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EFFECTS OF HUMAN DISTURBANCES ON THE SEED DISPERSAL OF BAT COMMUNITIES IN THE ECUADORIAN ANDEAN CHOCÓ

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Abstract.

In the northwestern forests of Pichincha, in Ecuador, some of the last Chocoan forests, located in the Mashpi mountains, have been fragmented due to deforestation and cattle ranching, which has impacts in ecosystem functioning. This study aims to assess how human disturbances influence seed communities dispersed by understory fruit bats (Phyllostomidae). We identified four different types of habitats, based on their conservation status and management strategies: primary forest (PF), secondary forest in natural regeneration (SF1), secondary forest in assisted regeneration (SF2), and pastures for cattle (P). Additionally, we studied the availability of plant resources that these animals can disperse in each habitat. Our results suggest that anthropogenic disturbances caused significant changes in the natural dynamics of seed dispersal in disturbed habitats (SF1, SF2, and P). These alterations are delaying the processes of secondary succession and species recruitment, making it difficult to predict the successional trajectories of these ecosystems.

*Key words***:** *Successional trajectories, priority effects, ecosystem services, edge effects.*

Introduction

Biodiversity represents the variety of different forms of life on earth, referring to the different number of species, the different genes these species possess, as well as the ecosystems they compose (Rawat & Agarwal, 2015). One of the emerging properties of biodiversity is the generation of ecosystem services, defined as the environmental conditions and natural processes through which ecosystems and biodiversity maintain human life (Lü & Wang, 2017). Ecosystem services are classified into supporting, regulation, provisioning and cultural services (Markl et al. 2012); which sustain human life by providing food, clean water, fresh air, medicine, clothing, raw materials, a pleasant climate, controlled diseases, fertile soil, cultural development, etc. (Martín-López et al. 2007). One of the least appreciated ecosystem services by society is the dispersal of seeds by animals, which maintain the natural dynamics of tropical ecosystems (Lacher et al. 2019); bats for example, are the most diverse seed dispersers in neotropical forests (Kelm et al. 2008).

Neotropical bats are very efficient as seed dispersers, as their accelerated metabolism allows that seeds consumed remain between 30-60 minutes in their digestive tract before being defecated (Saldaña-Vázquez, 2014). This fact, added to their high mobility, means this group can disperse seeds over great distances, including between forest mosaics and disturbed habitats, having great impacts on landscape dynamics (Kelm et al. 2008; Lacher et al. 2019). As such, they contribute to maintaining a high genetic variability between isolated plant populations, helping to maintain the dynamics of natural plant succession in healthy ecosystems, and promoting succession and regeneration in disturbed areas (Mesquita et al. 2001; Kelm et al. 2008; Novoa et al. 2011). Bats are essential for restoration and reforestation because they disperse a highly diverse plant community far away from the parental tree, which increases the probability of colonization of new forest patches, and ensures a higher survival rate for these seeds (Mesquita et al. 2001). However, a recent review of the ecosystem roles of bats across ecosystems and taxonomic groups showed that the assessment of ecosystem services provided by bats in transformed landscapes and agricultural crop areas remains largely unexplored (Ramírez-Fráncel et al. 2021).

Anthropic activities negatively affect the quality of ecosystem services provided by bats in neotropical forests (Kelm et al. 2008; Medellín et al. 2000). A meta-analysis carried out on a global scale shows that the ecosystem services most threatened by human activities are pollination and seed dispersal; without these plant regeneration processes, food security and the use of resources on which civilization depends are endangered (Neuschulz et al. 2016). The main human activities that contribute to altering the natural dynamics of seed dispersal and ecosystem functioning are deforestation, expansion of the agricultural frontier, habitat conversion, fires, and hunting (Markl et al. 2012; Wieland et al. 2011). In tropical forests worldwide, it is common for human activities to create open areas that are abandoned after a use (Kelm et al. 2008; Wieland et al. 2011). Under these circumstances, natural regeneration processes can be initiated in which seed dispersal influences the initial succession, giving rise to the growth of secondary forests (Kelm et al. 2008; Wieland et al. 2011).

In neotropical forests, previous land use and management methods are extremely variable in space and time (Mesquita et al. 2015; Norden et al. 2011). Furthermore, the type of disturbances that occurred in the past are usually only known thanks to anecdotal accounts (Mesquita et al. 2015), which avoids establishing cause and effect relationships in the successional trajectories of open areas (patterns of changes in the composition of species in an ecosystem) (Hooper et al. 2004; Mesquita et al. 2015). Several studies acknowledge the importance of land use history on vegetation composition as succession progresses, noting that disturbed areas can evolve into alternative and persistent states (Dent et al. 2013; Norden et al. 2011; Odion et al. 2010). Ramírez-Fráncel et al. (2021), review of bats and their vital role on ecosystem services highlight the fact that, even though most studies regarding seed dispersal of native or endemic species have been conducted within the Neotropical region, most of these lack an experimental approach regarding broader bat feeding ecology and their contribution to environmental function. Therefore, we are still unable to fully understand how bats impact ecosystems at different spatial scales, and how changes in land use affect seed dispersal by bats. For instance, initial colonizers can remain for a long time in a disturbed forest, and even cause succession to generate a forest type with a different plant composition in the area compared to the forest composition before the disturbance (Chazdon, 2003; Hooper et al. 2004; Mesquita et al. 2001).

It is estimated that succession in altered tropical forests could take between 100 - 200 years if the land use is of low intensity (Mesquita et al. 2001), and it could take up to 500 years to return the ecosystem to its original state if the land use was intense (Chazdon, 2003; Dent et al. 2013). Differences in successional trajectories may be caused by limited seed dispersal, by differences in abiotic factors (especially in soil quality), or by priority effects stemming from the competitive advantages of early colonizers (Hooper et al. 2004; Norden et al. 2011; Weidlich et al. 2021).

In Neotropical forests, the creation of open areas responds mainly to two treatments: clearcutting and the creation of pastures for cattle (Hooper et al. 2004; Longworth et al. 2014; Mesquita et al. 2015; Norden et al. 2011). In the first treatment, large and small trees are removed, leaving tree stumps that can regenerate quickly, burning is minimal and it is common for plants of the *Cecropia* genus to dominate after a while. Clearcuts represents a state of minimal disturbance because stumps can be regenerated and the soil seed bank is allowed to germinate, and as such, soil nutrients and properties are not affected (Hooper et al. 2004; Longworth et al. 2014; Mesquita et al. 2015; Norden et al. 2011). In the second treatment, in addition to cutting, land is also burned, eliminating stumps that could sprout and the soil seed bank. Exotic herbs are introduced into the land and the way is opened for livestock. Burnings are carried out annually, for 5 or 8 years, until the land is abandoned. This method commonly benefits the germination and dominance of plants like *Vismia* (Hooper et al. 2004; Longworth et al. 2014; Mesquita et al. 2015; Wieland et al. 2011). Thus, the creation of pastures suppresses the original plant composition of trees and seeds due to burning and competition with introduced species, and allows soil compaction, erosion, and loss of nutrients due to cattle trampling (Longworth et al. 2014; Mesquita et al. 2015).

Regeneration of tropical forests disturbed by anthropic activities can be slowed for years by the establishment of competitive pioneer species, such as those of the genus *Vismia* and *Cecropia* (Longworth et al. 2014; Mesquita et al. 2001; Wieland et al. 2011), because they inhibit the recruitment of new species of initial succession, becoming dominant (Mesquita et al. 2015; Wieland et al. 2011). The two types of land use replacement described above create less suitable habitats for bats because they offer fewer roosts as well as less diversity and abundance of food sources (Kelm et al. 2008). Several investigations find that the diversity and abundance of seeds dispersed by bats decreases in environments that had disturbances of anthropic origin (Aguilar-Garavito et al. 2014; Markl et al. 2012); with less seed input, natural regeneration processes are delayed (Kelm et al. 2008). In this way, the previous history of land use can not only affect the successional trajectories of the plant composition of the land, it also significantly influences seed dispersal (Hooper et al. 2004; Longworth et al. 2014; Mesquita et al. 2015; Wieland et al. 2011).

In Ecuador, in the Andean Chocó, especially in the Mashpi mountainous region, has been highly fragmented, mainly by the expansion of agricultural activities, forest deforestation and, in recent years, mining activities (Roy et al. 2018). This type of human intervention in Mashpi's past has affected the availability of plant resources in the ecosystem. This landscape is made up of mosaics of primary forests, secondary forests, and pastures suitable for analyzing the effect of anthropogenic disturbances on the composition of seeds dispersed by bats. Analyzing this type of data in South America is important to understand how the anthropogenic disturbances described above, are the main drivers of biodiversity loss worldwide, which has led to what is currently considered the ongoing sixth mass extinction (Ceballos et al. 2020; WWF, 2020). The impacts of these losses on nature, their ecological interactions, ecological functions, ecosystem services and different aspects of human life are being studied at small and large scales (Ceballos et al. 2020; Valiente-Banuet et al. 2015). Thus, this research is useful to compare effects on the ecosystem services provided by other mammalian species in other parts of the world.

Material and Methods

Study area

This work was carried out in four reserves (Mashpi Lodge, Pambiliño, Chontaloma and Mashpi Shungo) in the northwestern piedmont evergreen forests of the western Andes range (PEF) (MAE, 2013), in the province of Pichincha. These reserves had different land use histories which allowed us to make comparisons. Mashpi Lodge, is a private reserve with a past history of logging, so most of its territory is secondary forest, and the rest corresponds to primary forest, mainly located in steep and unexplored areas designated as protected forest. In Masphi lodge we surveyed in areas of primary or undisturbed forests. The agro-ecological reserves of Mashpi Shungo, Pambiliño and Chontaloma, are located 3.7 km away from Mashpi Lodge. In the years between 1980-2000 forests around these reserves suffered the loss of vegetation cover due to deforestation. Later, open areas were converted into pastures for cattle ranching, and in the last 12 - 15 years monocultures of heart of palm (*Bactris gasipaes*) and cacao (*Theobroma cacao*) were installed. Most of these reserves have secondary forests in natural regeneration that were used for our sampling, except in Mashpi Shungo where there are some areas of undisturbed forest that were also included. In Chontaloma we surveyed a 4-year-old patch of secondary forest in assisted regeneration, which has managed trees and shrubs that improve soil quality and create shade that eliminates grass. This area was used for cattle ranching in the past. Around Chontaloma there are several adjoining lands that are still used as pastures for cattle, we finally used a small part of these lands to understand how bats contribute in processes of initial succession . Today livestock is relatively scarce among the three reserves (Falchi & Solano com pers. 2021) (Supplementary material, Fig. S1).

Capturing bats and seeds

We carried out 45 bat capture sessions between the months of February and August 2021: 12 sampling nights in primary forest (PF) at Mashpi Lodge, 12 sampling nights in secondary forest in natural regeneration (SF1) and 12 nights in secondary forest in assisted regeneration (SF2) between the Pambiliño and Chontaloma reserves. In addition, a 9-night sampling trip was carried out between the Mashpi Shungo and Chontaloma reserves. In Mashpi Shungo, we carried out 3 sampling nights in primary forest (PF) and 3 sampling nights in secondary forest in natural regeneration (SF1), while in Chontaloma 3 sampling nights were worked in pastures of for cattle (P). In the study sampling sited were grouped by forest type (PF, SF, P)

For the capture sessions, we used 4-7 mist nets of variable sizes (6, 9 and 10 meters), opened between 19:00 pm to 00:30 am (Arias & Pacheco, 2019; Novoa et al. 2011). We placed capture stations on closed trails, mountain ridges, near water sources, and potential flight sites where bats could be intercepted (Kelm et al. 2008). Nets were checked in 15 to 20 minute intervals. Bat species were identified with the help of field guides (López-Baucells et al. 2016; Tirira, 2017). To obtain seeds, the animals were kept for an hour in cloth bags. Fecal samples obtained were preserved in 2 ml eppendorf tubes with 70% alcohol (Arias & Pacheco, 2019). We collected voucher specimens according to the guidelines of the American Society of Mammalogist (Sikes & Gannon, 2016). The specimens were deposited with their respective reference data in the Museo Ecuatoriano de Ciencias Naturales (MECN) of the Instituto Nacional de Biodiversidad (INABIO) under the research license with code MAE-ARSFC-2020-0.512 granted by the Ministerio del Ambiente Agua y Transición Ecológica del Ecuador (MAATE) (Appendix 1).

Counting seeds

Seeds collected were separated from the fecal remains in the laboratory with entomological tweezers. Once separated they were dried on paper envelopes and then photographed with a stereomicroscope (Arias & Pacheco, 2019). To count very numerous seeds such as those of the genus *Piper*, we used the AI app CounTThings from Photos (Dinamic Ventures INC, 2017), and for cases in which this application could not differentiate seeds from other fecal residues, we used ImageJ (Wayne Rasband (NIH), 2019) , which allows counting the seeds based on the size of their pixels. Seed identification was performed to the lowest taxonomic level possible using field guides (Kirkbride et al. 2006; Lobova & Mori, 2007; Magalhaes de Oliveira & Pereira, 2016). Counts were made by individual, then grouped by species and type of habitat (PF, SF1, SF2, P).

The seed collection was deposited in the MECN to act as a reference guide for other studies.

Availability of plant resources

To determine resource use vs availability, vegetation transects were established at each site: 6 in primary forest (PF), 5 in secondary forest in natural regeneration (SF1), 2 in secondary forest in assisted regeneration (SF2) and 3 in pastures for cattle (P) (Fig. S1). Each transect was 50 x 2 m, where richness, composition and frequency of woody plant species with a CBH (Circumference at Breast Height) greater or equal than 2.5 cm up to 10 cm were recorded (Mostacedo & Fredericksen, 2000). Additionally, herbaceous plants and shrubs less than 2 m tall were recorded in two 2 x 5 m transects at the corners of each sampling point (Mostacedo & Fredericksen, 2000).

Counts were summarized based on the abundance of each botanical family identified by habitat type.

To define which resources are potentially dispersed by bats, we carried out a literature review to determine whether within each identified botanical family there were genus or species reported as been dispersed by bats (Lobova & Mori, 2007; Magalhaes de Oliveira & Pereira, 2016) . This search helped us define the richness of botanical families that can be used by bats in each habitat with their respective abundance.

Diversity and differences on seed dispersal

We compared bats, seeds and plants diversity among sites using the Simpson (D), Shannon (H’), and Sørensen (CS) indices, calculated in RStudio with the packages Vegan and BiodiversityR (results of Sørensen are provided in supplementary material) (Kindt, 2021; Oksanen et al. 2020). To determine differences in abundance of seeds dispersed by bats among sites we applied a Kruskall Wallis test .

Ecological relationships

To understand which seed species are more commonly dispersed by bats in and within habitat types, we organized a matrix of ecological relationships and used the R package bipartite 2.16, and bipartite 3D to generate an interactive bipartite graph, following Dormann (2021) and Terry (2021) (Figs. S2-S6 or click here). Following Dormann (2021), we analyzed associations at the network level, thus we calculated the Shannon diversity index (H’) (in this context Shannon measures the diversity of interactions inside the network). We performed a null model with 1000 repetitions to evaluate the significance from this index.

Phylogenetic analysis

We also were interested in determining whether related species of bats are dispersing similar resources (seed species) in the different habitats studied, using a phylogeny built with mitochondrial mammal sequences and chloroplast plant sequences available in GenBank (cytochrome b gen (cyt-b) and from ribulose-1,5-bisphosphate carboxylase/oxygenase large subunit (rbcL) gen). Phylogenies obtained from this analysis were matched together with ecological relationships visualized among all the habitats (details of this analysis and GenBank accession numbers are explained in supplementary material, Methods S1)

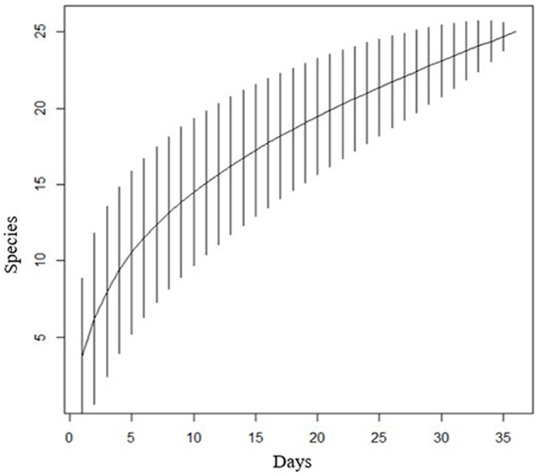


Figure 1. Species accumulation curve. CHAO1 = 44. Total sampling effort was 6002 m net/hour (net meters by hour) during 36 days.

Table 1: Bat, dispersed seeds and plant diversity in the three study habitats. PF = primary forest, SF1 = secondary forest in natural regeneration, SF2 = secondary forest in assisted regeneration, P = pastures for cattle.

Bat diversity				
Index α	**PF**	**SF1**	**SF2**	**P**
Shannon (H')	2.39	2.18	1.88	2.14
Simpson (D)	0.87	0.85	0.81	0.86
Richness	16	14	9	11
Dispersed seed diversity				
Index α	**PF**	**SF1**	**SF2**	**P**
Shannon (H')	2.52	0.62	0.49	1.35
Simpson (D)	0.82	0.2	0.17	0.59
Richness	55	59	25	14
Plant diversity				
Index α	**PF**	**SF1**	**SF2**	**P**
Shannon (H')	4.49	3.32	2.12	1.52
Simpson (D)	0.98	0.89	0.81	0.75
Richness	161	120	37	17

RESULTS

Bats diversity

We recorded a total of 249 bats distributed in 25 species of 13 genus and 3 families (Appendix 1, Table S1), data that was lower than the 44 species estimated by CHAO1 in for the study area (Fig. 1). Fecal samples with seeds were obtained from 20 species of bats, with a total of 173 samples (PF = 46, SF1 = 69, SF2 = 39, P = 19). The vast majority of samples were obtained from the most abundant species in this study: *Carollia brevicauda, Carollia perspicillata, Carollia castanea, Sturnira ludovici* and *Rhinophylla alethina*. In some bat species fecal samples did not contain seeds, so they were not used for the analysis.

Bat diversity was slightly higher in PF compared to the other habitat types (Table 1). The lowest diversity was recorded in SF2. Dominance was high in all habitats, with the most dominant species being those of the *Carollia* genus (Appendix 1).

Seed diversity

Regarding seeds, a total of 31.941 seeds distributed in 119 species, 15 genus and 13 families of plants were counted. The most abundant family was Piperaceae. The most dominant genus among habitats were *Piper*, *Philodendron*, and *Vismia* (Fig. 2). Seed diversity was higher in PF compared to the other habitats analyzed (Table 1). Here the most dominant seed species dispersed by bats were *Philodendron* sp2 and sp4, *Tarenaya* sp5, *Alocasia* cf. sp1 and *Piper* sp11 and *Piper* sp1. In SF1, SF2 and P the dominant species was *Piper aduncum*, representing 78% of the seeds collected. In P two other species dominated the habitat were *Piper* cf. sp25 and *Vismia* sp13. When comparing seed input among habitats, we found that bats are dispersing the same quantity of seeds among PF, SF1, and SF2 ($p > 0.05$), but this quantity is higher than P ($p < 0.05$). We also found that bats are dispersing a higher quantity of *Piper* in SF1 and SF2, compared with PF and P ($p < 0.05$).

Ecological relationships

Null models found significative values for Shannon diversity in network interactions among habitats ($p < 0.05$). Network interactions are very rich in PF in comparison with the other habitats (SF1, SF2 and P). The most important dispersers in disturbed habitats where *Carollia* spp and *S. ludovici*. Compared with primary forest, these species have a less diverse diet composition (Fig. 3, Figs. S2-S5). Some important seed genus like *Cecropia* and *Vismia* were scarce in disturbed habitats (SF1, SF2 and P). There was also a higher number of unidentified seed species (morphospecies) in primary forests, compared to the other habitats, which proposes these populations have a more diverse diet and a more important role in ecological dispersion in this habitat.

Furthermore, we observed that species that were more phylogenetically related also dispersed more

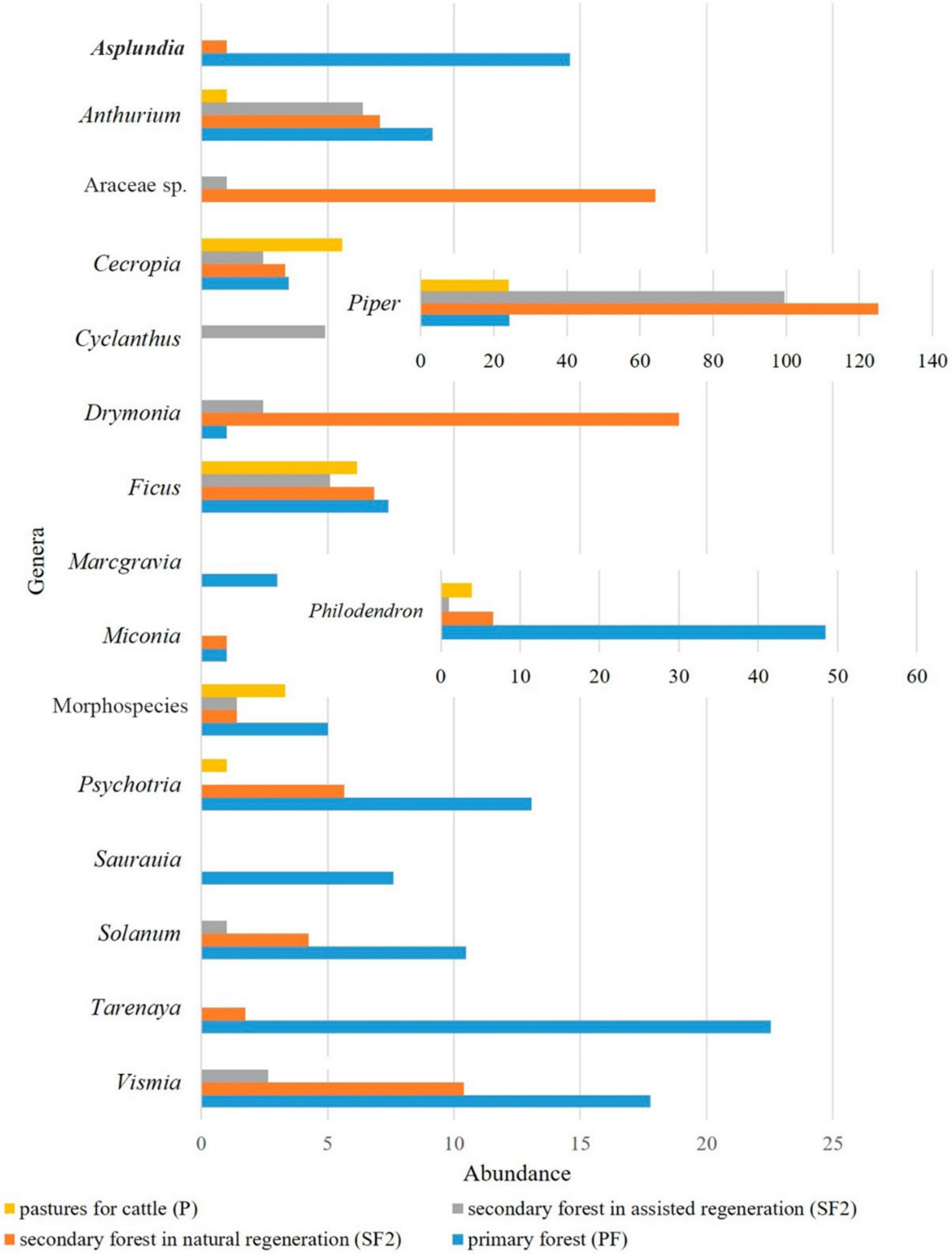


Figure 2. Seed abundance among 4 habitat types. Abundance is expressed as the square root of the original data due to the great difference in the number of individuals for some species. Additionally, to better appreciate the differences of *Piper* and *Philodendron*, each is shown inserted in the figure. Morphospecies are indeterminate species.

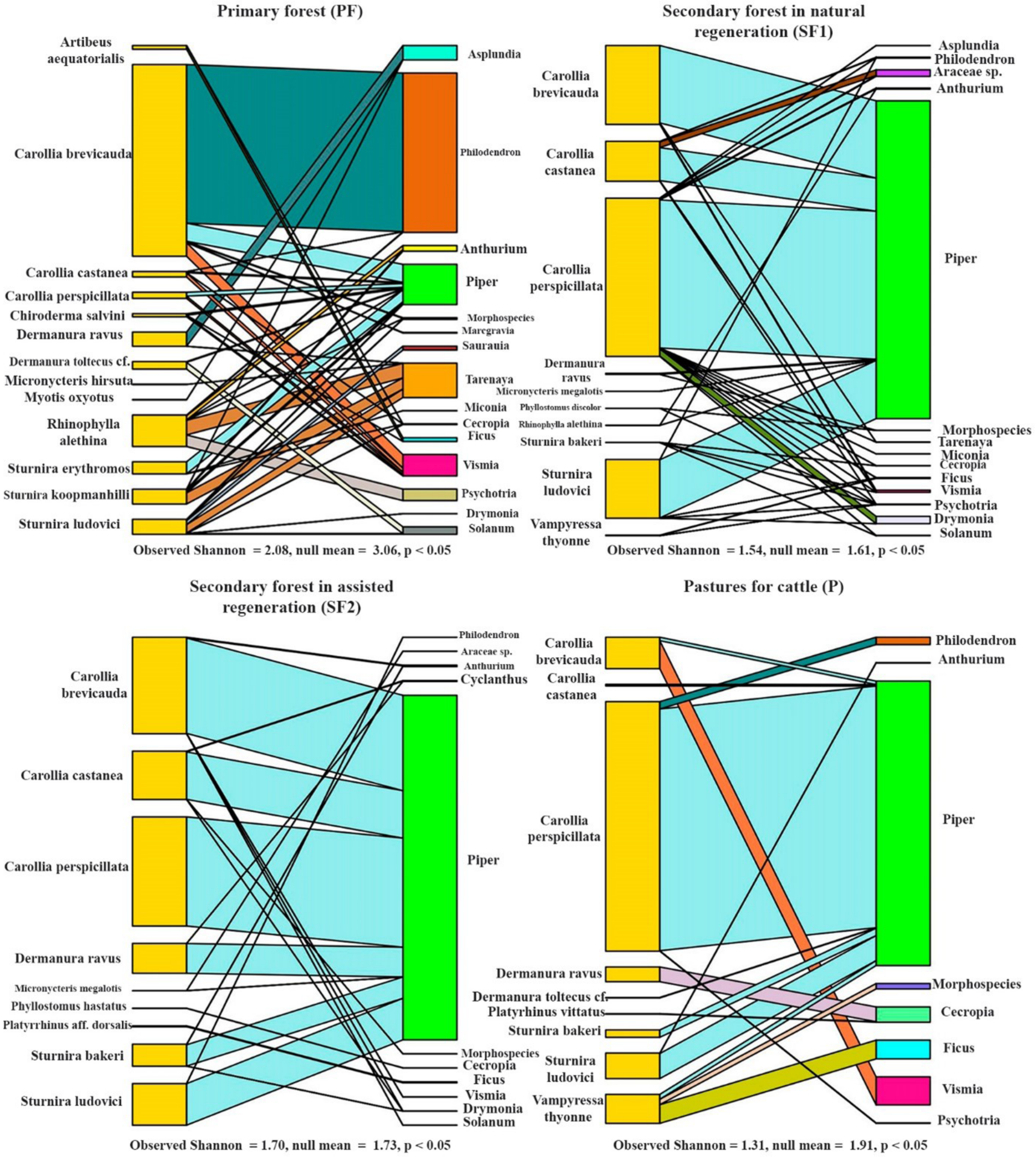
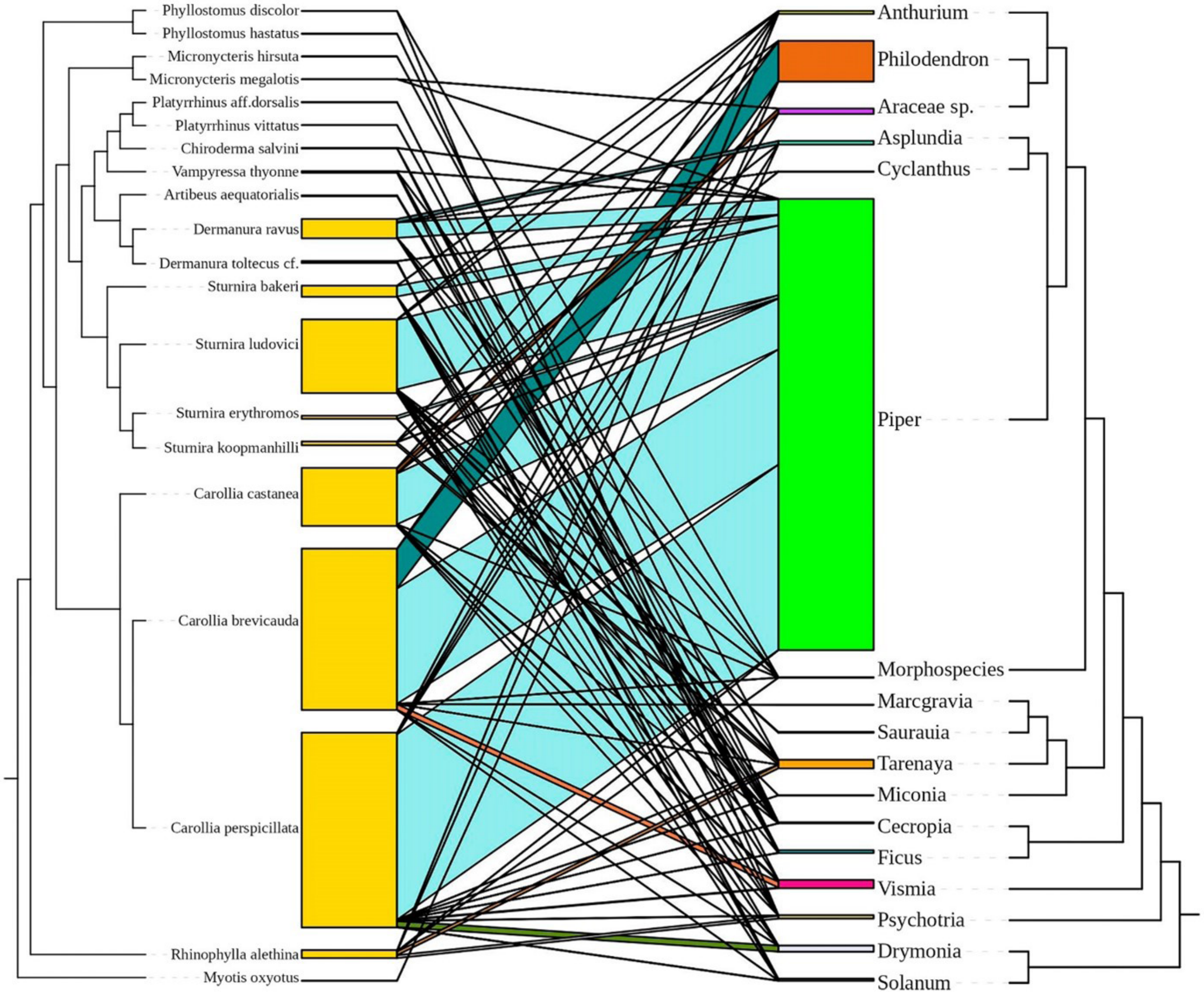


Figure 3. Ecological relationships between bat species and seed species dispersed in each habitat type. Results from null model analysis are shown at the bottom of each bipartite graph. Explore this relationships in an interactive map available in supplementary material or clicking here: (PF, SF1, SF2, P).



Observed Shannon = 2.09, null mean = 2.38, $p < 0.05$

Figure 4. Dendrogram of phylogenetic congruence showing species phylogenetic relatedness and dispersal of dietary items in the Ecuadorian Andean Chocó. Results from null model are shown at the bottom of the figure. Explore these relationships in an interactive way in supplementary material or clicking here.

similar seed species, which proposes a pattern of conservation in diet composition and plant specialization (Fig. 4, Fig S6). On the other hand, specific cases such as seeds of *Cecropia, Ficus, Anthurium and Philodendron* are dispersed by a wide variety of species, without any signal of phylogenetic conservatism.

Plant diversity

Regarding the diversity of plants registered in vegetation plots, to characterize resource availability), we found a total of 310 plant species, corresponding to 38 families and 55 genus. The most representative families across habitat types were Lamiaceae, Melastomataceae, Araceae, Euphorbiaceae Araliaceae and Rubiaceae. The diversity of plants decreases, in a gradient from primary forest to pastures (Table 1). All habitats presented a Simpson index very close to 1 due to the dominance of a few species at the understory level.

Availability of plant resources

The number of plant families that can potentially be dispersed by bats varied depending on habitat type. In primary forests there were 13 families that can potentially be used by bats, nine families in secondary forests 1, five in secondary forests 2 and only three in pastures (Fig. 5). With regards to resource

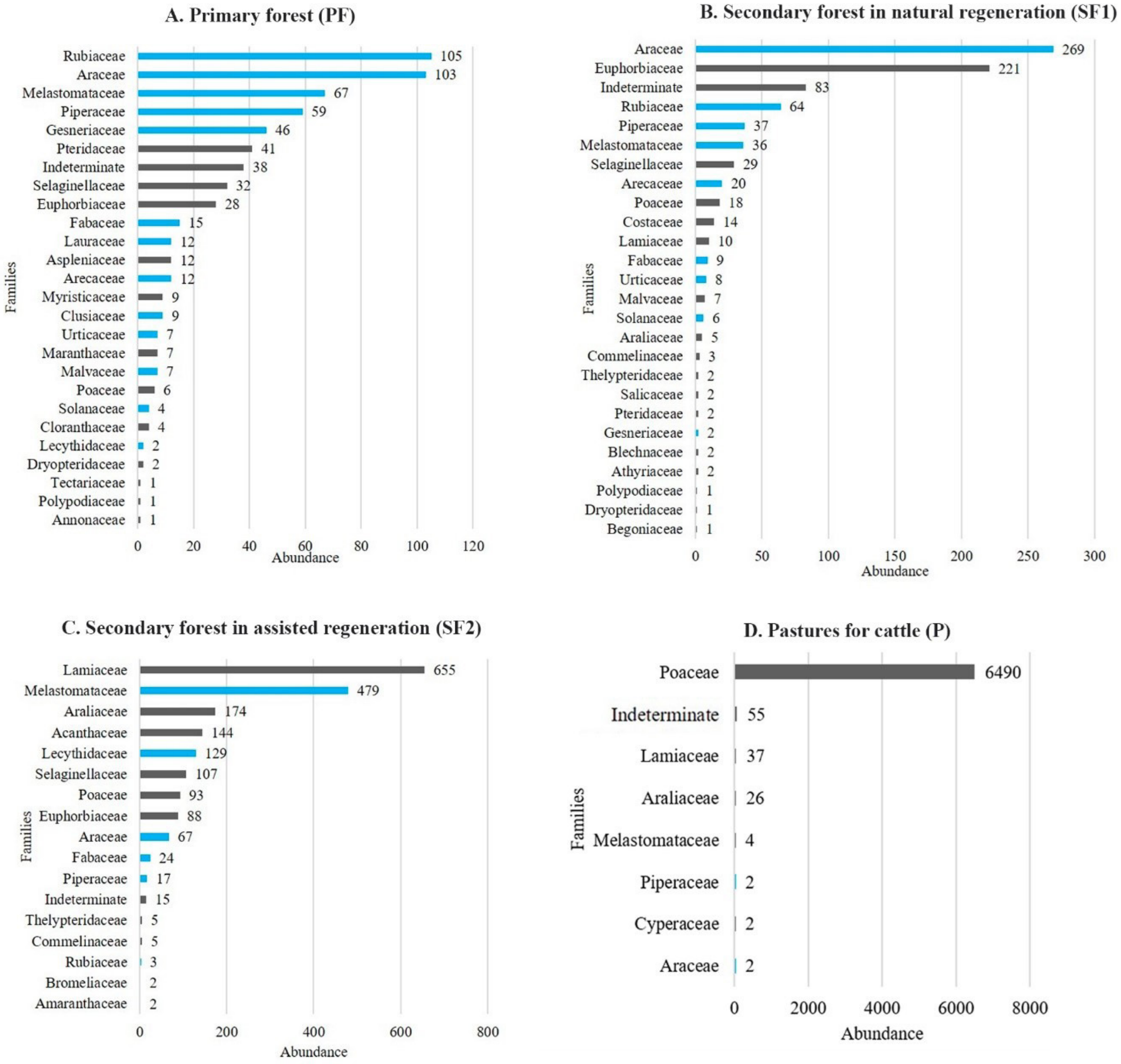


Figure 5. Plant species abundance recorded for each plant family across four study habitats: PF = primary forest, SF1 = secondary forest in natural regeneration, SF2 = secondary forest in assisted regeneration, P = pastures for cattle.

availability and their use by bats, there was a greater abundance of plants from the Rubiaceae, Araceae, Melastomataceae, Piperaceae, and Gesneriaceae families in primary forest (Fig. 5A); all these families were present in samples of seeds dispersed by bats in this habitat. These results are supported by the higher Shannon index registered here in comparison to other study habitats (Table 2). For secondary forest 1, the most common plant families registered were Araceae, Euphorbiaceae, Rubiaceae, Piperaceae and Melastomataceae (Fig. 5B). Of these, only Euphorbiaceae was not represented in seed samples dispersed by bats in this habitat. In this habitat type, the most dominant species was *Acalipha diversifolia* (Euphorbiaceae), which forms dense masses of shrubs that capture the light. This species was present in all habitats (PF, SF1, and SF2) except on pastures (P).

In secondary forests in assisted regeneration, 5 species were especially dominant *Marcipiantes* cf., *Aciotis* cf. *alata*, *Hydrocotyle bonplandii* , *Justicia* sp. and a type of *Gustavia* sp. (Fig. 5C). We did not find any seeds of these plant species in the seed samples dispersed by bats in this habitat. In this habitat type it was also common to find many introduced Poaceae due to their past use for livestock.

Finally, in pastures, out of the 8 families registered, only 2 have been registered as part of bat diets (Piperaceae and Araceae), and were poorly represented in the seed samples dispersed by bats (Fig. 5D). Pastures are mainly dominated by 4 types of grasses (Poaceae) used as fodder for cattle that dominate most of the land.

Discussion

Anthropogenic disturbances caused significant changes in the natural dynamics of seed dispersal by bats in secondary forests (SF1 and SF2) and pastures (P) when compared to bat community structure and seed dispersal in primary forests (PF). These alterations may be delaying processes such secondary succession and species recruitment, making it difficult to predict the successional trajectories that these habitats will follow in the future.

As expected, the diversity of bats and seeds and plants was higher in PF compared to habitats altered by anthropogenic disturbances (SF1, SF2 and P); this result is similar to a study conducted in Colombian montane forests (Aguilar-Garavito et al. 2014), where the diversity of bats and seeds decreased in response to disturbances. It is known that time since disturbance, added to the characteristics of the disturbance, such as the type of affectation, duration and intensity (Castro-Luna et al. 2007; Osman, 2015) can influence various components of diversity, thus affecting the processes of seed dispersal and forest regeneration (Aguilar-Garavito et al. 2014; Baniya et al. 2008; Osman, 2015). Thus, older or better conserved habitats tend to have a higher diversity of all groups and as such will present higher ecological stability and resilience (Baniya et al. 2008; Castro-Luna et al. 2007; Medellín et al. 2000; Piotto et al. 2019). This occurs because these habitats maintain greater reserves of resources (biotic and abiotic), different types of niches and refuges, a variety of microhabitats, and favorable environmental conditions that benefit species survival and development (Aguilar-Garavito et al. 2014; Castro-Luna et al. 2007; Medellín et al. 2000). This can also help understand the differences found in the diversity of bats and seeds dispersed between the two secondary forests with different management strategies.

Bat communities were moderately similar between habitats, which can be explained due to the high mobility of most species recorded, such as *Carollia* spp. and *Sturnira ludovici*, which is reflected in their wide distribution patterns (Fig. S7) (Ruelas, 2017; Velazco & Patterson, 2013). Many Neotropical bat species have shown a high tolerance to anthropogenic disturbances, as they can easily move among different types of habitats; this high vagility may explain the high number of species found across the four habitats. On the other hand, many other bat species have preferences for certain types of habitats and do not tend to move easily (for example, *Sturnira koopmanhilli*) (Tirira & Burneo, 2012). These species, sometimes considered rare, are sensitive to habitat modifications and can easily disappear from a community after a disturbance (Gorresen & Willig, 2004; Medellín et al. 2000). Several studies report that the responses of bat communities to habitat conversion and fragmentation are variable, and there may be species within the community that change their abundance depending on the type and intensity of the disturbance , and species that are simply not affected (Gorresen & Willig, 2004; Presley et al. 2009), which could explain the differences observed between communities for each type of habitat.

Differences in seed dispersal help us understand how anthropogenic disturbances alter the structure of natural communities, populations, ecosystems, and resource reserves that bats can disperse (Calderon-Aguilera et al. 2012). As we report in this study, the community of seeds dispersed by bats varied widely across habitat types. However, given the concept of dispersal limitation (Ricklefs 2004) it is expected that similarity across communities decreases as distance amongst them increases, because closer sites maintain similar environmental conditions and present fewer dispersal barriers for organisms (Soininen et al. 2007). However, in the in the case of seed communities dispersed by bats, spatial proximity does not seem to have this effect. The low similarity among habitat types reported here could be explained because of reduced dispersal distances for species that inhabit primary forests with high resource availability, avoid entering surrounding disturbed habitats, since these resources are usually limited and may have a low nutrient input (Boyle et al. 2012; Muñoz-Lazo et al. 2019). In fact, behavioral and resource use effects in bats, related to the dispersal process, are strongly influenced by variations in the characteristics of the matrix in the surrounding landscape (Meyer et al. 2016). In this study, the species dispersed by bats are fairly different from the surrounding plant communities, which makes dynamics of seed dispersal different in each habitat.

Our results show that bats play an important ecological role as seed dispersers in these Andean Choco ecosystems, as highlighted by the large abundance and diversity of seed species being dispersed when considering all habitat types (PF, SF1, SF2, and P); however, when analyzing seed community composition, this diversity decreased between habitats, being lower in secondary forests (SF1 and SF2) and pastures (P). The main seeds dispersed by bats in these habitats were those of the genus *Piper* spp. These species are abundant in agroforestry ecosystems in Colombia, where they are considered weeds, acting as pioneer species (Enríquez-Acevedo et al. 2020), which would indicate that these sampling points are in the initial stages of the process of ecological succession (Lepš et al. 2002; Longworth & Williamson, 2018).

Priority effects of bat-dispersed seeds are defined here as the influence that initial colonizers have on the structure and composition of a future community (Fukami, 2015). It has been reported that initial colonizers can have three types of priority effects: positive (facilitative), negative (inhibitory), or neutral (tolerant) (Weidlich et al. 2021). Effects on the structure and functioning of plant communities can be especially long-lasting if the effect is inhibition (Weidlich et al. 2021; Wilsey et al. 2015), which has important implications for restoration efforts in Chontaloma (SF1 and SF2). Differences in the order of arrival of the initial colonizers can cause different successional trajectories that can be classified as 1) alternative stable states, in which the differences in the historical sequences of the arrival of species to a locality lead to the formation of final communities completely different from the original community after the disturbance occurred; 2) alternative transient states, which occur when communities have not yet reached a stable state in succession; that is, they vary in the structure and composition of their species and energy flows; what happens because the immigration of new species on the ground is highly variable; and 3) compositional cycles, which occur when a community of species constantly changes in a cyclical sequence; the composition of the next community in this cyclical pattern depends on the sequence of the previous species (Fukami, 2015).

At the moment the successional trajectories in this zone of the neotropics are not well characterized due to the lack of longitudinal studies, so it is difficult to understand what are the priority effects exerted by seeds of the genus *Piper* and other genus dispersed by bats in secondary forests. (SF1 and SF2) and pastures (P). *Piper* species in this study are plants with herbaceous and shrubby habits, which reproduce by producing numerous seeds and have a short life cycle (being characteristics of pioneer species) (Dalling & Hubbell, 2002). It is inferred that *Piper* species could be behaving as facilitators by preparing the soil for other later species in succession, but further studies are necessary to confirm this hypothesis. Other pioneer species like *Acalipha diversifolia* have been considered to have inhibitory effects in tropical montane forest in Ecuador, by their competition habits, which slows natural forest regeneration process (Proaño et al. 2018).

Although bats are dispersing seeds of the genus *Vismia* and *Cecropia* among disturbed habitats (SF1, SF2 and P) not many seedlings of these species were found growing among understory. The species that dominated the understory were different from those reported in the literature in other studies from South America (Longworth et al. 2014; Wieland et al. 2011). In the case of *Vismia* seeds, dispersed by bats, the absence of seedlings could be explained because the land used was not subjected to continuous burning in the past, since fire has been recognized as the beneficial factor for the establishment of this genus (Hooper et al. 2004; Longworth et al. 2014; Mesquita et al. 2015; Wieland et al. 2011). *Cecropia* tends to be dominant when ground disturbance is minimal, as in the practice of clearcutting (Mesquita et al. 2015; Wieland et al. 2011), but the land use history for this sites was not logging but livestock.

The recruitment of seed species characteristic of primary forests in disturbed habitats can be very slow according to successional models for neotropical forests (Hooper et al. 2004), so it is possible that due to the short time elapsed since the disturbance in the habitats of SF1 (12-15 years), SF2 (4 years) and P (still in use), much more time is still needed for recruiting of primary forest seeds dispersed by bats; which occurs because the environmental and edaphic conditions are not favorable (Hooper et al. 2004; Longworth et al. 2014; Mesquita et al. 2015)

Coevolutionary processes are considered a crucial engine to the maintenance of ecosystem services, because they have governed the ecological relationships between organisms, through all the history of life in earth (Raguso, 2020). Our Network analysis for each habitat was important to understand how human disturbances are affecting the functioning and stability of forest ecosystems in disturbed habitats from the Ecuadorian Andean Chocó. Not many studies have explored the properties of mutualistic networks in relation to human disturbances, the vast majority of them, including our work, have focused in specific localities instead of greater regions, therefore, little is known about the community structure of bat-fruit interactions (Mello et al. 2011). Despite this, our Network analysis considering phylogenetic relatedness of species was congruent with other studies in the neotropics, where the genus, *Piper*, *Cecropia*, *Vismia*, *Solanum* and *Ficus*, compose the core in the feeding habits for related species of phyllostomid bats (Giannini & Kalko, 2004;Mello et al. 2011; Saldaña-Vázquez, 2014).

Our research fills the gap in the knowledge about the diet of many phyllostomid species, some resources like *Drymonia, Tarenaya, Saurauia, Asplundia, Cyclanthus* and *Psychotria* where new for the feeding habits known for this bat family (Lobova & Mori, 2007; Magalhaes de Oliveira & Pereira, 2016). Furthermore, morphospecies dispersed by bats, may belong to characteristic species from the final successional stages in primary forest (the climax community) (Longworth et al. 2014; Fukami, 2015). The identification of seeds was based on classic taxonomic, we recommend a formal revision with the use of DNA extraction, to support and better characterize the diet of species and their ecological relationships.

Differences in the number of fecal samples obtained for each habitat may be biased in regards to sampling effort, and similarly, the number of fecal samples was highly related to the most common bat species (*C. castanea, C, brevicauda, C. perspicillata,* and *S. ludovici*). This high dominance may influence our results observed, especially in pastures. According to Giannini & Kalko (2004), when studying seed dispersal in bats, it is important to try using a larger number of samples and balancing the sampling effort between habitats, with the objective to give a better support to inferences made. Here the only site with a lower sampling effort were pastures, which, given a normal low diversity due to disturbance we expect reflects natural conditions of that habitat type.

Finally, we consider that human disturbances analyzed and current threatens mentioned in the Ecuadorian Andean Chocó, are the main drives to the loss of ecosystem services, ecological relationships, coevolutionary processes, and biodiversity in this part of South America. Worldwide the effects of these type of losses for the human wellbeing still misinterpreted.

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Appendix 1. Voucher specimens deposited at MECN.

Carollia brevicauda (MECN6820, MECN6805, MECN6810, MECN6809), *Carollia perspicillata* (MECN6801)*, Carollia castanea* (MECN6808, MECN6822), *Dermanura ravus* (MECN6798, MECN6800, MECN6821)*, Myotis oxyotus* (MECN6807)*, Phyllostomus hastatus (*MECN6812*), Rhinophylla alethina* (MECN6814, MECN6803), *Sturnira ludovici* (MECN6804, MECN6813, MECN6815, MECN6817, MECN6819)*, Sturnira erythromos (MECN6816), Sturnira Koopmanhilli* (MECN6802, MECN6806)*, Sturnira bakeri* (MECN6797, MECN6811)*, Vampyressa thyone* (MECN6818), *Platyrrhinus aff. dorsalis* (MECN6799). The seed collection does not have a formal MECN code, today is called the INABIOs national bat-seed collection, many samples are associated with vouchers or original field numbers from researchers (example: MARS031/ MECN6802)

Supplementary material

Methods S1

Phylogenetic analysis

To analyze if related species of bats are dispersing similar seed species, we performed a phylogenetic analysis in MEGA11 (Tamura et al. 2021). For bats we used partial and complete mitochondrial sequences from the cytochrome b gen (cyt-b) deposited in Gene bank (accession numbers are detailed below). All the sequences belong to the current accepted species of bats occurring in South America (Wilson et al. 2019). For plants we used partial chloroplast sequences from ribulose-1,5-bisphosphate carboxylase/oxygenase large subunit (rbcL) gene deposited in Gene bank. We selected representative specimens from each seed genus identified in our study to construct a phylogenetic tree. We assumed that seeds not identified and resumed as morphospecies, must probably belong to known related families of plants, then we used sequences from a member of Fabaceae to represent this branch possibility in our phylogeny. It was expected that our analysis will not produce matching trees or cospeciating patterns between coevolving species, this because we focused at the level of genus instead of species (although matching trees or cospeciating are potential phylogenetic results, cospeciating or lack thereof is not evidence for or against coevolution) (Segraves, 2010). Our alignments were made with the Clustal W algorithm. Each locus alignment was run under a separate model of nucleotide substitutions selected using the Bayesian Information Criterium (BIC) as suggested by ModelTest available in MEGA: cyt-b (GTR+G) and rbcL (T92+G). We used these models to perform a Maximum likelihood analysis with a standard bootstrap method composed by 1000 repetitions. Our phylogenetic trees were modified with iTOL v6 (Letunic & Bork, 2021), and finally combined with our network visualization among all the studied habitats (Wang et al. 2020; Dormann 2021).

Gene bank accession numbers:

Bats: *Artibeus aequatorialis* (DQ869421.1), *Carollia brevicauda* (AF511960.1), *Carollia castanea* (MW193568.1), *Carollia perspicillata* (FJ589715.1), *Chiroderma salvini* (MN823718.1), *Dermanura ravus* (FJ179249.1), *Dermanura toltecus* (FJ376728.1), *Micronycteris hirsuta* (MN707461.1), *Micronycteris megalotis* (DQ077429.1), *Myotis oxyotus* (MH431033.1), *Phyllostomus discolor* (NC_065690.1), *Phyllostomus hastatus* (FJ155479.1), *Platyrrhinus dorsalis* (FJ154133.1), *Platyrrhinus vittatus* (FJ154178.1), *Rhinophylla alethina* (AF187028.1), *Sturnira bakeri* (KC753828.1), *Sturnira erythromos* (KC753788.1), *Sturnira koopmanhilli* (AF435203.1), *Sturnira ludovici* (KC753806.1), *Vampyressa thyonne* (AY157049.1)

Plants: *Asplundia liebmannii* (OP711522.1) , *Anthurium scandens* (OP711189.1), Araceae sp. (JX887612.1), *Cecropia peltata* (MZ478815.1), *Cyclanthus bipartitus* (OL536844.1), *Drymonia serrulata* (KT958453.1), *Ficus tinctoria* subsp. *swinhoei* (JQ773786.1), Marcgraviaceae sp.(JQ594916.1), *Philodendron fendleri* (OL537043.1), *Piper aduncum* (AY572252.1), *Psychotria poeppigiana* (MZ478945.1), *Saurauia* sp.(MG707309.1), *Solanum nigrescens* (KF546069.1), *Tarenaya parviflora* (KU739623.1), *Vismia guianensis* (HQ332126.1), *Inga edulis* (FJ173737.1) (this was the Fabaceae used to represent a branch possibility for morphospecies), *Miconia crenata* (MH143302.1)

Methods S1 References:

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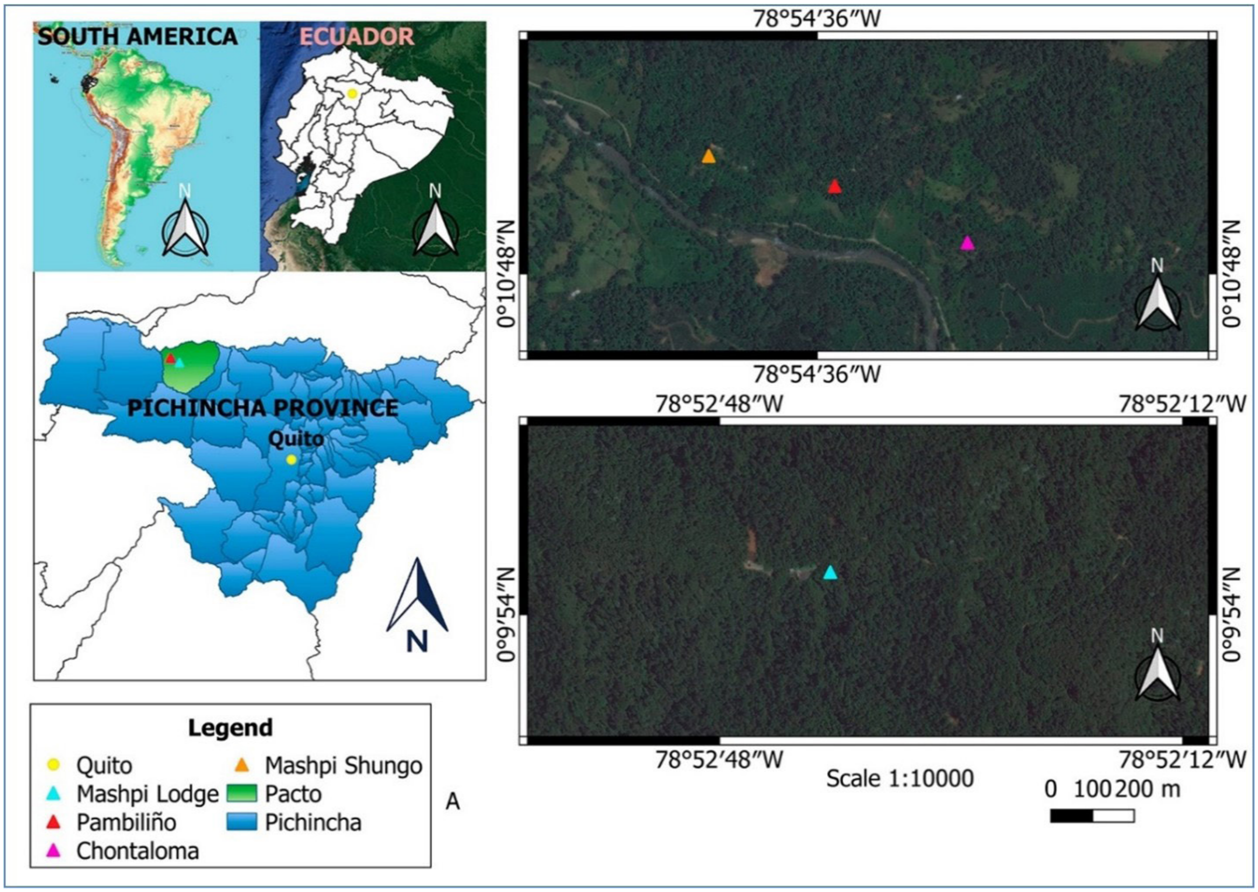
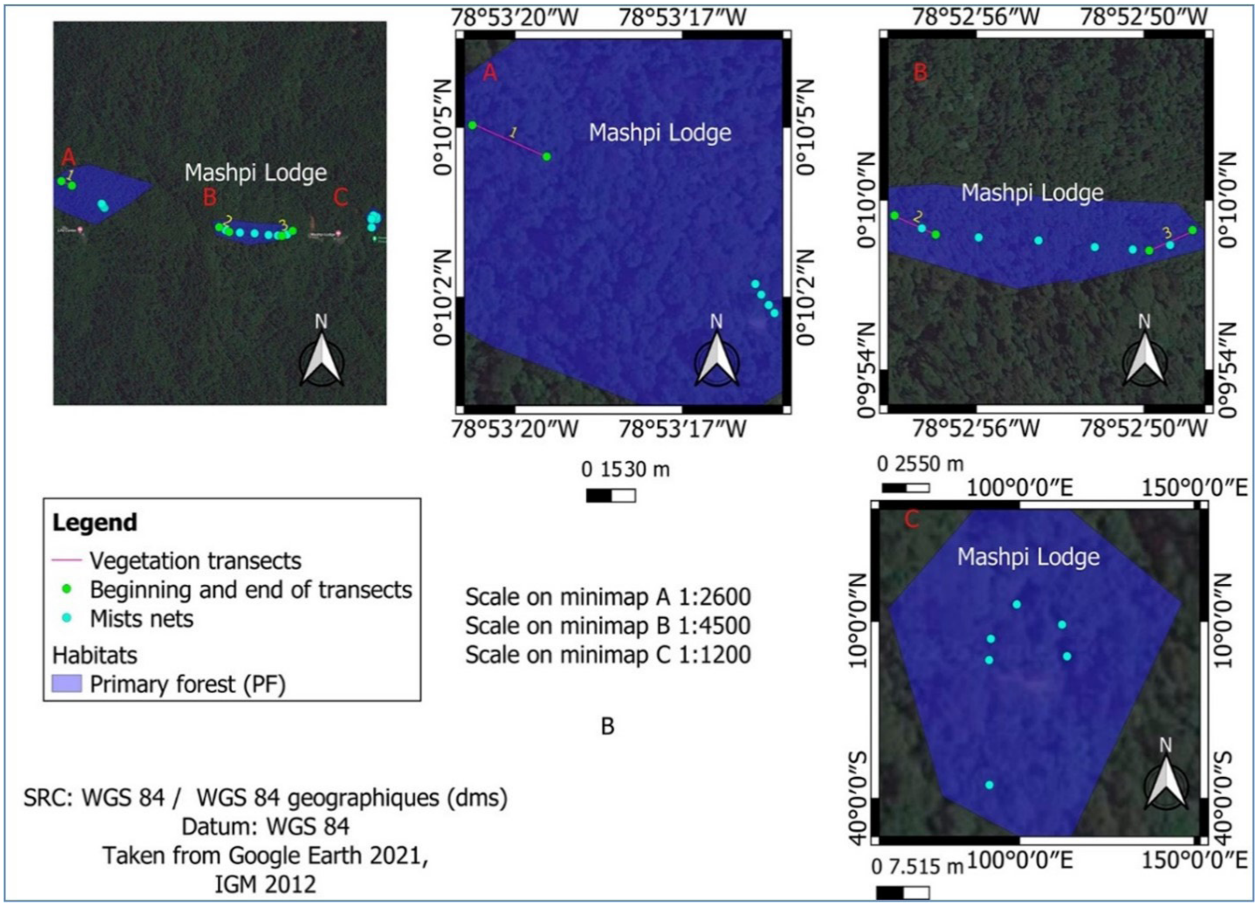
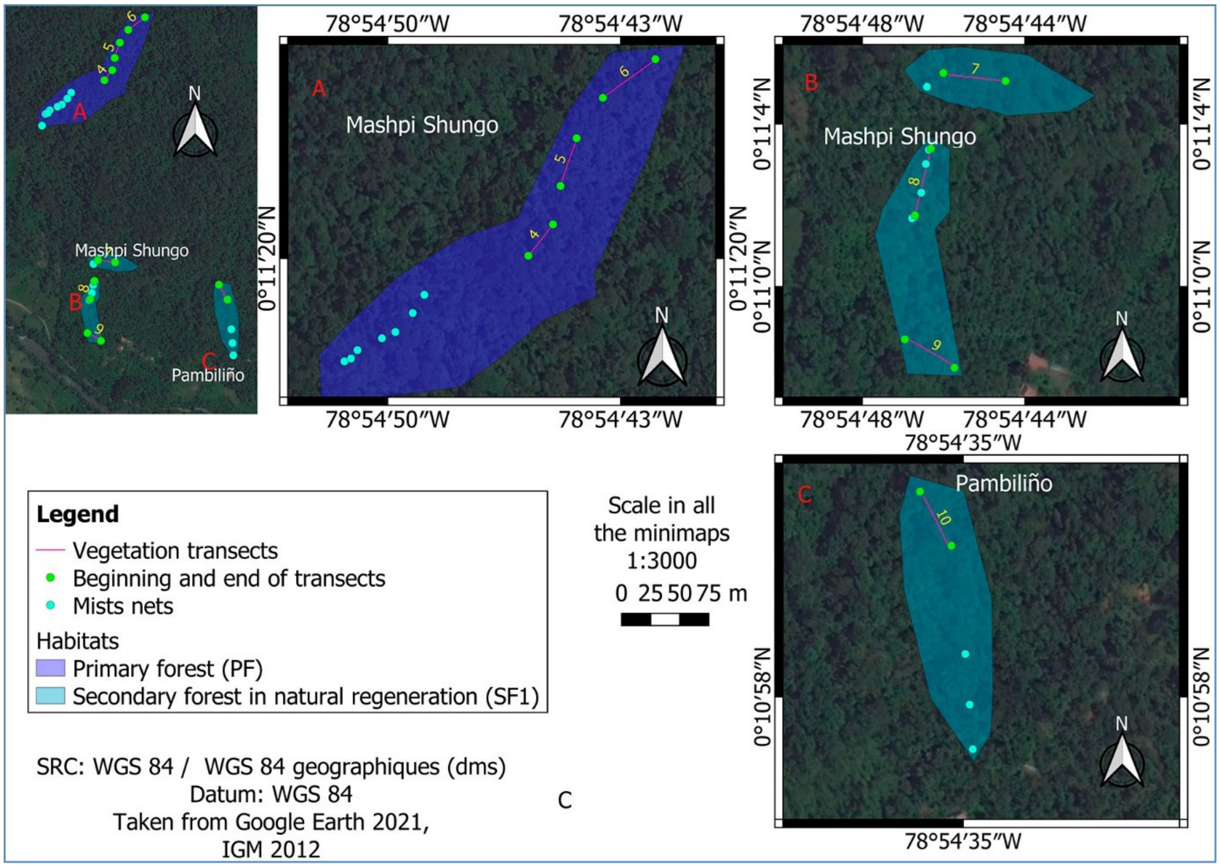
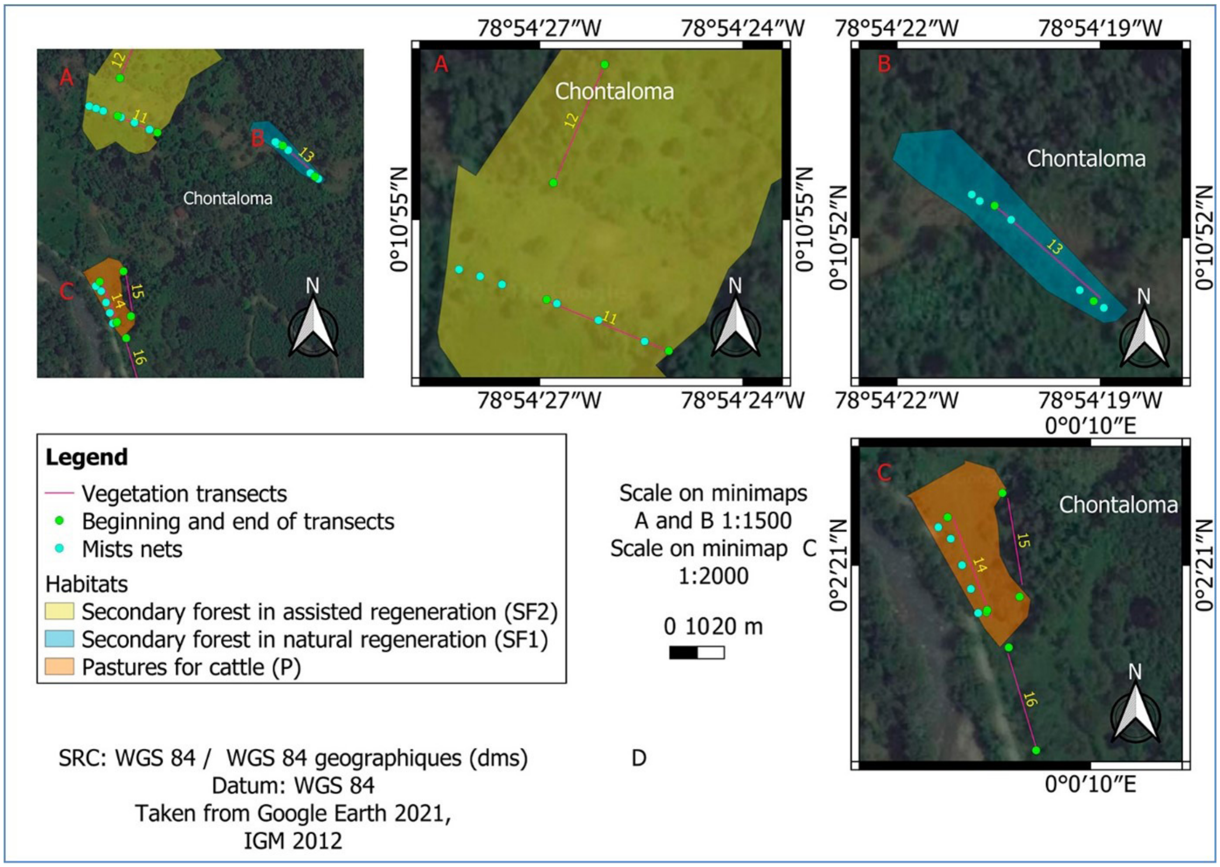
Figure S1. Study area. A = Location of the reserves visited in the Andean Chocó. B = Location of the mist nets and vegetation transects in the Mashpi Lodge reserve. C = Location of mist nets and vegetation transects in the Mashpi Shungo and Pambiliño reserves. D = Location of mist nets and vegetation transects in the Chontaloma reserve. We used 52 points to capture bats and 16 transects.




Mashpi Lodge
A
B
C
1
2
3
N
78°53′20″W
78°53′17″W
0°10′5″N
0°10′2″N
0 1530 m
78°52′56″W
78°52′50″W
0°10′0″N
0°9′54″N
0 2550 m
100°0′0″E
150°0′0″E
10°0′0″N
40°0′0″S
0 7.515 m
Legend
Vegetation transects
Beginning and end of transects
Mists nets
Habitats
Primary forest (PF)
Scale on minimap A 1:2600
Scale on minimap B 1:4500
Scale on minimap C 1:1200
B
SRC: WGS 84 / WGS 84 geographiques (dms)
Datum: WGS 84
Taken from Google Earth 2021,
IGM 2012


Mashpi Shungo
Pambiliño
A
B
C
4
5
6
7
8
9
10
N
78°54′50″W
78°54′43″W
0°11′20″N
78°54′48″W
78°54′44″W
0°11′4″N
0°11′0″N
78°54′35″W
0°10′58″N
Legend
Vegetation transects
Beginning and end of transects
Mists nets
Habitats
Primary forest (PF)
Secondary forest in natural regeneration (SF1)
Scale in all the minimaps 1:3000
0 25 50 75 m
SRC: WGS 84 / WGS 84 geographiques (dms)
Datum: WGS 84
Taken from Google Earth 2021,
IGM 2012
C



The next figures are online interactive widgets. You are able to interact with them by clicking or moving your mouse/finger in any bar color in front of any bat or plant species:

Figure S2. Ecological relationships in primary forest (PF), click on the next link: https://rpubs.com/Marszeo24/1060248

Figure S3. Ecological relationships in secondary forest in natural regeneration (SF1), click on the next link: https://rpubs.com/Marszeo24/1060250

Figure S4. Ecological relationships in secondary forest in assisted regeneration (SF2), click on the next link: https://rpubs.com/Marszeo24/1060252

Figure S5. Ecological relationships in pastures for cattle (P), click on the next link: https://rpubs.com/Marszeo24/1060253

Figure S6. Ecological relationships among all the study habitats in the Andean Chocó: https://rpubs.com/Marszeo24/1060247

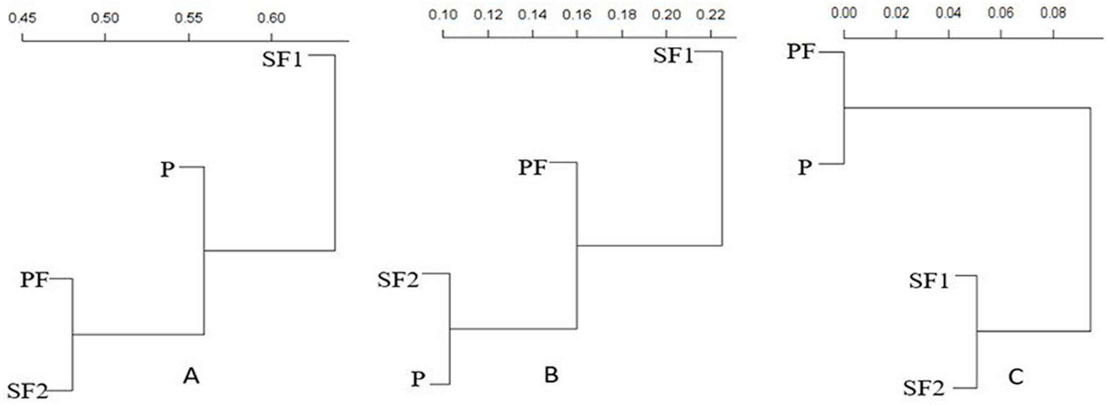


Figure S7. Dendrograms showing community similarity for A = bats, B = dispersed seeds and C = plants, between 4 habitat types. PF = primary forest, SF1 = secondary forest in natural regeneration, SF2 = secondary forest in assisted regeneration, P = pastures for cattle. All dendrograms are based on the Sørensen index, the scale at the top of the dendrogram indicates the degree of relative similarity. In general bat communities across habitats were moderately similar, seed communities were low similar in composition. Plant communities were fairly different.

Table S1: Species of bats recorded in each type of habitat and fecal samples obtained.

#	**Genus**	**species**	**Habitats**				**Total**	**Fecal samples**
			PF	**SF1**	**SF2**	**P**		
1	*Anoura*	*caudifer*‡§	4	0	0	0	4	1
2	*Artibeus*	*aequatorialis*	1	2	0	0	3	1
3	*Carollia*	*brevicauda*	15	14	12	7	48	36
4	*Carollia*	*castanea*†	5	10	4	2	21	16
5	*Carollia*	*perspicillata*	2	29	8	5	44	36
6	*Chiroderma*	*salvini*	2	0	0	0	2	2
7	*Dermanura*	*toltecus* cf.	6	1	0	1	8	5
8	*Dermanura*	*ravus*	2	12	3	1	18	8
9	*Mesophylla*	*macconnelli*§	0	1	0	0	1	0
10	*Micronycteris*	*hirsuta*	2	0	0	0	2	2
11	*Micronycteris*	*megalotis*	1	3	1	0	5	4
12	*Myotis*	*oxyotus*	1	0	0	0	1	1
13	*Phyllostomus*	*discolor*	0	1	0	0	1	1
14	*Phyllostomus*	*hastatus*	0	0	1	0	1	1
15	*Platyrrhinus*	*matapalensis*§	0	1	0	0	1	0
16	*Platyrrhinus*	aff. *dorsalis*	0	0	1	0	1	1
17	*Platyrrhinus*	*vittatus*	0	0	0	2	2	1
18	*Rhinophylla*	*alethina*	12	9	0	0	21	12
19	*Sturnira*	*bakeri*	0	5	4	6	15	9
20	*Sturnira*	*erythromos**	1	0	0	0	1	1
21	*Sturnira*	*Koopmanhilli*	3	0	0	0	3	3
22	*Sturnira*	*Ludovici*	6	16	9	5	36	28
23	*Sturnira*	*perla*§	0	0	0	1	1	0
24	*Thyroptera*	*tricolor*§	0	0	0	1	1	0
25	*Vampyressa*	*thyone*	2	4	0	2	8	4
Total			65	108	43	33	249	173

PF = primary forest, SF1 = secondary forest in natural regeneration, SF2 = secondary forest in assisted regeneration, P = pastures for cattle. * = sensu Velazco & Patterson, (2013), † = sensu Baker & Bradley (2006), ‡ = previously with the epithet *aequatoris* (Calderón-Acevedo et al. 2022). § = not used in seed dispersal analysis.

Table S1 References

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