ORIGINAL ARTICLE

Diet and trophic structure of frugivorous bats (Phyllostomidae) in forests and chagras of the Andean–Amazon piedmont, Ecuador

Martin Hinojosa[1] · Nataly Méndez-Romero[1] · Maria Cristina Peñuela[1,2]

Abstract

Ecuador is experiencing a rapid conversion of its natural habitats, especially in its Andean–Amazon piedmont forests, a conversion that in turn threatens the country's biodiversity. Frugivorous bats (Phyllostomidae) are not only an example of a taxa affected by habitat loss but may also play a role in overturning habitat loss and degradation. As important seed dispersers, bats are key to many ecological processes such as forest regeneration and succession. To understand Phyllostomidae diversity and trophic structure of Ecuador's piedmont forests, as well as the potential role of bats in forest recovery through seed dispersal, we sampled bats at both agroforestry (chagras) sites and patches of secondary forest in the buffer zone of the Colonso Chalupas Biological Reserve, Napo Province (750–900 m asl.). For 4 months, we used mist nets and seed traps to sample bats and the seeds they carried. In total, these efforts yielded 224 bats belonging to 33 species. We captured 224 bats belonging to 33 species of which 114 individuals from 24 species transported seeds. We captured more species but fewer individuals of bats in forests (17) than in chagras (15). The bats carried 15,685 seeds of 41 different morpho-seeds belonging to twelve plant genera, with *Piper, Cecropia,* and *Solanum* being those with the highest number of seeds. The main disperser we found was *Carollia brevicauda*, both in the forest (index value = 1.4) and in chagras (2.2). Bat-plant networks were more symmetric in forests (− 1.63) compared to chagras (− 9.28) and showed higher degrees of specialization in chagras. Our results show the great diversity of bats and the seeds they carry and highlight how this traditional agricultural system allows for connectivity between forest patches by providing food niches for seed dispersers. Therefore, we argue both bats and chagras must be considered in forest restoration programs.

Keywords Agroforestry · Dispersion · Interaction network · Metrics · Restoration · Seeds

Introduction

In recent decades, intensive agriculture has affected biodiversity through deforestation, soil degradation, and habitat fragmentation in tropical ecosystems (Loos et al. 2014; Lewis et al. 2015) (Sodhi and Ehrlich 2010; Loos et al. 2014). Ecuador, a hotspot of flora and faunal diversity (Myers et al. 2000), has the highest deforestation rate in Latin America (Armenteras and Rodríguez 2014). The Ecuadorian Amazon, for instance, includes ecosystems, from lowland humid forests to Andean foothills (Guevara et al. 2013). In these foothills, the evergreen piedmont forest ecosystem is located in a strip (approximately 400–1200 m asl.) between Andean and Amazonian regions (Etter et al. 2006; Ricaurte et al. 2012; Guevara et al. 2013). Sanchez-Villacis et al. (2017) found a significant loss of plant diversity in this type of forest mainly due to indiscriminate logging and predominance of few species. Capparelli et al. (2020) found several pollutants in the area related to mining and urbanization that seriously threaten the biodiversity of this area.

There are more than 440 species of mammals in Ecuador, 40% of them bats (Tirira et al. 2020). Bats define the structure and the reproductive success of vegetation because they disperse seeds (Muscarella and Fleming 2007; Lobova et al. 2009). Most of these bats are Phyllostomidae which

Handling editor: Danilo Russo.

✉ Maria Cristina Peñuela
crisantema1995@gmail.com

1 Department of Life Sciences, Universidad Regional Amazónica Ikiam, Km 8 vía a Muyuna, Tena, Napo, Ecuador

2 Grupo de Investigación en Ecosistemas Tropicales y Cambio Global, Universidad Regional Amazónica Ikiam, Km 8 vía a Muyuna, Tena, Napo, Ecuador

comprises 11 subfamilies. Bats eat fruits of both pioneer and advanced successional species (Fleming 1986; Medellin and Gaona 1999; Lobova et al. 2009; Vleut et al. 2015). Some specialize on certain plant species (da Silva et al. 2008; Mello et al. 2011a; Andrade et al. 2013; Sarmento et al. 2014; Vleut et al. 2015; Parolin et al. 2016; Castaño et al. 2018; Sánchez and Giannini 2018). For example, *Artibeus* bats eat mainly *Ficus* and *Cecropia*, *Carollia* bats *Piper*, and *Sturnira* bats *Solanum* and *Piper* (Fleming 1986).

Ecuador has at least 176 species of bats of 65 genera belonging to 8 families (Tirira et al. 2020) but we lack details about how these bats influence ecosystems. In southern Ecuador, Lindner and Morawetz (2006) compared the number of seeds dispersed by birds and bats in a humid mountain forest (1800–3150 m asl) and verified that bats were the major contributors to the forest's regeneration. Arguero et al. (2012) in the same region, but at a lower elevation (650–1360 m asl), highlighted the importance of less abundant and specialized fruit bats, which dispersed plant species not commonly carried by more generalist species. This contributes to the maintenance of the diversity of this ecosystem. On lower lands in Yasuní National Park (220–273 m asl), Ghanem and Voigt (2013) found a reduction in Phyllostomidae due to deterioration of environmental quality in salt licks. In the western Ecuadorian Amazon there have been inventories, such as a very short general data survey (Ordoñez et al. 2012) at 1800 m asl. in the Colonso Chalupas Biological Reserve as well as ecological niche projections done by Burneo and Tirira (2014) which consider the piedmont forest the ecosystem with the greatest potential richness of bats in Ecuador.

In the same region, in addition to protected areas, chagras or chacras (an agroforestry system, AFS) have gained relevance due to their sustainable management and great cultural importance (Luzuriaga-Quichimbo et al. 2019; Vera et al. 2019). AFS are polycultures that plant trees within agricultural practices to benefit both humans and ecosystems (Muschler 2016). AFS's provide habitats for species with some degree of tolerance to disturbance, preserve germplasm, reduce natural habitat conversion rates, provide connectivity between remnants of natural habitat, encourage animal dispersal movements, conserve biodiversity and provide other ecosystem services (Laurance 2004; Jose 2009; Muschler 2016). Hernández-Montero et al. (2015) found that if an AFS maintains an adequate vegetation structure, the trophic structure of chiropterochoric plant species between forest and chagras would not differ significantly, probably favoring dispersal of seeds among forest patches.

Kichwa Amazonian chagras are diverse with more than 90 plant species (Peñuela et al. 2016). They contribute to the food and health security of human populations, to biodiversity conservation, and to the mitigation of climate change local effects (Torres et al. 2015). We studied the role of bats

as seed dispersers and evaluated the diet and trophic structure of phyllostomid bats in secondary forests and chagras in the Andean–Amazon piedmont forest in Ecuador. We addressed the following questions: (1) What is the diversity of frugivorous bats in secondary forests and chagras? (2) What species of bats is the most important seed disperser in both types of land uses? (3) What seeds are transported by the frugivorous bats captured in forest and chagras? And, (4) are there significant differences among trophic networks of forests and chagras? We did not expect significant differences in the diversity of bats and the seeds transported.

Methods

Study area

We conducted our fieldwork in the province of Napo in the buffer zone of the Colonso Chalupas Biological Reserve (CCBR) (Fig. 1). The study area is part of the Piedmont Evergreen Forest ecosystem of the northeastern Andes (Guevara et al. 2013) that covers an elevational range of 750–900 m asl, has high precipitation (> 4000 mm per year) and humidity (90% on average) (van der Hoek 2018).

Experimental design

We sampled two sites separated by about 2.0 km (Fig. 1). Each site has chagra and forest (> 20 years old) zones, separated by at least 700 m. The forest has a canopy between 15 and 35 m high and is composed of several strata, with the following dominant families of trees: Euphorbiaceae, Fabaceae, Melastomataceae, Meliaceae, Moraceae, Myristicaceae, Rubiaceae, and Vochysiaceae. The understory is composed mostly of Melastomataceae and Rubiaceae (van der Hoek 2018). In the chagras, there were banana (*Musa* sp.), yucca (*Manihot esculenta*), pineapple (*Ananas cosmosus*), guayusa (*Ilex guayusa*), cocoa (*Theobroma cacao*), and guava (*Inga* sp.), among others (Peñuela et al. 2016).

We selected a strip-transect (400 × 2 m) per land use, at each site. In each strip-transect we placed eight mist nets set in pairs 100 m apart. We sampled bats during 23 nights Between October 2019 and January 2020, 12 nights in the forest and 11 in the chagra. We used two nets of 12 m and six nets of 6 m, opened them from 18:00 to midnight (00:00) and checked them every 15 min, for a total of 8280 m-hours (4320 in forest and 3960 in chagra). We did not sample on nights with heavy rains due to low bat activity (Bracamonte 2018). We held bats in individual cotton bags, waited for them to defecate, identified them using different field guides (Tirira 2017; López-Baucells 2018) and then released them.

We collected seeds directly from the cloth bags (Bonaccorso and Gush 1987) and from 1.5-m-wide plastics
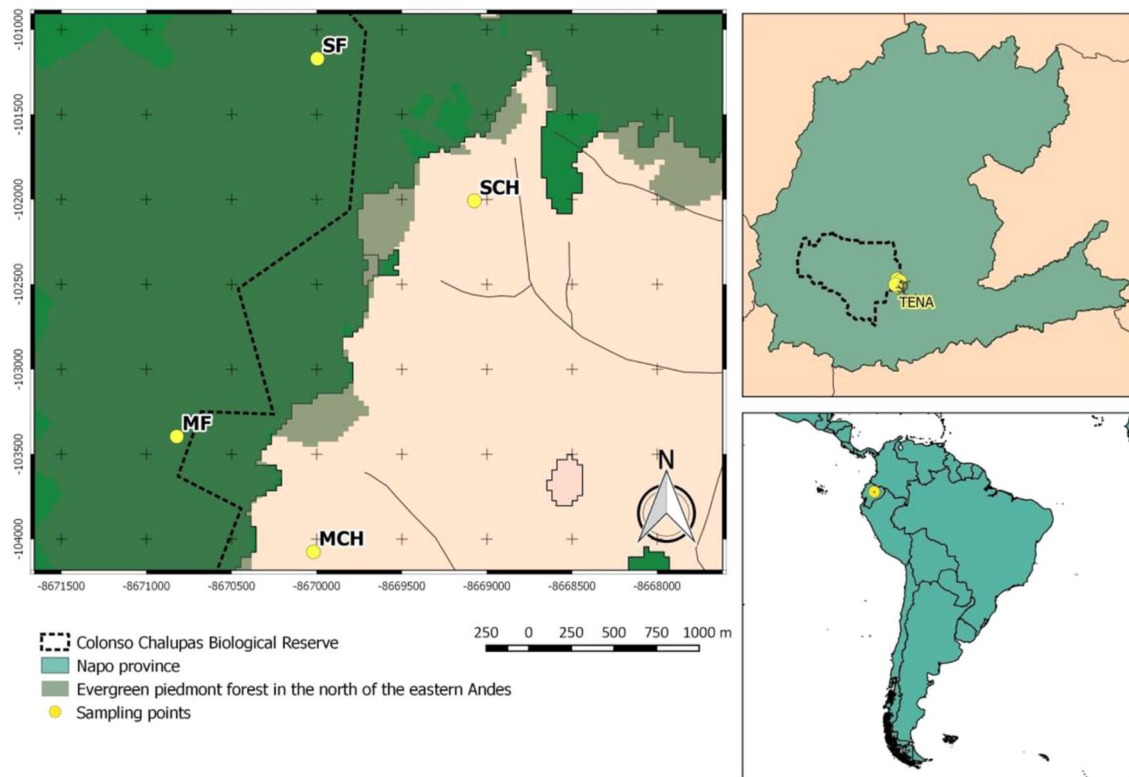
Fig. 1 Study area. Buffer zone of the Colonso Chalupas Biological Reserve in the province of Napo, Ecuador. (MF = Monos Forest: 0°55′51.25 "S 77°52′59.55 "W, MCH = Chagra Monos: 0°54′58.73 "S 77°52′32.22 "W, SF = Shitig Forest: 0°54′31.669′′'S 77° 53′ 2.043′′ W, SCH = Chagra Shitig: 0°56′5.59 "S 77°53′2.79 "W)

placed under the nets to capture seeds that were released by the individuals once they were trapped (Galindo-González et al. 2009). We cleaned the bags, between each capture, to avoid contaminating the samples. We separated fecal samples and stored them in paper sleeves at 4 °C to avoid deteriorating the samples (Morales et al. 2012). Then, we separated, counted, photographed, measured, and identified the seeds using identification guides (Cornejo and Janovec 2010; Lobova et al. 2009) and plant seed identification websites (OARDC, Seed ID Workshop and USDA, Agriculture Research Service).

Data analysis

We considered dispersal events as the variable allowing us to have a standardized measure of the contribution of each seed morphotype to the bat´s diet. A dispersal event is one record of the interaction between a bat and a plant. Thus, if a fecal sample contained more than one seed morphotype we counted each seed as separate records (i.e. different dispersal events) (Galindo-González et al. 2000).

Diversity indices

To identify the best diversity indicators that show the differences among bat species that consume seeds because there is no index universally applicable to all ecological assemblages (Magurran 2004), we used the DER algorithm (Guisande et al. 2017) which considers all the diversity indicators in a single analysis. The DER function from the R package *EcoIndR* (Guisande et al. 2017; Guisande 2019) and the RWizard software (Guisande et al. 2014) considers two indices of rarity, 14 indices of heterogeneity, seven indices of evenness and two indices of taxonomic diversity (see Table 1 of Guisande et al. 2017). We compared how the morpho-seeds consumed by bats using four components of diet diversity (rarity, heterogeneity, evenness, and taxonomic diversity) and looked at differences between forest and chagra. Therefore, we choose from all of the estimated indices, one per each of the diversity components. The selection of the indices is based on the maximization of the differences among the morpho-seeds considering the four diversity components of the diversity plot.

Important seed dispersal bats

We assessed the importance of bats as seed dispersers through the dispersion importance index (DII = (B) (s) / 1000) for each species that presented dispersal events (Galindo-Gonzalez et al. 2000). This index is based on the relative abundance of a species (B) and the percentage of fecal samples containing seeds (s). The values of the DII index vary between 0 and 10, where 0 refers to a bat species that does not disperse any of the collected seeds, while a value of 10 corresponds to a species that disperses all seeds recorded.

Interaction networks

We explored bat-plant association using canonical correlation analysis (CCA) and then we carried out an interaction network analysis using binary and weighted adjacency matrices, wherein bat species were in columns and morpho-seeds in rows. The cell values correspond to the dispersal events, but not to the number of seeds transported.

We conducted the analysis of the interaction networks with the bipartite package 2.13 (Dormann 2019), as recommended in other studies (Mello et al. 2011a; b; Castaño et al. 2018). We calculated measures of centrality (Grade, Intermediate, Proximity) to evaluate the importance of bat species in the structure of the food web.

We measured networks structured as cohesive subgroups, using the modularity value (Mello et al. 2011b). Then, we compared this value with a null model based on the generation of 1000 trophic networks with random interactions to verify if it effectively supported the formation of subgroups within the network. If the observed modularity value was greater than two standard deviations, it meant that the network was significantly modular, which represented the formation of groups of bats that were specialized on groups of plants. Finally, we evaluated the metrics of each network using the 'visweb' function of the same package (Dormann et al. 2019) and included connectance, links per species, nestedness, specialization asymmetry, niche overlap, and centrality.

Results

Diversity of bats

We captured 224 bats from 33 species of Phyllostomidae: 114 individuals (14 genera, 24 species) presented dispersal events. We registered a total of 159 dispersal events, 88 of in chagras and 71 in forest (Fig. 2). Our sample included 69 Carollinae, 41 Stenodermatinae, one Phyllostominae (*Phyllostomus elongatus*), one Glossophaginae (*Anoura*

aequatoris) and two Glyphonycterinae (*Trinycteris nicefori* and *Glyphonycteris daviesi*).

We captured 47 individuals of 10 genera and 17 species in the forest, compared to 67 (8 genera, 15 species) in the chagra. The genera *Anoura*, *Uroderma* and *Vampyressa* were restricted to the chagra, while *Enchisthenes*, *Glyphonycteris*, *Phyllostomus*, *Trinycteris*, and *Vampyriscus* were restricted to the forest (Table 1). In the chagra the most frequently captured bat species were: *Carollia brevicauda* (26.9%), *Carollia perspicillata* (23.9%), *Sturnira giannae* (14.9%) and *Rhinophylla pumilio* (9.0%), contributing 74.7% of the captures. In the forest the most frequent species were: *C. brevicauda* (44.7%), *S. giannae* (8.5%), and *Sturnira oporaphilum* (6.4%); *Artibeus glaucus*, *Artibeus planirostris*, *Enchisthenes hartii*, *Rhinophylla fischerae*, and *Vampyriscus bidens* made up 4.3% of the records each.

The algorithm selected the diversity indices that better showed the difference among the bats through their consumption of morpho-seeds. First, Guisande's rarity index for the diversity component of rarity, second richness, third evenness with Pielou index-evenness, and fourth taxonomic diversity (Fig. 3). In the forest, the morpho-seeds FMof6 (*Vismia*), FMof21 (*Ficus*) and FMof29 (*Cecropia*) (see Fig. 3 upper panel) showed values close to the maxima for the four components of diversity. It means that these three morpho-seeds are consumed by many bat species (high species richness), including those with a lower presence of seeds (high rarity index), with similar frequencies of consumption among the bat species (high evenness) and by bat species belonging to different taxa (high taxonomic diversity). In the chagra, only CMof22 (*Solanum*) was close to this group, with values closer to the maximum of the four components of diversity (Fig. 3 lower panel). In the forest, eight morpho-seeds (FMof8, FMof11, FMof13, FMof27, FMof28, FMof33, FMof34 and FMof35), with low values of the four diversity components belong to the genera *Muntingia, Piper*, *Gaulteria, Vismia* and two morpho-seeds of *Solanum* and two of *Ficus*. In the chagra, four morpho-seeds showed these characteristics (CMof1, CMof18, CMof31 and CMof35), which belong to *Piper*, *Solanum*, *Vismia,* and one unidentified morphotype. These morpho-seeds are consumed only by *Carollia brevicauda*.

Some morpho-seeds are consumed by a few species (high rarity index), although the values of the other diversity components (richness, uniformity, and taxonomic diversity) are lower. In the chagra, there were nine seeds with this characteristic: CMof4, CMof5, CMof10, CMof12, CMof13, CMof19, CMof20, CMof23, and CMof25 that belong to the genera *Solanum, Piper*, *Philodendron*, *Annona*, *Protium*, *Vismia*, *Iriartea* and two unidentified morpho-seeds. In the forest, there were six morpho-seeds: FMof22, FMof26, FMof30, FMof31, FMof36 and FMof41 that belong to *Solanum*, *Vismia, Protium*, Cecropia, and two unidentified
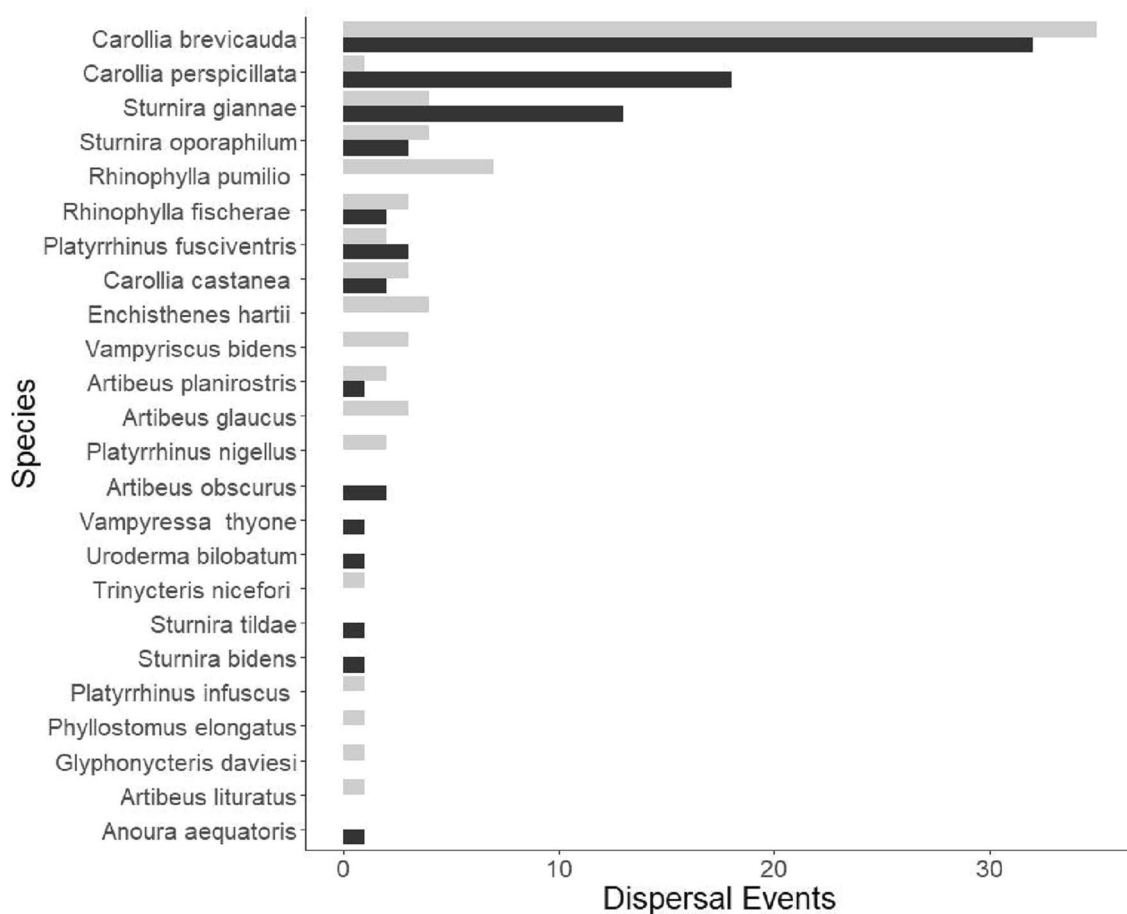
Fig. 2 Number of bat dispersal events recorded in forest (grey bars) and chagra (black bars) in the Colonso Chalupas Biological Reserve. A dispersal event refers to the recording of the interaction between a bat and a plant, which varies between 1 (if it interacts) and 0 (if it does not). Because of this if a sample contained more than one morpho-seed it was counted as different dispersal events

morpho-seeds. An intermediate diversity of bat species consumed the remaining morpho-seeds.

Important seed dispersal bats

Bats transported 15,685 seeds with an average of 137.5 seeds per sample. Some bats were generalists transporting different morpho-seeds, and others were much more specific, transporting a single type of seed (Tables 2 and 3). *Carollia brevicauda* was the main seed dispersal agent, both in the chagra and in the forest, with a dispersion importance index value of 1.4 and 2.2 respectively (Fig. 4). It dispersed 26 of the 43 morpho-seeds found; in the forest study place it transported 45.8% of the species and in the chagra's 64.3%.

Seeds transported by frugivorous bats

We identified forty-one morpho-seeds and classified 38 of them, into 12 genera: *Annona*, *Cecropia*, *Ficus*, *Gaultheria*, *Gurania*, *Iriartea*, *Muntingia*, *Philodendron*, *Piper*,

Protium, Solanum and *Vismia.* We were not able to identify five morpho-seeds.

More seeds were collected in chagras (64.04%) than in the forest (35.95%). Forest and chagras shared 15 morpho-seeds, 15 morpho-seeds were only found in the forest, and 13 only in the chagra. The most abundant genera in the chagra were: *Piper* 53.3%; *Cecropia* 14.0%; and *Solanum* 13.6%, whereas in the forest we found: *Cecropia* 22.8%; *Piper* 28.8%; *Solanum* 10.6%; *Ficus* 10.1%; *Vismia* 9.9%; and *Muntingia* 9.7% (Table 4).

Interaction networks

Discriminant analysis (Fig. 5) showed that in the forest, the genus *Carollia* was close to the genera of plants *Piper*, *Muntingia* and *Gaulteria*; the genus *Sturnira* to *Solanum* and the tribe Ectophyllini which comprises the genera (*Artibeus, Enchisthenes, Platyrrhinus, Uroderma, Vampyressa, Vampyrodes*) to *Ficus*, *Cecropia* and *Protium*. On the other hand, in the chagra we observed that *Carollia*

Table 1 Phyllostomidae bats in forest and chagra in the buffer zone of the Colonso-Chalupas Biological Reserve

Genus	Species	Forest	Chagra	Total
Anoura	*Anoura aequatoris*		1	**1**
	Artibeus glaucus	2		**2**
	Artibeus lituratus	1		**1**
Artibeus	*Artibeus obscurus*		2	**2**
	Artibeus planirostris	2	1	**3**
	Total	5	3	**8**
	Carollia brevicauda	21	18	**39**
Carollia	*Carollia castanea*	1	2	**3**
	Carollia perspicillata	1	16	**17**
	Total	23	36	**59**
Enchisthenes	*Enchisthenes hartii*	2		**2**
Glyphonycteris	*Glyphonycteris daviesi*	1		**1**
Phyllostomus	*Phyllostomus elongatus*	1		**1**
	Platyrrhinus fusciventris	1	3	**4**
Platyrrhinus	*Platyrrhinus infuscus*	1		**1**
	Platyrrhinus nigellus	1		**1**
	Total	7	3	**10**
	Rhinophylla fischerae	2	2	**4**
Rhinophylla	*Rhinophylla pumilio*		6	**6**
	Total	2	8	**10**
	Sturnira bidens		1	**1**
	Sturnira giannae	4	10	**14**
Sturnira	*Sturnira oporaphilum*	3	2	**5**
	Sturnira tildae		1	**1**
	Total	7	14	**21**
Trinycteris	*Trinycteris nicefori*	1		**1**
Uroderma	*Uroderma bilobatum*		1	**1**
Vampyressa	*Vampyressa thyone*		1	**1**
Vampyriscus	*Vampyriscus bidens*	2		**2**
Total		**47**	**67**	**114**

Genera, number of individuals per species and total per genera

grouped with most of the plants, and the tribe Ectophyllini clustered with *Ficus* and *Iriartea*. We found that *C. brevicauda* was the main disperser both in the chagra and in the forest. It dispersed 26 of the 43 morpho-seeds found; in the forest it transported 45.8% of the species and in the chagra 64.3%., with a value of DII = 1.4 and DII = 2.2 respectively (Fig. 4).

Both types of land use formed groups but without specific patterns. *C. brevicauda* formed groups in both types of land use and dispersed a great variety of plant species. In the forest (Fig. 6A), bats belonging to the Ectophyllini tribe were grouped in a module, and we found that these were mainly related to plants of the genus *Cecropia* and *Ficus*. On the other hand, in the chagra (Fig. 6B) most species of the genus *Sturnira* formed a group and fed on *Solanum*, *Vismia* and *Annona*.

The modularity value confirmed significant differences between our data and that of the null model in forest ($Q = 0.47$, $z = 1.41$) and chagras ($Q = 0.5$, $z = 5.0$). Table 5 shows metrics for the interaction networks. We plotted centrality values by bat species (Fig. 7). In the forest, *C. brevicauda* had a high value that decreased, whilst in the chagra, the opposite happened to *S. giannae*. In addition, *C perspicillata* had a high degree of centrality in the chagra, contrary to the forests where it was a peripheral species.

Discussion

Diversity of bats

From the 33 species of Phyllostomidae bats, 29 are new records for the Colonso Chalupas Biological Reserve; 24 transported seeds. The number of species is similar to the ones found in Arguero et al. (2012) and Lindner and Morawetz (2006) in southern Ecuador when correcting for sampling effort. However, we found a higher number of morpho-seeds (27:41) compared to Lindner and Morawetz (2006), probably due to differences in elevation and vegetation, highlighting the importance of bats as seed dispersers of this ecosystem and the importance of considering them in restoration programs.

We found three morpho-seeds with a high value of the four diversity components, belonging to the genera *Vismia*, *Ficus*, and *Cecropia* in the forest and only one morpho-seed with similar characteristics in the chagra of the genus *Solanum*. These results show a higher diversity of food resources for bats in the forest, consequently a diversification of their diet (Sánchez and Giannini 2018) towards species of higher forest strata (Lobova et al. 2009).

Some seeds have a low value in the four diversity components and correspond to morpho-seeds that are carried only by *C. brevicauda*. In the chagra, the morpho-seeds belong to the genera *Piper, Solanum, Vismia* and in the forest to *Muntingia, Piper, Gaulteria, Vismia*, as well as to two morpho-seeds of *Solanum* and two of *Ficus*. This result is related to the value of the dispersal importance index, since *C. brevicauda* is the species that consume the greatest number of morpho-seeds and confirms that *C. brevicauda* diversifies its diet depending on the environment in which it is found. This type of variation is recorded in sites with different seasons throughout the year, where *Carollia* modified its diet according to the abundance of available plants (Mello et al. 2004). Therefore, a reduction in the abundance of plants of the genus *Piper* in the forest would affect the feeding intake of *C. brevicauda*.

There were seeds transported only by one species of bat (high value of the rarity index). This apparently tight interaction, could be important to consider in environmental

Fig. 3 Four diversity indices Rarity.G (Guisande's rarity index), richness, PielouE (Pielou index-evenness) and D (taxonomic diversity) of the bat species that consume each morpho-seed making the differentiation between forest (upper panel) and chagra (lower panel). Circles are labelled C for chagra and F for forest. The size of the circles increases with richness, and the gradient of color indicates the rarity index. Numbers in circles represent number of bat species consuming the morpho-seed
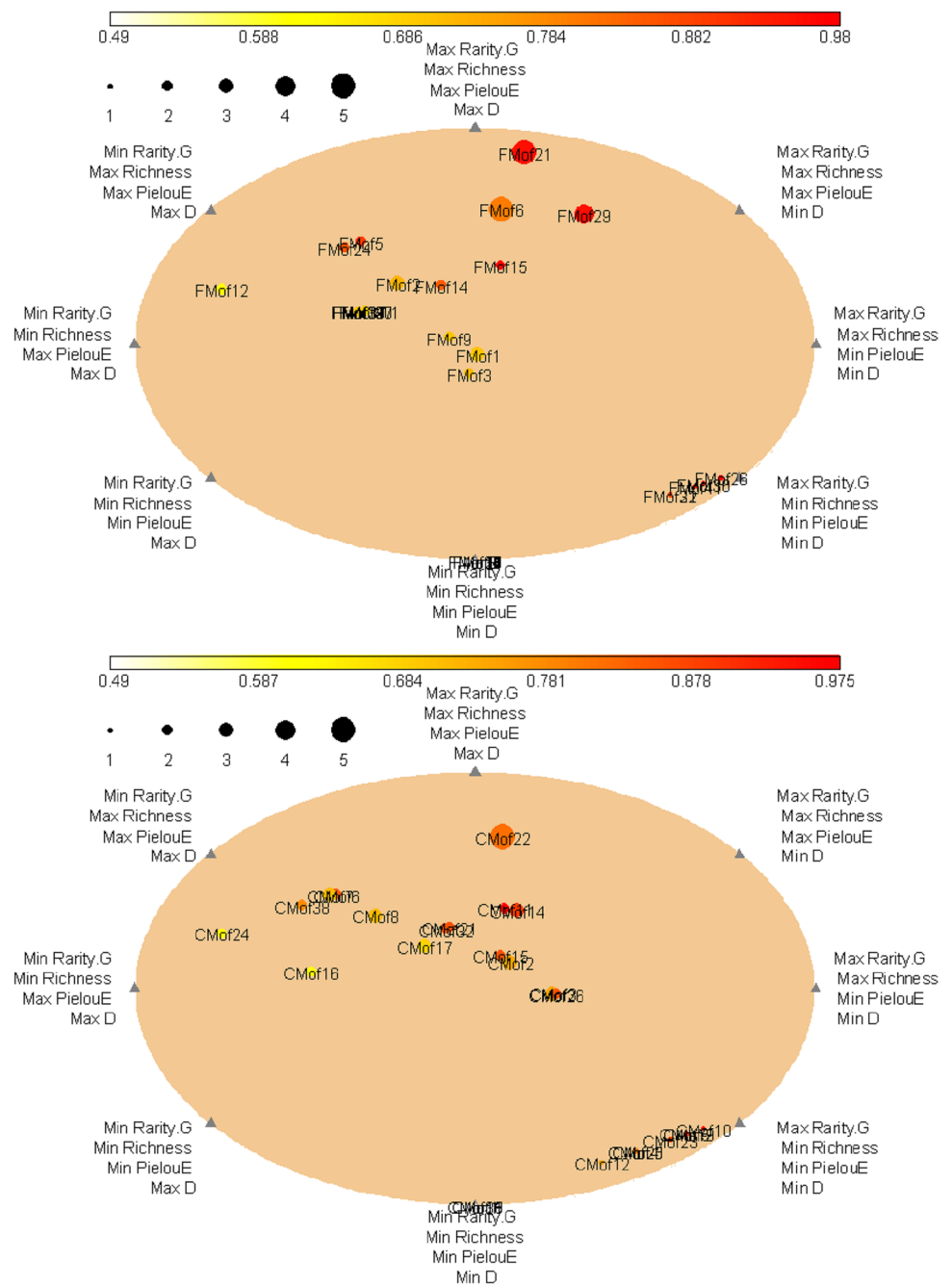
restoration programs. In the forest, *S. oporaphilum* was the only one who consumed morpho-seed 22 (*Solanum*), which corresponds with the feeding preferences recorded for this genus of bats (Castaño et al. 2018). Furthermore, morpho-seed 30 *(Protium)* was only recorded on *A. glaucus*, morpho-seed 36 *(Ficus)* was only consumed by *A. planirostris*, and morpho-seed 44 *(Cecropia)* only by *E. hartii*. This may be related to species classified as nomadic frugivores that forage in the canopy (Soriano 2000), while the genera *Protium*, *Ficus,* and *Cecropia* correspond to canopy-forming plants with a height of over 15 m (Parolin 2002; Schöngart et al. 2007; Tostes et al. 2018).

In the chagra, only *C. castanea* consumed the morpho-seed 5 (*Vismia)* and *A. planirostris* the morpho-seed 10 (*Iriartea deltoidea*), plant species that probably are transported from forest to chagras (Vera et al. 2019). On the other hand, *S. lilium* was the only bat that consumed the morpho-seed 12 (*Solanum*), which corresponds with the widely reviewed feeding preferences (Andrade et al. 2013; Castaño et al. 2018; Sánchez and Giannini 2018). Finally,

Table 2 Seeds transported by bats in chagras in the buffer zone of the Colonso Chalupas Biological Reserve

Species (total number of seeds)	*Cecropia*	*Ficus*	*Piper*	*Solanum*	*Vismia*	*Iriartea*	*Muntingia*	Others
Anoura aequatoris (83)	100.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Artibeus obscurus (196)	93.4	6.6	0.0	0.0	0.0	0.0	0.0	0.0
Artibeus planirostris (1)	0.0	0.0	0.0	0.0	0.0	100.0	0.0	0.0
Carollia brevicauda (3931)	0.0	0.0	80.1	9.5	3.8	0.0	2.1	4.5
Carollia castanea (1481)	0.0	0.0	99.5	0.0	0.5	0.0	0.0	0.0
Carollia perspicillata (1337)	4.8	0.0	45.4	24.2	20.3	0.0	0.0	5.2
Platyrrhinus fusciventris (525)	100.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Rhinophylla fischerae (97)	61.9	0.0	0.0	0.0	38.1	0.0	0.0	0.0
Rhinophylla pumilio (969)	0.0	0.0	9.2	0.4	13.4	0.0	74.6	2.4
Sturnira bidens (134)	0.0	0.0	0.0	100.0	0.0	0.0	0.0	0.0
Sturnira giannae (884)	55.7	4.6	4.6	27.5	0.0	0.0	0.0	7.6
Sturnira oporaphilum (58)	0.0	0.0	0.0	19.0	55.2	0.0	0.0	25.9
Sturnira tildae (279)	0.0	0.0	0.0	100.0	0.0	0.0	0.0	0.0
Uroderma bilobatum (67)	0.0	100.0	0.0	0.0	0.0	0.0	0.0	0.0
Vampyressa thyone (3)	0.0	100.0	0.0	0.0	0.0	0.0	0.0	0.0

Diet of the 15 species of bats found in this type of land use, in relation to the seven most frequent plant genera

Table 3 Seeds transported by frugivorous bats in the forest of the buffer zone of the Colonso Chalupas Biological Reserve

Species (total number of seeds)	*Cecropia*	*Ficus*	*Piper*	*Solanum*	*Vismia*	Others
Artibeus glaucus (8)	0.0	0.0	0.0	25.0	75.0	0.0
Artibeus lituratus (139)	100.0	0.0	0.0	0.0	0.0	0.0
Artibeus planirostris (113)	0.0	99.1	0.0	0.0	0.0	0.9
Carollia brevicauda (2566)	0.2	3.9	39.1	6.1	14.1	36.5
Carollia castanea (674)	0.0	0.0	91.7	0.3	7.7	0.3
Carollia perspicillata (174)	79.9	0.0	0.0	0.0	20.1	0.0
Echisthenes hartii (253)	74.7	14.2	0.0	0.0	5.9	5.1
Glyphonycteris daviesi (203)	0.0	100.0	0.0	0.0	0.0	0.0
Phyllostomus elongatus (3)	0.0	0.0	0.0	100.0	0.0	0.0
Platyrrhinus fusciventris (9)	100.0	0.0	0.0	0.0	0.0	0.0
Platyrrhinus infuscus (743)	100.0	0.0	0.0	0.0	0.0	0.0
Platyrrhinus nigellus (117)	0.9	99.1	0.0	0.0	0.0	0.0
Rhinophylla fischerae (153)	23.5	0.0	0.0	0.0	44.4	32.0
Sturnira giannae (482)	11.2	0.0	0.0	88.8	0.0	0.0
Sturnira oporaphilum (17)	0.0	0.0	0.0	41.2	47.1	11.8
Trinycteris nicefori (17)	0.0	0.0	0.0	0.0	100.0	0.0
Vampyriscus bidens (116)	95.7	3.4	0.9	0.0	0.0	0.0

Diet of the 17 species of bats found, in relation to the five most frequent plant genera

R. pumilio was the only one that consumed morpho-seeds 13 (*Piper*) and 19 (*Philodendron*), which makes sense as it is considered the main disperser of *Philodendron* (Rinehart and Kunz 2006*)* and also belongs to the subfamily *Carollinae* which is associated with the genus *Piper*.

Important seed dispersal bats

C. perspicillata showed the highest number of dispersal events, mainly in the chagra (94.7%), which indicates that this species does not forage in the forests and that there are

Fig. 4 Dispersion importance index DII (Galindo-González et al. 2000) for frugivorous bat species shared between forest (grey bars) and chagra (black bars) in the buffer zone of the Colonso Chalupas Biological Reserve. The values range from 0 a bat species that does not disperse any seeds to 10, a species that disperses all the morpho-seeds found
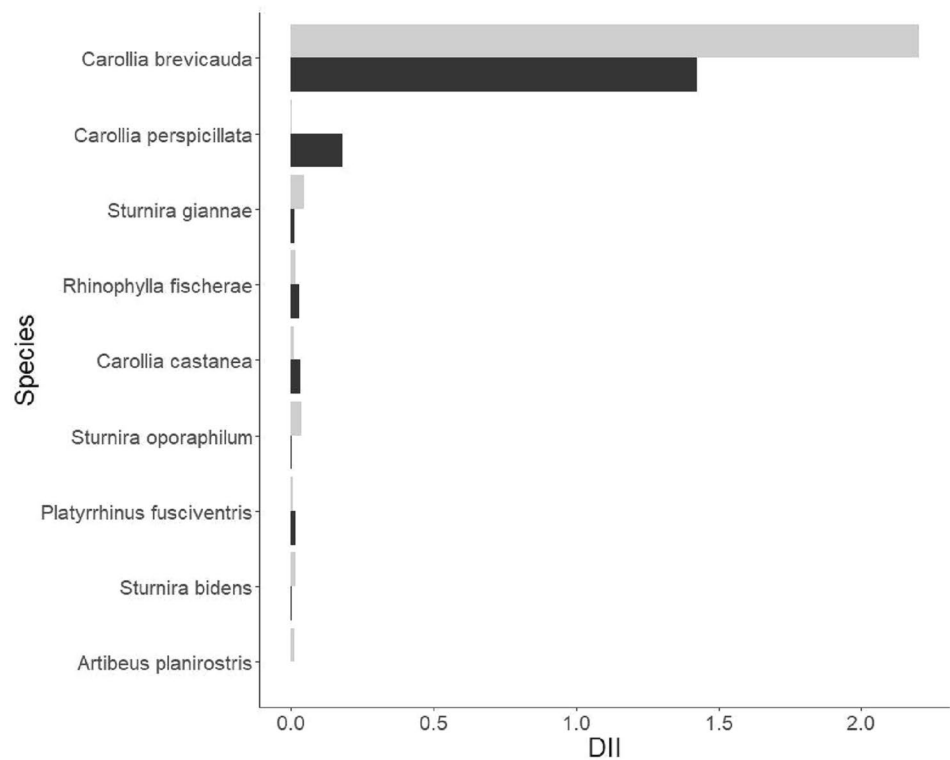
Table 4 Percentage of seeds by genus found in bat fecal samples in forest and chagra in the buffer zone of the Colonso Chalupas Biological Reserve

| Genus	Forest	Chagra
Annona	0	0.15
Cecropia	22.8	14.01
Ficus	10.1	1.23
Iriartea	0	0.01
Gaultheria	6.3	0
Gurania	0.2	0
Muntingia	9.7	8.01
Undetermined	0.1	0.79
Philodendron	1.4	2.56
Piper	28.8	53.35
Protium	0.0	0.03
Solanum	10.6	13.62
Vismia	9.9	6.24
Total	100.0	100.0

species of the genus *Carollia* and *Sturnira* as has been reported in other sites with greater disturbance (Medellín and Gaona 1999; Estrada and Coates-Estrada 2002; Castro-Luna and Galindo-González 2012; Casallas-Pabón et al. 2017). These differences can be explained by the structure of the vegetation, which in turn is influenced by the feeding habits of the bat species (Muscarella and Fleming 2007; da Silva et al. 2008).

We captured *A. aequatoris* in the chagra and presented dispersal events associated with *Cecropia*. This species belongs to the subfamilies Glossophaginae, classified as opportunistic (Rojas et al. 2011). Although, it's possible it was visiting the banana flowers, since it has been reported as a pollinator of these plants, and other species of the same genus have been associated with these crops (Muchhala and Serrano 2015; Pedrozo et al. 2018).

Seeds transported by frugivorous bats

We found that seeds of the genus *Piper* are highly dispersed both in the chagra 53.3% and forest 28.8%. This is consistent with other studies that report *Piper* as the main food source for the three species of the genus *Carollia*: *C. brevicauda* (80.1%), *C. castanea* (99.5%), *C. perspicillata* (45.4%) (Bonaccorso and Gush 1987; Thies and Kalko 2004; Saldaña-Vázquez 2014). In the forest, *Piper* was also the main food source for two species: *C. brevicauda* (39.4%) and *C. castanea* (91.7%), although we observed that the

differences in the food niche within this genus. In general, the values of dispersion importance index (DII) found in this study were low. However, the DII found for *C. perspicillata* (0.18) in both forest and chagra were very similar to Galindo-González et al. (2000) in Mexico (0.19). *C. brevicauda* presented the highest index value (DII = 1.4 in the Chagra and DII = 2.2 in the forest) which indicates that it includes a high diversity of plants in its diet.

The forest presented more bat-dispersion events, whereas the chagra showed a greater abundance, specifically of

Fig. 5 Canonical Correspondence Analysis (CCA) of plant genders, bat genders and Ectophyllini tribe. **A** Forest, where CA1 comprises 59.63% of the variance and CA2 the 22.25%. **B** Chagra, where CA1 comprises 69.64% of the variance and CA2 the 16.09%
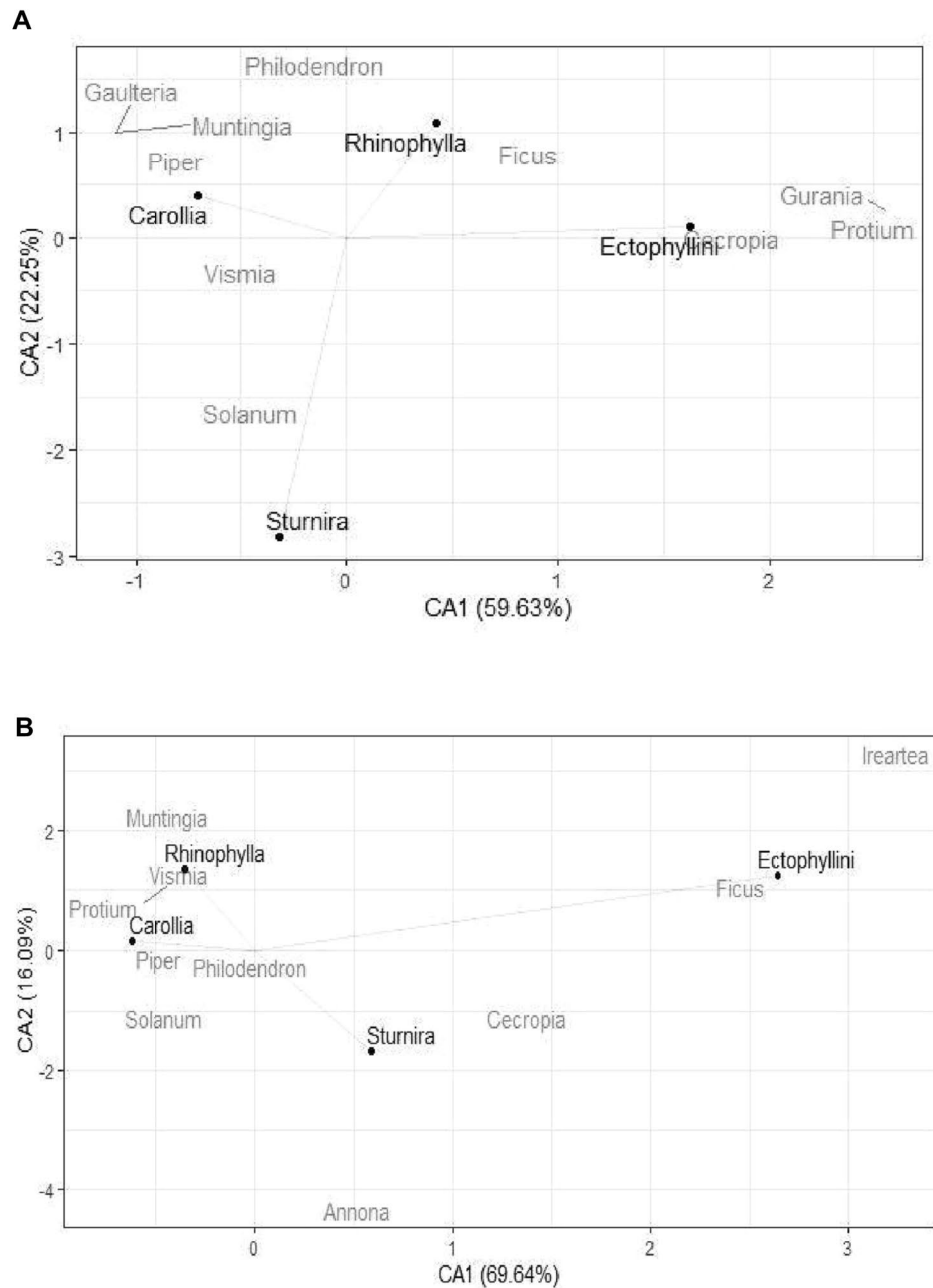

diet within this genus was varied, possibly by a greater diversity of food sources. There are reports of abundance of *Carollia* and *Sturnira* in sites with higher degree of disturbance (Estrada and Coates-Estrada 2002; Castro-Luna and Galindo-González 2012; Casallas-Pabón et al. 2017), such as chagras, and that they are specialists in plant genera such as *Piper* and *Solanum*. On the other hand, the bat species found in the forest belong mainly to the Ectophyllini tribe including *Artibeus*, which are considered specialists in *Cecropia* and *Ficus* (Fleming 1986).

The genus *Muntingia* was representative in the sampling, contributing 9.7% of the total seeds analyzed in the forest

and 8.0% in the chagra. It represented 74.6% of the diet of *Rhinophylla pumilio*, which is the first report for this species, increasing the number of species of its broad diet (Lobova et al. 2009). *R. pumilio* is also associated with *Vismia* in the western Amazon (Gorchov et al. 1995), and in this study, corresponded to 13.4% of the diet of this bat species.

Interaction networks

We obtained higher modularity values (0.47 for the forest and 0.50 for the chagra) than those presented by Mello et al. (2011b) (0.2 and 0.4) showing a greater division into
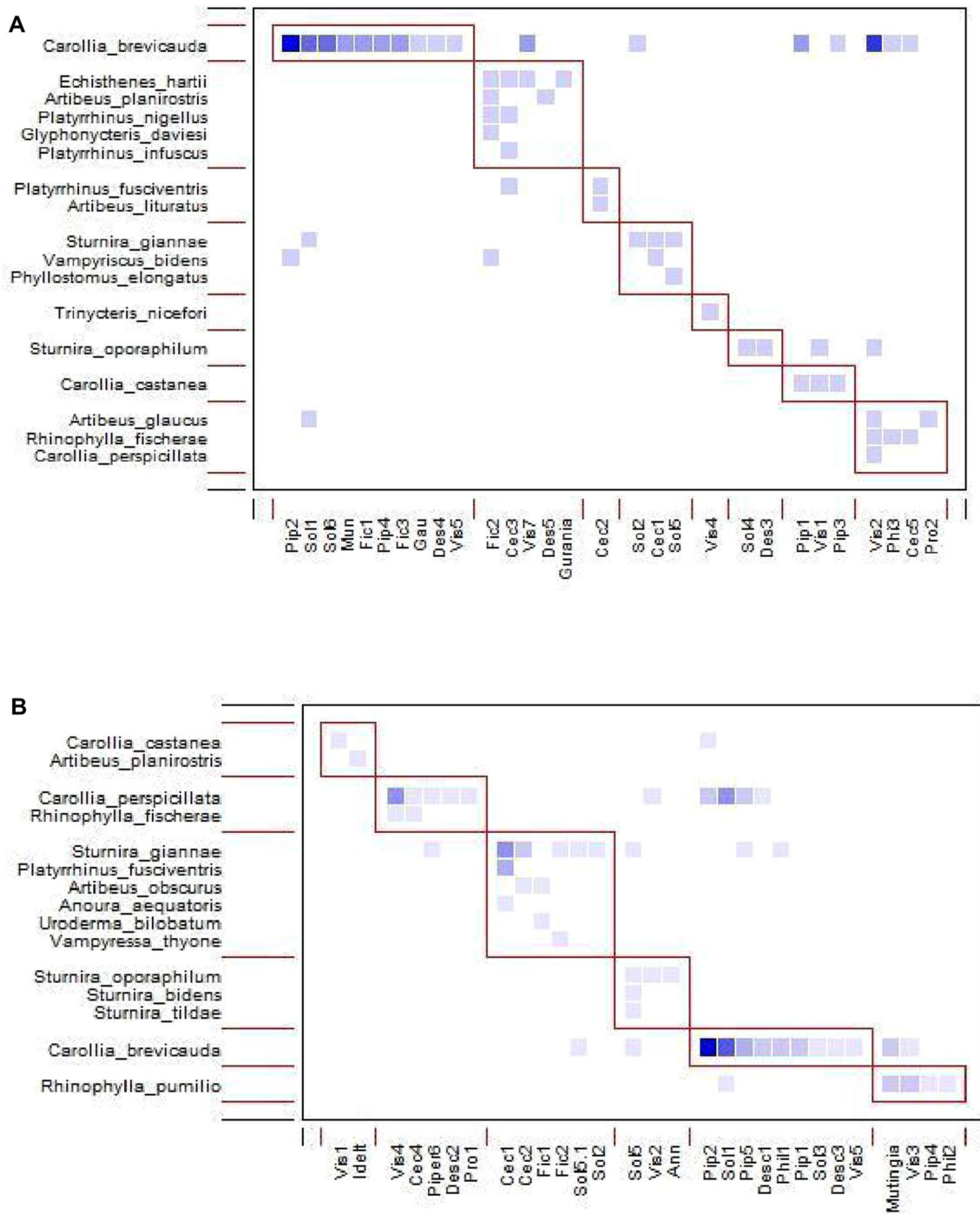
Fig. 6 Interaction network between bats and plants in the Piedmont forest and chagra of the Colonso Chalupas Biological Reserve

subgroups than usual. In addition, this value indicates that more groups were formed in the chagra than in the forest, which supports the hypothesis that, in places with high biodiversity the diet of frugivorous bats shifts due to the diversity of food resources (Sánchez and Giannini 2018;

Dormann and Strauss 2013). The relationship between *A. planirostris* and *I. deltoidea* although important, when considering the dominance and variety of ecosystem services provided by this palm throughout the Amazon (Anderson and Putz 2002; Renninger et al. 2009), should be carefully

Table 5 Metrics of food webs in forest and chagra in the buffer zone of the Colonso Chalupas Biological Reserve

Metrics	Forest	Chagra
Connectance	0.105	0.121
Links per species	1.14	1.2
NODF	2.212	2.022
Specialization asymmetry	− 1.63	− 9.28
Niche overlap (plants)	0.264	0.217
Niche overlap (animals)	0.094	0.072

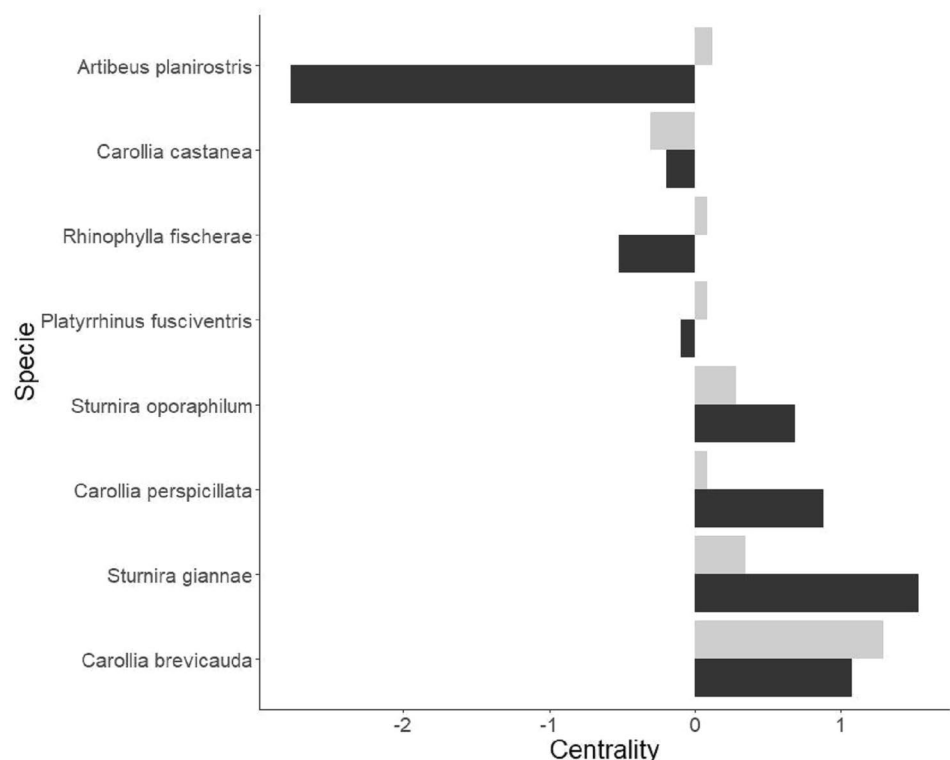Values calculated with the bipartite package and based on Dormann and Strauss (2013)

considered, because we observed this relationship just once. It is also important to clarify that although a dispersal event is evidence of seed transport, the effectiveness of dispersion will depend on both the number of seeds bas disperse and the probability of a seed germinating (Schupp 1993), an aspect not covered in this study.

The connectance observed was low and could be related to a high number of interactions as reported by Jordano (1987). Concerning specialization asymmetry, the specialization we found in the chagra (− 9.28) vs. the forest

(− 1.63) supports the hypothesis that there is greater specialization in areas with less diversity of food resources due to interspecific competition (Saldaña-Vázquez 2014). Finally, niche overlap was low for both plants and animals indicating that there are changes in the roles of the species within the structure of the network. The values of nestedness were lower than those presented in the literature (Mello et al. 2011b), which could indicate a lack of sampling effort to observe a nesting pattern as expected in this kind of interaction (Andrade et al. 2013). This effort will be also useful to increase the sample coverage values for the interactions which were low in this study 29.4% in forest and 44.5% in chagra.

Finally, our study strengthens the idea of chagras being a system that promotes biodiversity (Torres et al. 2015; Luzuriaga-Quichimbo et al. 2019; Vera et al. 2019), and that like other AFS, promotes the presence of bat seed dispersers (Olimpi and Philpott 2018). Our results reinforce the need to conserve such traditional AFS which are threatened by changes in the food systems of Amazonian Kichwa communities (Rodríguez and Castillo 2005; Zurita-Benavides et al. 2021). Consequentially, we recommend them to be included in future restoration programs and land management strategies.

Fig. 7 Centrality values in chagra and forest in the buffer zone of the Colonso Chalupas Biological Reserve. The values of *C perspicillata, S. giannae* and *C. brevicauda* in forest and chagras show significant differences

Declarations

Conflict of interest The authors declare that they have no conflict of interest.

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