their food (Klingbeil and Willig, 2009). In forest there are more species and more individuals of plants of the families Piperaceae and Solanaceae than in bracken (Lippok et al., 2013, 2014). In addition, the abundance of frugivorous bats is higher in forest compared to bracken

FIGURE 3
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 histories. Large circles (Pioneer) and triangles (non-pioneer) with error bars denote means $\pm$ 95% CI estimated by the GLMMs, small circles denote the observed values at each of the eight study sites.

(Gallegos et al., 2024). Thus, our results for bats could be related to higher abundance of frugivorous bats and their food resources in forest compared to bracken.

We found that birds and bats present in the bracken area carried significantly more seeds of pioneer species than birds and bats captured at the forest. This could be related to the fact that the majority of birds and bats that disperse seeds into bracken area were small frugivorous and omnivorous species that mostly consume fruits with small seeds (Snow, 1981; Arteaga et al., 2006; Emer et al., 2018) 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 from deforested areas, and are rare in the forest. On the other hand, non-pioneer, shade-tolerant plant species that usually have large seeds (Thompson and Rabinowitz, 1989; Khurana and Singh, 2006) are mostly dispersed by large specialist frugivore birds (Snow, 1981; Carlo

et al., 2022) and large mammals (Cramer et al., 2007), which were rare in the bracken areas. For instance, Saavedra et al. (2015) and Ssali et al. (2018) found a lack of non-pioneer and large-seeded plants in the seed rain in bracken areas of south America and Africa, respectively, suggesting that there was very little dispersal of such species from the forest. In the forest interior and forest edge of tropical mountain forests there are several species of Lauraceae, and species such as *Rhamnus* sp*haerosperma, Symplocos arechea* that have large seeds (>10 mm) and are non-pioneer species (Oosterhoorn and Kappelle, 2000; Günter et al., 2007; Lippok et al., 2014; Saavedra et al., 2015; López et al., 2024). Bracken fosters the establishment of non-pioneer species, but not of pioneer species (Gallegos et al., 2015; Ssali et al., 2019; López et al., 2024). Although pioneer species arrive into bracken areas, the recruitment of these species is hindered by the low light conditions under bracken, that is detrimental to light demanding pioneer species

(Gallegos et al., 2015, 2016; López et al., 2024). In this study, we 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 a plant that remains in the deforested area or that bats defecate in flight and drop seeds. Future studies can analyze aspects related to the behavior of seed dispersers, for example, analyze if birds that consume fruits in the forest are able to go out to bracken areas and deposit seeds in these deforested areas.

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). We 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 birds and bats actually deliver to deforested sites is mist netting which allowed us to estimate the actual seed-dispersal functions by birds and bats. It is important to recognize that this method primarily captures small frugivores and may underestimate the role of large and other frugivorous animal groups. The characteristics of seed-dispersal interactions vary according the forest strata (Schleuning et al., 2011; Thiel et al., 2021). Our results reflect the interactions of species that actively use the understory. Additional studies using alternative methods are needed to assess the effects of communities in other forest strata and their role in forest regeneration.

Since most bird and bat species dispersed mainly pioneer species that rarely establish in bracken areas, our results suggest that seed dispersal of non-pioneer species is limiting natural regeneration dynamics in bracken-dominated areas. Thus, active restoration techniques are needed, such as planting species that can growth in the presence of bracken, reduce their dominance and facilitate the establishment of non-pioneer species (Toledo-Aceves et al., 2022). Moreover, the installation of perches increases the seed rain and seedling establishment of bird-dispersed species in bracken areas (Mayta et al., 2024). These strategies could help to reestablish seed dispersal of non-pioneer species by large animals in bracken-dominated areas, which is crucial for the maintenance and regeneration of tropical forests.

Data availability statement

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

Ethics statement

The animal study was approved by Direccion General de Biodiversidad, Ministerio de Medio Ambiente y Agua (permit: CAR/MMAYA/VMABCCGDF/DGBAP/MEG 0012/2020). The study was conducted in accordance with the local legislation and institutional requirements.

Author contributions

CM: Data curation, Formal analysis, Writing – original draft. MS: Formal analysis, Writing – review & editing. CL: Data curation, Writing – review & editing. MV: Data curation, Writing – review & editing. IH: Funding acquisition, Supervision, Writing – review & editing. SG: Project administration, Supervision, Writing – review & editing.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Generative AI statement

The author(s) declare that no Generative AI was used in the creation of this manuscript.

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Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2025.1567678/full#supplementary-material.

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