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Conservation

Avifauna of cloud forest riparian corridors in a degraded landscape in eastern Mexico

Avifauna de corredores ribereños de bosque de niebla en un paisaje degradado del este de México

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Abstract

Cloud forests are known for their remarkable biodiversity and provide many ecosystem services. However, this biodiversity is in jeopardy due to the conversion of forests to other land uses. At its northernmost range in the Neotropics, cloud forest persists in remnant fragments immersed in an agricultural matrix that still has arboreal elements, such as riparian corridors. In this study we characterize the avifauna present in cloud forest riparian corridors in a highly degraded landscape of Mexico. We classified the avifauna in terms of migratory and conservation status, trophic guild, body mass, forest stratum and habitat preference. In 14 riparian corridors we recorded 86 bird species (75% were resident). Insectivorous and frugivorous species represented 79% of total richness. Almost 65% of species prefer the mid-story or canopy forest strata, while 46% were habitat generalists. Despite crossing open agricultural areas, cloud forest riparian corridors still harbor a diverse assemblage of bird species, which includes not only those tolerant to disturbance, but also species that are typical of old-growth cloud forest. We suggest that these remnants may be crucial for forest birds that move across the fragmented landscape.

Keywords: Riparian strips; Bird community; Fragmented landscape; Reservoirs

Resumen

Los bosques de niebla son conocidos por su notable biodiversidad y sus servicios ecosistémicos. Sin embargo, esta biodiversidad está en peligro debido a su conversión a otros usos de suelo. En su distribución más septentrional en el Neotrópico, el bosque de niebla persiste en remanentes inmersos en una matriz agrícola que aún conserva elementos arbóreos, como los corredores riparios. En este estudio caracterizamos la avifauna presente en dichos corredores en un paisaje altamente degradado de México. Clasificamos a la avifauna en términos de su estatus

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migratorio y de conservación, gremio trófico, masa corporal y preferencia de hábitat y estrato forestal. En 14 corredores riparios registramos 86 especies de aves. Las especies insectívoras y frugívoras representaron 79% de la riqueza total. Casi 65% de las especies prefieren los estratos forestales medios o de dosel, mientras que 46% fueron generalistas de hábitat. Aunque los corredores riparios atraviesan zonas agrícolas, siguen albergando un conjunto diverso de aves, que incluye no solo aquellas tolerantes a las perturbaciones, sino también especies características del bosque de niebla conservado. Sugerimos que estos remanentes pueden ser cruciales para las aves forestales que se desplazan por el paisaje fragmentado.

Palabras clave: Franjas riparias; Comunidad de aves; Paisaje fragmentado; Reservorios

Introduction

Tropical montane cloud forest (hereafter, cloud forest) is one of the most important terrestrial ecosystems worldwide. It provides environmental services such as carbon sequestration and water capture, and also mitigates flooding and drought (Bruijnzeel et al., 2011). Cloud forest is among the most biodiverse ecosystems in the world and hosts a remarkable diversity of flora and fauna in which spatial variation is prominent (i.e., high beta diversity), as well as a high proportion of endemic species (Aldrich et al., 2000; Karger et al., 2021). Mexican cloud forests are particularly rich in species of trees, shrubs and epiphytes, along with amphibians, reptiles, birds and mammals (Gual-Díaz & Rendón-Correa, 2014). It is estimated that Mexican cloud forests are home to 551 bird species (i.e., 50% of the total richness of the avifauna in the country), and the cloud forests in the state of Veracruz are home to 346 bird species (Navarro-Sigüenza et al., 2014). The richness of cloud forest avifauna in other parts of the country ranges from 196 to 335 species per region (Hernández-Baños et al., 1995; Navarro-Sigüenza et al., 2014). Despite its relevance, Mexican cloud forest is currently in jeopardy, not only because of agricultural expansion and uncontrolled urban growth, but also due to the illegal extraction of its species and unsustainable use of its resources (Toledo-Aceves et al., 2011). In the central part of Veracruz in the 1990s, it was estimated that there were 426 km² of cloud forest, an area that was reduced to 279 km² by 2003 (Muñoz-Villers & López-Blanco, 2008). Even though the rate of Mexican cloud forest deforestation has slowed over the last decade, today it is estimated to cover only 175 km² in Veracruz (Bonilla-Moheno & Aide, 2020). Cloud forest remnants are currently found as numerous fragments of different sizes (1 to 30 ha, usually), which are immersed in an extensive agricultural matrix (Williams-Linera et al., 2002) that still contains distinct arboreal elements such as isolated trees, living fences and forested riparian corridors. The presence of these arboreal elements within the agricultural matrix, which also include small patches (< 5 ha) of secondary forest, could be relevant to the maintenance of different groups of native flora and fauna in anthropic landscapes (Toledo-Aceves et al., 2014).

Cloud forest riparian corridors are single rows of trees growing along each side of permanent streams or rivers that have been left uncut by farmers when converting the forest to crop fields or pastures. These narrow, elongated belts or strips of tall trees have a dense woody undergrowth (riparian corridors, hereafter) and extend along rivers for kilometers. They are usually the most conspicuous arboreal element in agricultural landscapes. Forested riparian corridors that cross agricultural plots provide several environmental services, such as riverbank stabilization, nutrient recycling and enrichment, and filtering and retention of agrochemical pollutants in surface runoff, among other services (Cole et al., 2020). Additionally, riparian corridors contribute to the conservation of several taxonomic groups in anthropic landscapes, including native woody plant species (Hernández-Dávila et al., 2020), amphibians (Rodríguez-Mendoza & Pineda, 2010), bats and non-flying mammals (Griscom et al., 2007; Zarazúa-Carbajal et al., 2017). For birds, forested riparian corridors have been shown to function as refuges, foraging and nesting sites, as well as habitat corridors or stepping stones for moving across fragmented landscapes (Domínguez-López & Ortega-Álvarez, 2014; Kontsiotis et al., 2019; Lees & Peres, 2008). In lowland tropical regions that have been converted to agriculture, relatively wide riparian corridors connected to large forest remnants have been found to harbor a higher richness and abundance of forest birds than narrower and unconnected riparian corridors (Arizmendi et al., 2008; Domínguez-López & Ortega-Álvarez, 2014; Pliscoff et al., 2020). The presence of linear arboreal elements within the agricultural matrix might help to maintain bird diversity in anthropic landscapes (de Zwaan et al., 2022). To date, the majority of studies on the avifauna that uses riparian corridors in anthropic or/and fragmented landscapes has been done in lowland areas originally covered by tropical rainforest or seasonally dry tropical forest (Graham et al., 2002; Latta et al., 2012; Villaseñor-

Gómez, 2008). In particular, for riparian strips of tropical montane cloud forest, Hernández-Dávila et al. (2021) found that landscape composition (i.e., urban and forest area) and vegetation structure (mean height of vegetation) positively influence the richness and abundance of generalist and specialist birds using riparian strips. However, the bird community of cloud forest riparian habitats that could potentially be using these remnants in anthropic landscapes has not been characterized to date. In this sense, taking into account that the original area covered by cloud forest has been drastically reduced by human activities and that the remaining forest fragments are surrounded by an extensive agricultural matrix, in which still there are arboreal riparian strips, we wanted to determine and characterize the composition and structure of the bird community present in these remnants. The latter, in order to find out if these riparian strips can serve as biodiversity reservoirs or landscape connectors, that facilitate the movement of birds across the landscape and which bird species use them. The objectives of this paper were: *1)* to determine the richness, diversity and composition of birds that use riparian corridors of cloud forest in a highly modified anthropic landscape, and *2)* to characterize the avifauna that uses these corridors in terms of their conservation and migratory status, trophic guild, and habitat preference. To date, no characterization of the bird community present in riparian corridors of cloud forest has been carried out. Given that the cloud forest is fragmented and natural or semi-natural remnants, such as arboreal riparian corridors, can support different groups of flora and fauna, it is necessary to determine and analyze the avifauna present in these corridors. This knowledge is needed to design and implement management strategies of riparian corridors and improve the odds of native cloud forest species conservation in current landscapes.

Materials and methods

The study area is located in the central part of the state of Veracruz, Mexico in the upper basin of the La Antigua River within 19°31’59”-19°22’42” N, 97°05’36”-96°57’43” W (Fig. 1). The original vegetation was cloud forest (i.e., Tropical Montane Cloud Forest) with an average annual temperature of 18 °C and total annual precipitation from 1,500 to 2,000 mm/year. Fourteen riparian corridor sites (with elevations from 1,190 up to 1,780 m asl) were selected for bird sampling. The sites selected are near to the cities of Xalapa, Coatepec, and Xico and are part of a highly fragmented landscape and are representative of the riparian corridors in the region (i.e., narrow linear bands of remnant cloud forest 2 to 5 m wide growing on both sides of permanent rivers). Since riparian corridors can be several kilometers long, we delimited each of our 14 sampling sites as a riparian tract or segment approximately 400 m long (± 16 m, s.e.) with a continuous tree canopy (i.e., uninterrupted arboreal cover). The 14 riparian segments selected were all separated by more than 1 km. Most of the segments of riparian corridors that we selected for bird sampling cross open cattle pastures, with a few of them adjoining small patches (< 4 ha) of secondary old-growth forest or different types of crop fields (mostly maize or shaded coffee plantations). Dominant tree species in the sampling sites include *Platanus mexicana*, *Liquidambar styraciflua*, *Palicourea padifolia*, *Styrax glabrescens*, and *Perrottetia longistylis*. The canopy of these riparian corridors is formed by tall trees usually 15 to 20 m in height, with some surpassing 30 m, however, the average tree height in the sampling sites was 6.3 (± 7.0) m. See Hernández-Dávila et al. (2020) for more details on the vegetation structure and composition of the sites sampled.

The richness and number of birds visiting each sampling site were recorded at 2 fixed point counts set along each segment at least 250 m apart (Gregory et al., 2004). Field observations were conducted in October 2017, and in January, April and July 2018, for a total of 4 visits per point over the course of 1 year, with a 75-day interval between visits to each point. For each point count, all bird sightings were recorded with binoculars over the course of 15 minutes and within 35 m distance by one of us between sunrise and 10:30 am, except on rainy days. It took 3 days to complete the 28 points of a given period. The starting point during each period was alternated to cover the whole morning schedule of observation at each point. Only birds that were perching on the woody vegetation or on the ground or riverbank were recorded. Those flying overhead or perching in open areas nearby outside the riparian corridor were not counted. Thus, a total of 112 counts (14 sites × 2 points/site × 4 visits/site) were done at 28 points, totaling 28 h of observation. In addition to the visual records, we also set mist nets to capture birds to record understory birds visiting some of the sampled corridors, but owing to time and monetary constraints, we were only able to place the nets in 6 of the 14 riparian corridor sites. These 6 sites were chosen randomly and in each of them a total of 15 nets (10 × 2.5 m, each) were set parallel to the river flow on both riversides and at least 50 m apart along the sampled segment. From August 2016 to July 2017, one of the 6 riparian corridors was selected each month for mist-netting. Nets were left in place for 3 consecutive days avoiding rainy days and opened twice a day from sunrise to 11:00 and from 16:00 to sunset. This was done at each site twice over the sampled year. Sampling effort was 1,743 h and 2,250 m² of nets (25 m²/net × 15 nets × 6 sites) in 2 sampling periods at each site.

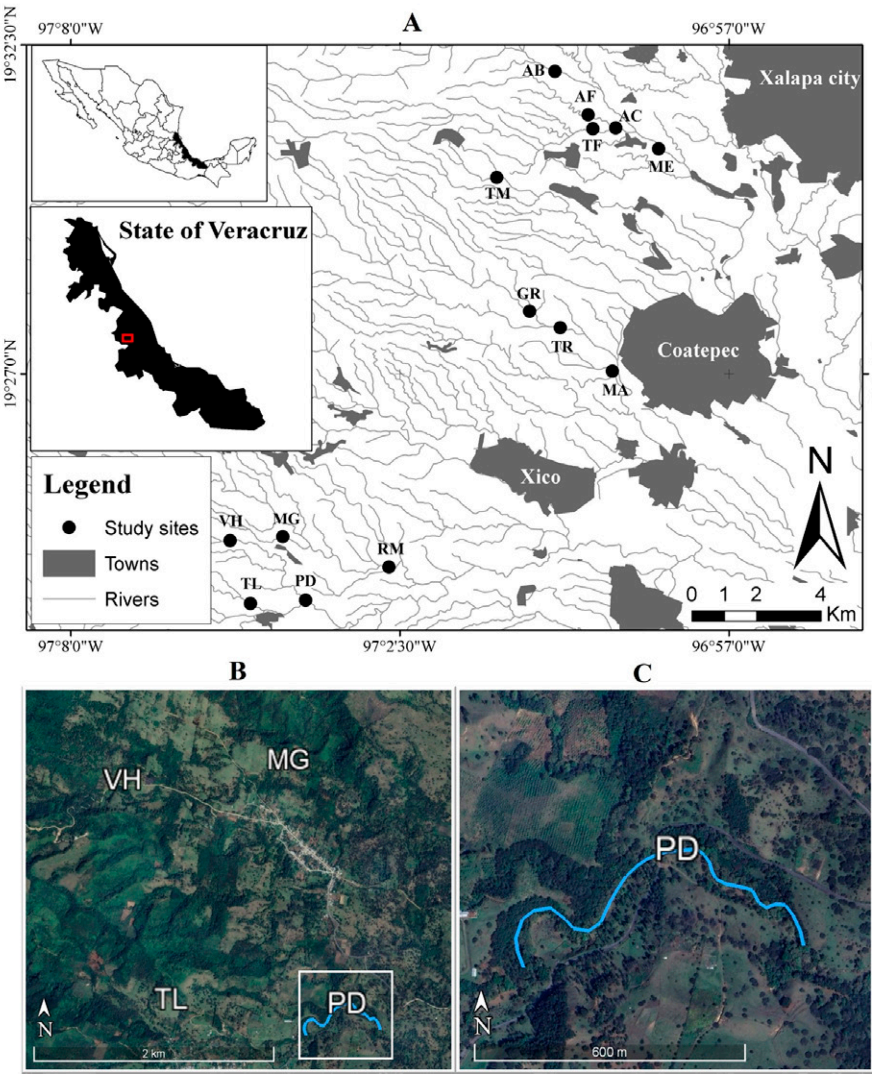

Figure 1. A, Location of the 14 segments of cloud forest riparian corridors (black circles) selected for bird sampling in central Veracruz, Mexico. The main river or streams (lines) and cities (polygons) are shown in gray. Sampling sites: Agua Bendita (AB), Agüita Fría (AF), Acuario (AC), Trucha Feliz (TF), Mariano Escobedo (ME), Truchas Martin (TM), Granada (GR), Trianon (TR), Marina (MA), Rio Matlacobatl (RM), Puente de Dios (PD), Monte Grande (MG), Tlalchy (TL) and Vista Hermosa (VH); B, image (Google Earth - Pro V 7.3.6.9345) is a close-up of 4 of the riparian corridor segments sampled (VH, MG, TL, PD); C, close-up of the PD site, with the river indicated by a blue line. Map by O. Hernández-Dávila.

Nets were inspected by 2 people every 30 minutes or less, depending on capture intensity. Each captured bird was marked by trimming a notch at the tip of one of the tail feathers to recognize recaptured individuals. Birds were released in situ immediately after sexing, weighing, and measuring (tarsus, tail, and total length; wing chord length; beak length, width, and depth).

Bird species were identified using the Sibley (2000) and Howell and Webb (1995) field guides. Nomenclature follows the IOC World Bird List checklist (Gill et al., 2024). Recorded birds were classified as either migratory from North America or resident species, and we also noted whether they were endemic, following Navarro-Sigüenza et al. (2007). The conservation status of each species was based on Mexican federal law NOM-059 (Semarnat 2010), and The IUCN Red List (IUCN, 2024). For trophic guild, each species was classified as: carnivore, insectivore, frugivore, granivore, nectarivore and omnivore (González-Salazar et al., 2014). Additionally, species were categorized into 3 size categories (body mass): small (< 40 g), medium (40 - 100 g) and large birds (> 100 g). Forest stratum preferences were based on Martínez-Morales (2001) and classified as: canopy species (those associated with the upper forest stratum, > 10 m above the ground); midstory species (those that preferentially use forest stratum between 5 and 10 m above the ground); midstory and canopy species (those using both midstory and canopy strata); understory species (those that frequent the forest floor up to 5 m above the ground); understory and midstory species (those using both understory and midstory strata); and all strata species (those that use all forest strata). Finally, main habitat preference was also based on Martínez-Morales (2001) and noted as: forest interior species (those which prefer forest sites away from the forest edge); forest edge species (those that preferentially use the fragment edge less than 100 m away from open areas); forest generalist species (those that are common both at the edge and the interior of forest fragments); and vegetation matrix species (those associated with the agricultural matrix or open areas). For species not reported by Martínez-Morales (2001) we did not assign categories for forest stratum preference and habitat preference. For these cases, species were classified as unknown.

The total richness recorded in riparian corridors was determined by the sum of records obtained from point records and those from mist-nets. Each bird species was characterized in relation to its migratory and conservation status, size, trophic guild, and habitat and forest stratum preferences. Due to the differences in the number of riparian corridors sampled by each sampling method (i.e., 14 for count points and 6 for mist nets) and their differences in data obtained from each method, for all the remaining analyses, only data from count points were taken into account: species accumulation curve and sample coverage were estimated to assess the sample completeness. Hill numbers were calculated to analyze the diversity of bird species in terms of effective number of species (q0), effective number of abundant species or Shannon diversity (q1) and effective number of dominant species or Simpson diversity (q2) (Hsieh et al., 2016; Jost, 2006). The rank-abundance curve of overall recorded avifauna was drawn to show graphically the structure of the bird community (Kindt & Coe, 2005). Analyses of accumulation curves, Hill numbers and range-abundance curves were performed for all riparian strips combined and separately. Finally, similarity in species composition among the 14 sampling sites was estimated using the Jaccard index distance, which varies from 0 to 1. Zero indicates that no species are shared between compared sites, and 1 indicates that species composition is identical between the sites. All analyses were run in R software using the vegan (Oksanen et al., 2020) and BiodiversityR (Kindt, 2021) packages.

Results

We recorded a total of 86 bird species in the 14 riparian corridors. These 86 species belonged to 9 orders, 27 families and 67 genera (Table 1). The richest families were Parulidae (16 species); Tyrannidae (13 spp.); Trochilidae (9 spp.) and Turdidae (6 spp.). Of the 86 bird species, there were 67 recorded at the point-counts and 48 trapped in the nets, with 29 recorded with both field methods (Table 1).

Of the 86 recorded species, 65 were resident species and 21 were migratory. Only 2 of the recorded species are endemic to Mexico: *Melanotis caerulescens* (Blue Mockingbird) and *Cardellina rubra* (Red Warbler). Four species are under special protection status by Mexican federal law (Semarnat, 2010): *Accipiter striatus* (Sharp-shinned Hawk), *Cinclus mexicanus* (American Dipper), *Psarocolius montezuma* (Montezuma Oropendola) and *Catharus mexicanus* (Black-headed Nightingale-thrush), and 1 species is threatened: *Catharus frantzii* (Ruddy-capped Nightingale-thrush). One species, *Selasphorus rufus* (Rufous Hummingbird), is regarded as Near Threatened in the IUCN list. The richest trophic guilds were insectivorous (63% of species) and frugivorous birds (15%) (Fig. 2A). Regarding forest stratum preference, 18% of the species recorded prefer the midstory to canopy strata, and 17% are midstory specialists (Fig. 2B). For habitat preference, habitat generalists were the most strongly represented accounting for 30% of richness, followed by forest-interior species with 18% (Fig. 2C). Most recorded species (66%) were relatively small with a body mass < 40 g, and only 12% of species were heavier than 100 g (Fig. 2D).

During the 28 point counts we recorded a total of 816 detections of 67 bird species using the corridors. In the mist nets placed in 6 of the corridors, we captured 273 birds belonging to 48 species. The species accumulation curve for all corridors reached a sample completeness of 97%. According to Hill numbers the bird diversity was of 67 species observed (q0), 18 common species (q1) and 8 dominant species (q2) (Fig. 3). Individually, the sample completeness for each of the 14 riparian segments varied between 79% and 93% per segment; and regarding diversity, q0 ranged from 9 to 24 bird species per segment, while q1 ranged from 5 to 13 species and q2 from 2 to 13 species (Fig. 4).

Table 1

List of the 86 bird species recorded in 14 cloud forest riparian corridors in the anthropic landscape of central Veracruz, Mexico. Shown are the number of visual detections (# detections) of each species estimated by point counts and the number of birds captured in mist nets. Seed dispersing birds are indicated with an asterisk (*). Species are ordered by rank (only for data obtained by point counts). We also show for each species: migratory status, resident (R), North American migrant (M). Protection status: threatened (A), special protection (Pr), least concern (LC), near threatened (NT). Trophic guild: insectivore (In), frugivore (Fr), nectarivore (Ne), omnivore (Om), granivore (Gr), carnivore (Ca). Size (body mass in g): small < 40 g (1), medium-sized 40 - 100 g (2), large > 100 g (3). Habitat preference: forest interior (FI), forest edge (FE), forest generalist (FG), vegetation matrix (VM), and no information available (-). Forest stratum preference: understory (U), understory and midstory (UM), midstory (M), midstory and canopy (MC), canopy (C), and no information available (-). See below for bibliographic sources.

Species	# detections by point counts	# captures in mist nets	Migratory status	Protection status	Trophic guild	Size category	Habitat preference	Stratum preference
*Chlorospingus flavopectus**	234	17	R	-/LC	In-Fr	1	FG	MC
Cardellina pusilla	102	15	M	-/LC	In	1	FG	A
*Psilorhinus morio**	79	2	R	-/LC	Om	3	FG	MC
*Myadestes occidentalis**	51	10	R	-/LC	Fr	2	FG	MC
Empidonax difficilis	36	18	R	-/LC	In	1	FG	M
*Myiozetetes similis**	33	3	R	-/LC	In-Fr	1	VM	C
*Parkesia motacilla**	20	14	M	-/LC	In-Fr	1	FI	U
*Psarocolius montezuma**	20	-	R	Pr/LC	Fr	3	-	-
Setophaga townsendi	12	-	M	-/LC	In	1	FG	MC
Sayornis nigricans	11	2	R	-/LC	In	1	-	-
*Tityra semifasciata**	9	-	R	-/LC	In-Fr	2	-	-
*Turdus assimilis**	9	6	R	-/LC	Fr	2	FE	M
*Turdus grayi**	9	6	R	-/LC	Fr	2	FE	M
Cinclus mexicanus	8	-	R	Pr/LC	Ca	2	-	-
Leiothlypis ruficapilla	8	1	M	-/LC	In	1	FI	MC
Mitrephanes phaeocercus	8	-	R	-/LC	In	1	FG	M
*Quiscalus mexicanus**	8	1	R	-/LC	Om	3	-	A
*Vireo solitarius**	8	3	M	-/LC	In-Fr	1	FG	M
*Henicorhina leucophrys**	7	4	R	-/LC	In-Fr	1	FG	U
*Melanerpes aurifrons**	6	-	R	-/LC	In-Fr	2	-	-
*Thraupis abbas**	6	1	R	-/LC	Fr	2	FE	C
Contopus pertinax	5	1	R	-/LC	In	1	FG	C
*Cyanolyca cucullata**	5	-	R	-/LC	Om	3	FI	MC
*Euphonia hirundinacea**	5	9	R	-/LC	Fr	1	-	-
Lepidocolaptes affinis	5	3	R	-/LC	In	1	FG	M
Mniotilta varia	5	1	M	-/LC	In	1	FI	MC
Myioborus miniatus	5	1	R	-/LC	In	1	FI	M
Chloroceryle americana	4	-	R	-/LC	Ca	2	FE	MC
Empidonax hammondii	4	-	M	-/LC	In	1	-	-
*Melanerpes formicivorus**	4	-	R	-/LC	In-Fr	2	FE	MC
*Piranga leucoptera**	4	-	R	-/LC	In-Fr	1	-	-

Table 1. Continued

Species	# detections by point counts	# captures in mist nets	Migratory status	Protection status	Trophic guild	Size category	Habitat preference	Stratum preference
*Catharus frantzii**	3	4	R	A/LC	Fr	1	FI	UM
*Momotus coeruliceps**	3	2	R	-/LC	In-Fr	3	FG	M
*Myiarchus tuberculifer**	3	1	R	-/LC	In-Fr	1	FG	M
Polioptila caerulea	3	-	M	-/LC	In	1	FG	MC
*Ptiliogonys cinereus**	3	-	R	-/LC	In-Fr	1	FG	C
Rupornis magnirostris	3	1	R	-/LC	Ca	3	-	-
*Vireo cassini**	3	-	M	-/LC	In-Fr	1	-	-
Amazona albifrons	2	-	R	-/LC	Gr	3	-	-
*Basileuterus belli**	2	11	R	-/LC	In-Fr	1	FI	UM
Basileuterus rufifrons	2	-	R	-/LC	In	1	FG	UM
*Chlorophonia elegantissima **	2	-	R	-/LC	Fr	1	FI	MC
Dendrocincla homochroa	2	1	R	-/LC	In	2	-	-
Leptotila verreauxi	2	-	R	-/LC	Gr	3	FG	U
Pyrocephalus rubinus	2	-	R	-/LC	In	1	-	-
Saltator atriceps	2	2	R	-/LC	Fr	2	-	-
Setophaga tigrina	2	-	M	-/LC	In	1	-	-
Setophaga virens	2	-	M	-/LC	In	1	FI	MC
Sporophila morelleti	2	1	R	-/LC	Gr	1	-	-
Campylorhynchus zonatus	1	-	R	-/LC	In	2	-	-
Cardellina rubra	1	-	R	-/LC	In	1	-	-
*Catharus mexicanus**	1	12	R	Pr/LC	Fr	1	FG	U
Corthylio calendula	1	-	M	-/LC	In	1	FG	U
*Dives dives**	1	2	R	-/LC	In-Fr	2	VM	A
*Dumetella carolinensis**	1	2	M	-/LC	In-Fr	2	VM	M
Empidonax minimus	1	-	M	-/LC	In	1	-	-
*Icterus bullockii**	1	-	R	-/LC	In-Fr	1	FE	M
*Megarynchus pitangua**	1	-	R	-/LC	In-Fr	2	-	-
*Ortalis vetula**	1	-	R	-/LC	Fr	3	FE	M
Pachyramphus aglaiae	1	-	R	-/LC	In	1	FI	MC
*Piaya cayana**	1	-	R	-/LC	In-Fr	3	FG	M
*Piranga flava**	1	-	R	-/LC	In-Fr	1	FE	MC
*Piranga rubra**	1	-	M	-/LC	In-Fr	1	FI	MC
Seiurus aurocapilla	1	1	M	-/LC	In	1	FI	U
Setophaga nigrescens	1	-	M	-/LC	In	1	-	-
Setophaga ruticilla	1	-	M	-/LC	In	1	-	-
Tyrannus melancholicus	1	-	R	-/LC	In	1	VM	C
Accipiter striatus	-	1	R	Pr/LC	Ca	3	-	-
Archilochus colubris	-	1	M	-/LC	Ne	1	FI	UM

Table 1. Continued

Species	# detections by point counts	# captures in mist nets	Migratory status	Protection status	Trophic guild	Size category	Habitat preference	Stratum preference
*Arremon brunneinucha**	-	14	R	-/LC	In-Fr	2	FG	M
Basileuterus culicivorus	-	2	R	-/LC	In	1	FG	UM
Campylopterus hemileucurus	-	20	R	-/LC	Ne	1	-	-
Cardellina canadensis	-	1	M	-/LC	In	1	FI	U
*Catharus aurantiirostris**	-	2	R	-/LC	Fr	1	FG	U
Chlorestes candida	-	1	R	-/LC	Ne	1	-	-
Eugenes fulgens	-	2	R	-/LC	Ne	1	FE	M
Lampornis amethystinus	-	21	R	-/LC	Ne	1	FG	U
*Melanotis caerulescens**	-	1	R	-/LC	In-Fr	2	FE	U
*Myiodynastes luteiventris**	-	2	R	-/LC	In-Fr	2	FI	MC
Pampa curvipennis	-	12	R	-/LC	Ne	1	VM	UM
*Pitangus sulphuratus**	-	1	R	-/LC	In-Fr	2	FG	A
Saucerottia beryllina	-	12	R	-/LC	Ne	1	-	-
Saucerottia cyanocephala	-	19	R	-/LC	Ne	1	FE	UM
Selasphorus rufus	-	1	M	-/NT	Ne	1	-	-
Stelgidopteryx serripennis	-	1	R	-/LC	In	1	FG	C
*Vireo gilvus**	-	1	R	-/LC	In-Fr	1	FI	C

*Seed dispersing birds: based on field data from Hernández-Dávila et al. (2022) and Hernández-Ladrón De Guevara et al. (2012). Migratory status: from Howell and Webb (1995) and Sibley (2000). Size: from Martínez-Morales (2001), Sibley (2000), and birds captured in mist nets (this study). Habitat preference and stratum preference: from Martínez-Morales (2001).

The most common species recorded visually was *Chlorospingus flavopectus* (Common Chlorospingus) with 234 detections (Fig. 5A), followed by *Cardellina pusilla* (Wilson's Warbler) with 102, *Psilorhinus morio* (Brown Jay) with 79 and *Myadestes occidentalis* (Brown-backed Solitaire) with 51 detections (see species detection data in Table 1). These 4 dominant species accounted for 45% of total detections recorded in the point counts. There were 10 species with only 2 detections (i.e., doubletons) and 18 species with only 1 (singletons), and these 28 extremely rare species accounted for less than 5% of total detections and 42% of the 67 species recorded in the point counts. In general, the pattern of dominance by the 4 species mentioned occurred in each riparian corridor sampled, concentrating most of the bird detections at each site, with several species having much fewer detections per site (Fig. 5B).

Bird species richness per site estimated in point counts varied from 9 (TM site) to 33 species (MA site), with 10 of the 14 segments sampled having fewer than 20 species each. Similarity between sites was low (Jaccard index, $J < 0.4$) for most of the paired comparisons (Table 2), with the highest level of similarity between the TL and AB sites (0.53) and the lowest between MA and AF (0.10).

Discussion

In general, and pooling all sampled riparian corridors, the sample completeness was high (97%), recording a total richness of 86 bird species in the 14 segments sampled in the fragmented cloud forest landscape of central Veracruz, Mexico. This richness is comparable to that reported in similar studies carried out in relatively large (> 3 ha) remnant fragments of cloud forest in the same region, where up to 75-100 bird species have been detected (Rueda-Hernández et al., 2015; Serna-Lagunes et al., 2023). These 14 riparian corridors harbor 24% of the bird richness reported for cloud forest throughout the entire state of Veracruz (Navarro-Sigüenza et al., 2014). The richness recorded in our study represents between

Table 2

Similarity distance in bird species composition (Jaccard index) among the 14 riparian corridors sampled (upper-right side of Table) with point counts (see Materials and methods), showing the number of species shared between riparian corridors (lower-left side), and the total number of species in each corridor (diagonal black cells). Gray-shaded cells highlight the highest and lowest values of similarity distance. The names of riparian corridors sampled are abbreviated as in Figure 1.

	AC	AB	AF	TR	GR	MA	ME	MG	PD	RM	TL	TF	TM	VH
AC	21	0.36	0.39	0.39	0.37	0.26	0.31	0.37	0.43	0.29	0.26	0.34	0.30	0.27
AB	9	13	0.33	0.35	0.43	0.24	0.30	0.38	0.39	0.32	0.53	0.35	0.38	0.32
AF	9	6	11	0.21	0.24	0.10	0.14	0.29	0.36	0.17	0.33	0.26	0.43	0.28
TR	11	8	5	18	0.52	0.24	0.29	0.21	0.32	0.27	0.19	0.29	0.23	0.25
GR	11	10	6	13	20	0.33	0.32	0.24	0.39	0.33	0.27	0.36	0.32	0.33
MA	11	9	4	10	13	33	0.31	0.17	0.27	0.43	0.21	0.28	0.17	0.25
ME	9	6	3	7	8	11	13	0.21	0.33	0.37	0.18	0.35	0.29	0.25
MG	10	8	6	6	7	7	5	16	0.35	0.25	0.32	0.42	0.32	0.27
PD	12	9	8	9	11	11	8	9	19	0.30	0.33	0.48	0.33	0.35
RM	10	9	5	9	11	17	10	8	8	24	0.32	0.40	0.22	0.24
TL	7	9	6	5	7	8	4	7	7	9	13	0.29	0.29	0.25
TF	10	8	6	8	10	11	8	10	12	12	7	18	0.35	0.43
TM	7	6	6	5	7	6	5	6	8	6	5	7	9	0.40
VH	7	6	5	6	8	9	5	6	10	7	5	9	6	12

25 and 43% of the avifauna reported in other regions of Mexico with cloud forest, where 196 to 335 bird species have been found (Martínez-Morales, 2007; Navarro-Sigüenza et al., 2014). The richness detected suggests that riparian corridors are important elements in deforested landscapes of cloud forest for numerous birds. Other studies in different sites have shown that these elements of the landscape can serve as refuges, foraging areas and even as reproductive (nesting) sites (Hawes et al., 2008; de Zwaan et al., 2022), as well as making it possible for birds to move across large open areas in agricultural landscapes (Gillies & St. Clair, 2010; Pliscoff et al., 2020). Both resident species and migratory birds, visit and use forested riparian corridors during their autumn-winter stay in the tropics (Skagen et al., 1998; Villaseñor-Gómez, 2008). As shown in our results: 24% of the recorded species were North American migratory species. The migratory bird *Cardellina pusilla*, abundant in cloud forest as well as in shaded coffee plantations in Veracruz (Navarro-Sigüenza et al., 2014), was the second most common species in our study. By far, the most dominant species in our study was *Chlorospingus flavopectus*, a resident bird regarded as a forest generalist that is common to old-growth forest, forest edge habitats and patches of secondary forest (Cruz-Angón et al., 2008; Martínez-Morales, 2007; Renner et al., 2006). *Myadestes occidentalis* was the fourth most dominant species in riparian corridors, which is considered a typical cloud forest species (Caballero-Cruz et al., 2020). This pattern of dominance is similar to that recorded by Martínez-Morales (2001) who reported *C. flavopectus*, *M. occidentalis*, *Henicorhina leucophrys*, *Catharus mexicanus*, and *Trogon mexicanus* as the most dominant species in conserved fragments of cloud forest. Except for *T. mexicanus*, the mentioned species were recorded in this study. Another very common bird in our study was *Psilorhinus morio*, a habitat generalist associated with disturbed areas, and common in small forest fragments of cloud forest (Serna-Lagunes et al., 2023), in rainforest riparian corridors that cross pastures (Graham et al., 2002), as well as in open agricultural areas with scant arboreal cover (Cerezo et al., 2009). It is important to mention that *P. morio* is a large species (> 100 gr), only 12% of the species recorded belong to this size category, while 65% are small species (< 40 gr). The conversion of forest for agricultural purposes mainly affects the presence of large bird species due to the reduction in food availability as well as fewer nesting and roosting sites (Gomes et al., 2008; Martínez-Morales, 2001). Thus, large bird species are the most strongly affected by the reduction of forest cover, while small birds are more vagile and tolerant to

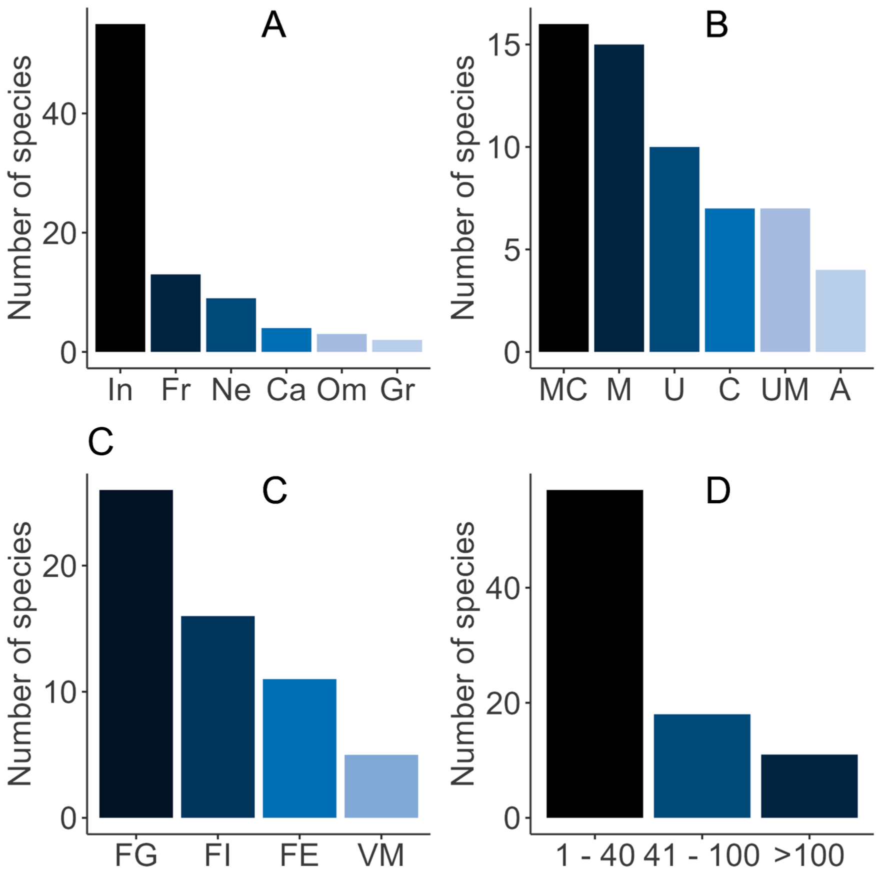

Figure 2. Characterization of the avifauna recorded in 14 segments of cloud forest riparian corridors sampled in central Veracruz, Mexico. A, Trophic guild: insectivore (In), frugivore (Fr), nectarivore (Ne), carnivore (Ca), omnivore (Om), and granivore (Gr); B, forest stratum preference: canopy (C), midstory and canopy (MC), midstory (M), understory and midstory (UM), understory (U), and all strata (A); C, habitat preference: forest generalist (FG), forest interior (FI), forest edge (FE), and vegetation matrix (VM); D, size (body mass): small (1 - 40 g), medium (40 - 100 g) and large (100 - 500 g).

deforestation, explaining the predominance of species smaller than 40 g in the riparian corridors studied.

Insectivorous birds were the richest and most abundant trophic guild in the riparian corridors sampled and are also the most common guild in intact cloud forest (Martínez-Morales, 2007). Frugivorous birds were the second richest guild and were relatively abundant in our riparian corridors. These species, together with omnivorous species, are particularly important in forest regeneration due to their role as seed dispersers of forest plants. Some of the most important frugivores that are efficient dispersers of cloud forest trees, shrubs and other zoochorous plants include *M. occidentalis*, *C. flavopectus*, *P. morio*, and several species of the genera *Turdus*, *Catharus*, and *Euphonia* (Hernández-Dávila et al., 2022; Hernández-Ladrón De Guevara et al., 2012), all of which were recorded in our study. Seed dispersal by birds is crucial for cloud forest restoration since most plant species native to this forest depend on vertebrate frugivores for dispersal (Jordano et al., 2011). Forest frugivores usually avoid open areas that are devoid of perching sites, and this is one of the strongest limitations to forest restoration due to the limited or absent immigration of woody plant seeds into agricultural areas (Holl et al., 2000). However, it has been recorded that the density of linear forest or wooded patches such as riparian strips and live fences can increase bird diversity in agricultural landscapes (Wilson et al., 2017). In this sense cloud forest riparian corridors could contribute to species movement across the landscape. Thus, forested riparian corridors within

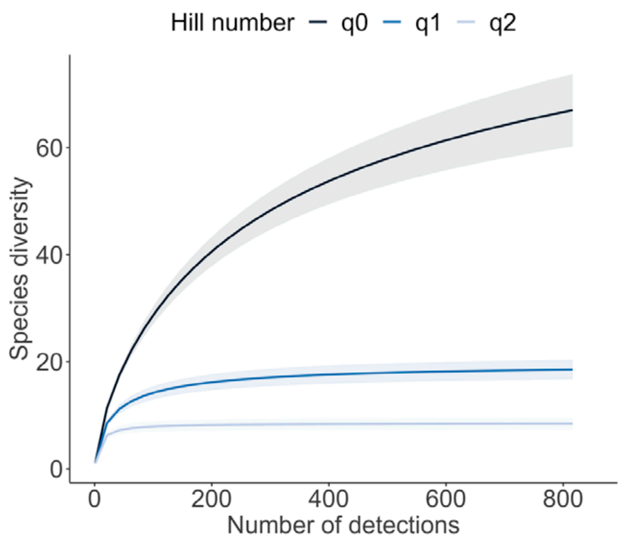

Figure 3. Species accumulation curve and Hill numbers of the bird community recorded in 14 cloud forest riparian corridors. Shaded area delimits 95% confidence intervals.

the agricultural matrix facilitate that frugivorous birds will visit these disturbed sites and disperse seeds across and into the site. Another group of birds that is crucial for plant reproduction are the nectarivorous species, with several species of hummingbirds being particularly important. Of the 26 hummingbird species reported for Mexican cloud forest (Navarro-Sigüenza et al., 2014), 9 were recorded in the riparian corridors that we studied. The presence of birds that are seed or pollen vectors in riparian corridors contributes greatly to connectivity in anthropic landscapes and are essential to biodiversity conservation and forest regeneration and restoration in these landscapes.

As expected by the high degree of anthropic disturbance in the landscape we studied, the richest groups of birds in the cloud forest riparian corridors were forest generalist species and those associated with the vegetation of the agricultural matrix (*sensu* Martínez-Morales, 2001), which together represented 53% of the avifauna we recorded. The presence and wide distribution of different arboreal elements within the current anthropic landscape could explain the presence of forest interior bird species in riparian corridors. Changes in the structure and floristic composition of the original vegetation of a given site, resulting from human activities also lead to changes in the community attributes of the avifauna (Martínez-Morales, 2005). Among the most salient changes in the forested riparian corridors that cross agricultural areas is the high abundance of plants that are common in large canopy gaps or associated with disturbed sites, including several species of the families Piperaceae, Melastomataceae, and Rubiaceae, which were common in our study (Hernández-Dávila et al., 2020). These vegetation changes are more favorable to habitat generalists than to bird species associated with the interior

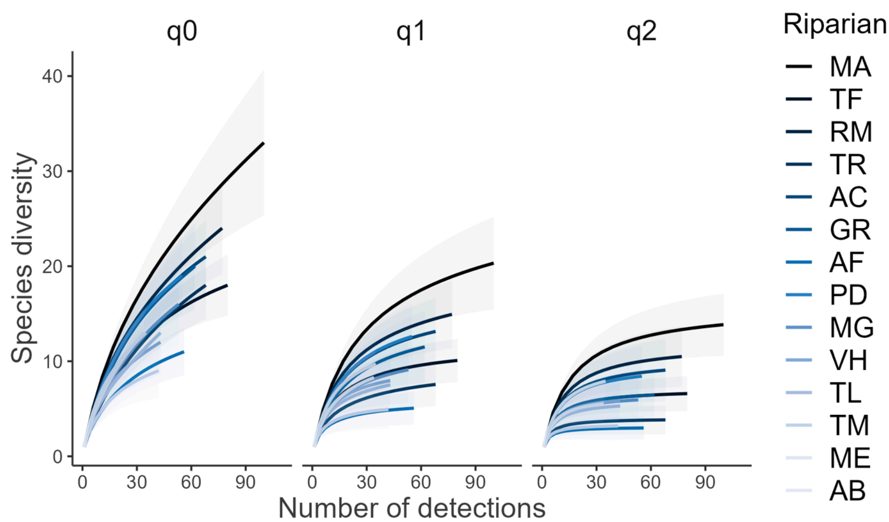

Figure 4. Species accumulation curve and Hill numbers (q0, q1, and q2) of birds recorded in each riparian corridor. Sites are ordered according to richness; dark blue curves correspond to the riparian corridors with the highest richness (e.g., MA), while light blue curves correspond to the sites with the lowest richness (e.g., AB). Shaded area delimits 95% confidence intervals. Abbreviations of riparian corridors can be found in Figure 1.

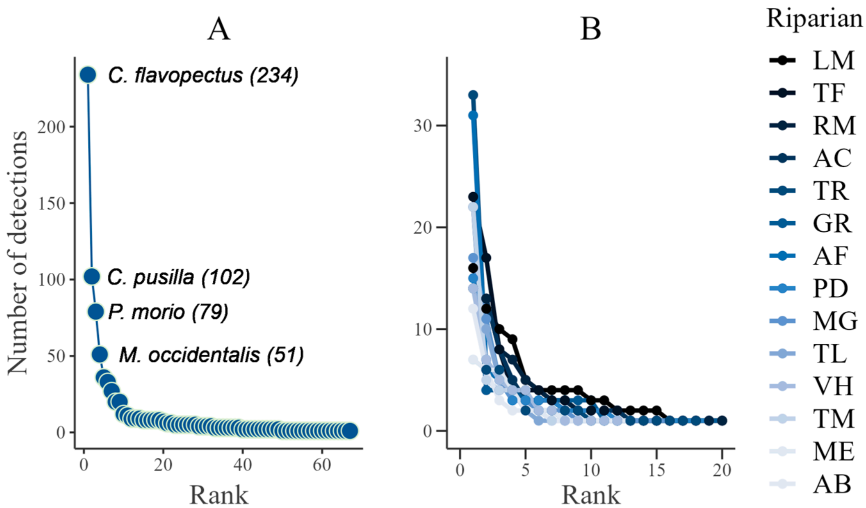

Figure 5. A, Rank-abundance curve for the avifauna recorded in 14 segments of cloud forest riparian corridors in central Veracruz, Mexico. The 4 most common species were: *C. flavopectus*, *C. pusilla*, *P. morio*, and *M. occidentalis*, the number of total detections is given in parenthesis; B, Rank-abundance curve in each riparian corridor. Sites are ordered according to number of detections; dark blue curves correspond to the riparian corridors with the highest number of detections (e.g., LM), while light blue curves correspond to the sites with the lowest number of detections (e.g., AB). Abbreviations of riparian corridors can be found in Figure 1.

of large forest fragments, explaining the lower proportion of species whose preferred habitat is the forest interior in our results. Studies in different regions report an increase in the richness and abundance of habitat generalist birds in forest edge habitats, where forest interior birds decrease (de Zwaan et al., 2022; Watson et al., 2004; Wilson et al., 2017).

For cloud forest, Martínez-Morales (2005) found that fragment size positively affects the richness and abundance of both generalist and forest-interior birds. In addition, for riparian corridors of cloud forest, Hernández-Davila et al. (2021) found that the richness and abundance of generalist and specialist birds showed a differential response to the amount of forest and urban cover in the vicinity of riparian strips. The percentage of urban cover near the riparian strip negatively affected the abundance of forest interior species and positively affected generalist species, whereas surprisingly the amount of forest area nearby the strip does not seem to influence the richness and abundance of birds using the riparian strip. These results could explain the differences between the number of generalist and interior species found in our study, as well as the differences of the Hill diversity values among the sampled corridors. Although this study did not analyze explicitly aspects of landscape configuration, it is relevant to mention that, although the riparian corridors are narrow remnants of just a few meters wide (< 10 m), both generalist and forest interior species were recorded in them. This suggests that these remnants may harbor a wealth of bird species regardless of their habitat preference. In fact, 2 of the bird species recorded are endemic to Mexico, another 4 are protected by law and 1 is threatened. This highlights the importance of riparian corridors as reservoirs of birds within anthropic landscapes, particularly species native to the cloud forest including resident and migratory birds. It is important to note that 3 of the species recorded in riparian corridors; *Quiscalus mexicanus*, *Rupornis magnirostris*, and *Pyrocephalus rubinus* could be regarded as urban birds (Maya-Elizarrarás, 2011; Ruelas & Aguilar, 2010).

As far as we know, this study is the first to describe and characterize the avifauna present in riparian corridors of the threatened cloud forest, however, it is important to take into account that, despite the fact that our point counts had a sufficient separation and elapsed time between observations to warrant independent detections and no overflying individuals or auditory recordings were included, we might have overestimated species abundances, in particular because birds move frequently along the forest strips (personal observation, OHD). Also, because mist nets capture understory species more frequently, species richness of mid- to high- strata birds are usually underestimated with nets. This study focused on riparian corridors and did not include other types of natural remnants or conserved forest fragments present in the region and part of the current mosaic of the anthropic fragmented landscape. Therefore, more studies are needed to determine the importance of riparian corridors for conserving bird diversity in comparison with other natural remnants of cloud forest.

In conclusion, our results show that the cloud forest riparian corridors that cross open agricultural areas harbor a diverse assemblage of bird species, which includes not only those tolerant of or associated with disturbance, but also species that are typical of intact patches of old-growth cloud forest. These would be absent in areas that are completely devoid of trees. Additionally, several of the birds recorded in our study are effective seed dispersers of cloud forest plants. For current deforested landscapes, this strongly suggests that cloud forest riparian corridors could be key elements in forest restoration efforts and for the conservation of bird biodiversity in agricultural landscapes. Landscape management plans designed to encourage the permanence and sustainable management of these forested corridors within the agricultural matrix will not only help in the conservation of the avifauna, but also in the restoration of degraded landscapes, thanks to the ecosystem services provided by birds, including the pollination and seed dispersal of plants native to the cloud forest.

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