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ORIGINAL ARTICLE

Vertebrate diversity and biomass along a recovery gradient in a lowland tropical forest

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Abstract

Deforestation of tropical forests have resulted in extensive areas of secondary forests with the potential to restore biodiversity to former old-growth forest levels. The recovery of vertebrate communities is an essential component of biodiversity and ecosystem restoration, as vertebrates provide key ecosystem functions. However, little is known about the recovery trajectories and habitat preferences of vertebrates in tropical landscapes with differing land-use legacies. We used camera traps covering 3 weeks to study the activity of ground-based mammals and birds in the understory of 57 sites along a forest recovery gradient, ranging from active agriculture, such as pastures and cacao plantations, to naturally recovering forests and old-growth forests in the Chocó rainforest in north-western Ecuador. Our results show that diversity and biomass of wild vertebrates are highest in old-growth forests and late recovery stages, while for domestic vertebrates, these indices are highest in agricultural

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land. Additionally, while species-habitat networks showed low habitat specificity for vertebrate species, an indicator species analysis found no species to indicate old-growth forests, *Dasyprocta punctata* and *Tayassu pecari* to indicate all forest types, and *Aramides wolfi* and *Pecari tajacu* to indicate late regeneration forests. We suggest that these patterns are caused by a high habitat connectivity and large amounts of remaining old-growth forest in our study area. Our findings indicate that secondary forests have a high potential for the recovery of vertebrate species diversity and biomass to old-growth level in lowland tropical forests with short regeneration times.

Abstract in Spanish is available with online material.

KEYWORDS

biodiversity, forest recovery, indicator species, land-use, legacy effects, networks, rainforests

1 | INTRODUCTION

Tropical forests face many threats, such as deforestation, hunting, and climate change (Wright, 2010). Globally, tropical forest cover decreased with an annual rate of 0.49% since 1990 (Achard et al., 2014). However, forests can recover, and regenerating forest ecosystems account for a sizable amount of forest habitat (Global Forest Resources Assessment, 2020). For instance, among Amazonian countries, secondary forests make up more than half of the forested area in Ecuador, Guyana, and Peru (Smith et al., 2021). Due to the crucial importance of tropical forest recovery (Watson et al., 2018), the United Nations General Assembly (UN) declared 2021–2030 the “UN Decade on Ecosystem Restoration” to reverse deforestation and defaunation of the past decades (UN General Assembly, 2019). At large scales, natural forest regeneration is the most cost-effective strategy for forest restoration (Chazdon & Guariguata, 2016; Crouzeilles et al., 2017; Meli et al., 2017), and it is usually chosen over assisted restoration programs.

Compared to other biomes, vertebrate species have experienced the strongest population declines in tropical forests (Dirzo et al., 2014; Jenkins et al., 2013), which harbor 62% of global terrestrial vertebrate species (Pillay et al., 2022), making them a particularly vulnerable group (WWF, Living Planet Report 2022, Almond, 2022). In addition to habitat loss by deforestation, vertebrates are threatened by habitat modification, hunting, pollution, climate change, and the introduction of diseases and invasive species (Redford, 1992; Young et al., 2016). Besides the continuing decrease of old-growth forests and the accompanied threat to forest dwelling vertebrates, it is argued that second-growth forests could mitigate the losses of old-growth forests, giving vertebrate species the chance to recover (Chazdon et al., 2009). A meta-analysis on vertebrates in regenerating tropical forests has shown that diversity recovers after approximately 40 years of succession, whereas recovery of species composition and some functional groups took longer (Acevedo-Charry & Aide, 2019).

However, processes of forest regeneration, including the recovery of different animal taxa, are not fully understood yet and the strategies for successful biodiversity restoration and conservation are still being debated, for example, whether landscapes should be actively restored or be set aside for natural regeneration (Crouzeilles et al., 2017; Langhammer et al., 2024). To assess the restoration success and conservation value of regenerating forests, biodiversity assessments are needed. These provide quantitative metrics that serve as first step for successful conservation planning and the selection of protected areas (Margules & Pressey, 2000).

This study aims to contribute to the assessment of the current status of Ecuador's secondary forests. We investigated the occurrence of vertebrates along a natural forest recovery gradient in the highly threatened Chocó tropical lowland rainforest in northwestern Ecuador. The Chocó is a global biodiversity hotspot (Orme et al., 2005), with less than 11% remaining old-growth forests left (Fagua et al., 2019). Using a camera trap approach, we captured ground-based vertebrates along a chronosequence selected in the framework of the Reassembly research unit (www.reassembly.de). In our analyses we addressed the following questions: (1) Do wild vertebrate species diversity and biomass recover to old-growth level in regeneration forests? As previous studies identified a fast recovery of vertebrates (Acevedo-Charry & Aide, 2019), we expect similar levels of recovery in older regenerating forests and old-growth forests. (2) Are there differences in the recovery patterns and habitat specializations of wild mammals and wild birds? As meta-analyses have shown that globally mammals are less impacted by human disturbance than birds (Gibson et al., 2011), we hypothesize a faster recovery of mammals than birds. (3) Are there indicator species specific to old-growth forest? As species composition and certain functional vertebrate groups often take longer to recover (Acevedo-Charry & Aide, 2019), we test the specificity of old-growth forest with the aim to identify indicator species that could be of importance in conservation efforts. Based on this, we expect that some habitat specialist species in our study area could be specific to old-growth forests. (4) To which extent do domestic vertebrates use forests as habitat in our study area? Domestics are frequently reported in camera trap studies in South America (Antunes et al., 2022; Lima et al., 2017), but the forest ages in which they occur is rarely considered. The role of domestics in forests is largely understudied, although it could be significant given the substantial biomass of species such as cattle and horses and possible consequent ecological impacts. In our study, we expect to find domestics in forests with different regeneration ages along the chronosequence.

2 | METHODS

2.1 | Study site and plot design

The study was conducted in a lowland rainforest located in northwest Ecuador (Esmeraldas Province) within the Reserva Río Canandé and Reserva Tesoro Escondido (Figure 1). Fieldwork was performed during the dry seasons (October–November) of 2021 and 2022 as dry seasons are the standard for camera trapping in the tropics (Jansen et al., 2014). The landscape is characterized by a patchy distribution of small-scale agriculture (pastures and cacao plantations), human settlements, and regenerating and old-growth forests (Figure 2a). Forest cover within a 1-km radius of each plot averaged 74% (SD ± 11; CI 68–79; ranging from 3% to 99%), whereas mean distance to the nearest old growth forest from each plot was on average 59 m (SD ± 46; CI 48–70; ranging from 0 to 202 m) based on analysis of current and historic land cover (Escobar et al., 2024).

We assessed vertebrate occurrences on a total of 65 plots. Plots in actively used agricultural land measured 16 × 16 m, while all other plots were 50 × 50 m. From these, we excluded eight plots due to technical issues with camera trapping. These issues comprised cases in which cameras did not function correctly or vision was reduced by vegetation, such as dropping leaves that blocked the vision. In the following we describe and analyze the data of the remaining 57 plots.

Our plot selection represents a recovery gradient ranging from agricultural land ($n = 14$) over regenerating forests ($n = 28$) to old-growth forests ($n = 15$). We categorized the sites into four land-use categories based on land-use legacy and regeneration ages [Agriculture: 7 pastures; 7 cacao plots; Recovery I: forests with regeneration times between 1 and 20 years (6 former pastures; 9 former cacao plantations); Recovery II: forests with regeneration times between 20 and 38 years (7 former pastures; 6 former cacao plantations); and, Old-growth forest plots (15)]. Agricultural land was still actively managed while recovering pastures and cacao plantations experienced no or only little anthropogenic disturbance similar to old-growth forests. Depending on the analysis, we used these four categories based on the regeneration times or sorted into seven subcategories when including the legacies of active or regenerating pastures and cocoa plantations (PA: Pasture Active; CA: Cacao Active; PRI: Pasture Regeneration 1; PRII: Pasture Regeneration 2; CRI: Cacao Regeneration 1; CRII: Cacao Regeneration 2; OG: Old-Growth Forests). The dates of land purchased by the nongovernmental organization Fundación Jocotoco as well as interviews with park rangers and farmers, revealed the regeneration ages and former land-use legacy (pasture or cacao plantation) of the forests. Further plot details, such as location and regeneration age, are provided in the Table S4.

2.2 | Camera trapping

On each plot, we installed one camera trap (Reconyx Hyperfire). The cameras were deployed over a course of 3 weeks and retrieved in the same order. In doing so, each camera operated over a period of 3 weeks. Plots were selected by the Reassembly research unit (www.reassembly.de) to investigate different reassembly processes along a forest recovery gradient from agriculture to old growth forests. We placed cameras within the plot on a tree at 30–80 cm height to face open areas or animal trails with the aim to increase detection probability. Camera traps were set to take three images per trigger event with a delay of 1 s between triggers. Vertebrates (birds and mammals) on the single images were then identified to species level (Billerman et al., 2022; Ridgely & Greenfield, 2006; Tirira et al., 2023) using the camera-trap management software TRAPPER (Bubnicki et al., 2016). Species identification was conducted by Jörg Müller and his team, which is experienced in identifying species based on images derived by camera traps. In a few ambiguous cases local experts were consulted. For assessing the number of species occurrences, we defined an event for a species as a single image or a consecutive sequence of images of one or several individuals of the same species at the same camera trap location, with a minimum interval of 5 min from the last image or image sequence (Henrich et al., 2022; Rovero & Marshall, 2009). When several individuals of the same species occurred on an image or an image sequence, we counted each individual as an individual event. For most of our captured species, the identification and differentiation of individuals was not possible and single individuals might have been counted several times. Hence, the number of species events in our study represents the habitat use of a specific plot and thus their functional role rather than the species abundance in the area.

Besides wild vertebrates, we also counted individual events of domestic animals as they are functionally present on the plots, for example, as a source of dung, as herbivores, or as prey. To evaluate the use of the various land-use categories, we only counted domestic animals when roaming freely on the plot, not when they accompanied humans (such as horses and donkeys).

We summarized all observed events, but included only ground-based vertebrates in our analysis as these species are the focal group of our investigation. We categorized vertebrates as ground-based when they spend the majority of their time foraging on the ground. The classification was based on information published in the Elton Traits database (Wilman et al., 2014), Birds of the World (Billerman et al., 2022) and expert opinion.

Additionally, we excluded local people from analyses as we assumed humans were not functionally present as described above for the domestic vertebrates.

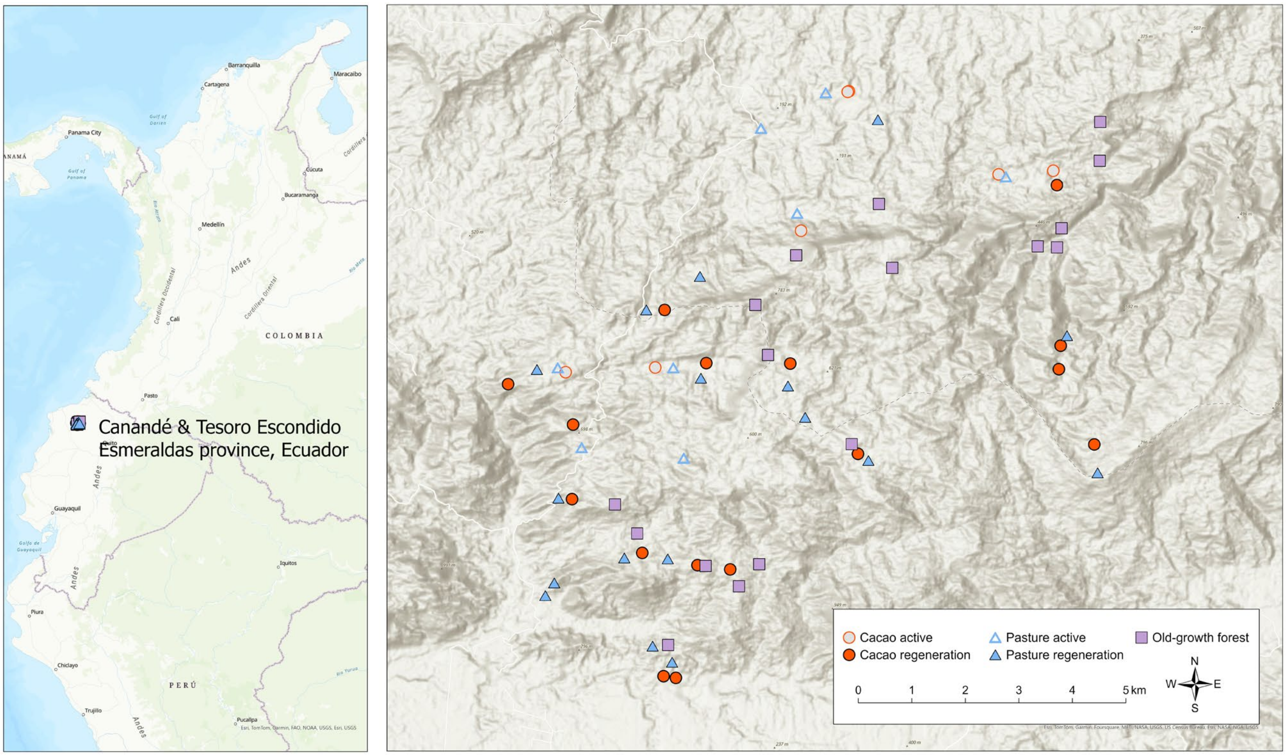

FIGURE 1 Distribution of the 65 study plots of the REASSEMBLY project in the reserves Río Canandé and Tesoro Escondido in the Ecuadorian Chocó rainforest. Symbols indicate different habitats and land-use legacies.

2.3 | Statistical analyses

All analyses were conducted with R version 4.2.0 (R Core Team, 2022). We calculated species diversity and biomass of vertebrates sorted into three groups: wild mammals, wild birds, and domestic vertebrates (comprising both domestic mammals and birds) separately for seven land-use categories described above. Diversity is often expressed with indices such as species richness, Shannon index, Shannon-Weaver index or Simpson index. However, the use of the term species richness has been criticized as it does often not consider the effects of abundance and sampling effort (see Gotelli & Colwell, 2001). As a standardization of our data is not possible due to low numbers of observations in many plots (e.g., for the calculation of species richness), we used the Hill numbers q0 and q1 (Hill, 1973) to quantify species diversity as follows: as the first Hill number (q0) we used the number of observed species. It was calculated using the "specnumber" function from the *vegan* package (Oksanen et al., 2022). As the second Hill number (q1) we calculated in a first step the Shannon indices for our plots with the "diversity" function from the *vegan* package. In a second step, we calculated the exponential function of the Shannon index (exp(Shannon)). This gives weight to abundance as well and as effective number of species it provides a number of statistical advantages (see Jost, 2006).

Biomass data for vertebrates was gathered from published sources (*Sporophila nigricollis* (yellow-bellied seedeater): Dunning Jr., 2007; *Equus caballus* (domestic horse): Carroll & Huntington, 1988; *Equus africanus* (domestic ass): de Aluja et al., 2005; all other vertebrates: Wilman et al., 2014) and then multiplied with the frequency of events per plot for each species to calculate the biomass per plot (Table S7). Similar to our definition of events, in our study, the biomass based on camera trap captures does not represent the plot's actual biomass as individuals could be captured several times. However, we assume that multiple captures of the same individuals indicate a high usage and hence a high impact of the captured species on the plots. Thus, although we do not display actual biomass on the plots, our calculated biomass represents the functional biomass of vertebrates on the plots.

We analyzed species diversity and biomass differences between the different land-use categories using generalized linear models. Land-use categories were set as ordered categories to reflect the order in which the temporal progression of the land-use gradient occurs from active agriculture to regenerating forests to old-growth forests. Pasture was ranked first before cacao, because of its open, grass-dominated habitat. In our generalized linear models, we chose a Gaussian distribution for continuous logarithmic transformed data (species diversity (q1) and biomass+1), to reach normal distribution, and a negative binomial distribution for count data (species diversity (q0)). We tested for spatial independence of the model residuals with cross-correlograms using the "spline.correlog" function of the *nfc* package.

We predicted estimated species diversity (q0), Shannon diversity, and biomass values for each vertebrate group in all 65 plots (including plots with failed cameras), in a generalized additive model (Table S5). We included land-use category, space (latitude,

FIGURE 2 The landscape of Reserva Rio Canandé (Ecuador) consists of forests of different ages intermingled with human settlements and agriculture (a). Habitats can be used by different vertebrate groups. One pasture plot, for example, was used by humans (b), domestic animals like cows, chicken, and horses (c, d), and wild mammals like pumas (e) within 48 h.

longitude), and elevation as input variables as well as forest cover within a radius of 1 km, distance to the nearest forest, and distance to the nearest forest edge. Spatial independence of the model residuals with cross-correlograms was performed as described above (Figure S4). The predicted estimations for all plots can be used in future investigations of our study area, that take into account these landscape variables.

For analyzing habitat specialization, we generated networks of the three vertebrate groups across our four land-use categories using the *bipartite* package (Dormann et al., 2008). As input we used events per species and plot as surrogates for abundance, hence the width of the network links represents the frequency of a species in the respective land-use category. The complementary specialization index (H2'), an indicator for specialization (Blüthgen et al., 2006), was calculated using the function "H2fun". We tested it against a null model with 1000 networks generated with the method "r2dtable" based on the Patefield algorithm. Networks were visualized using the "plotweb" function.

We conducted an indicator species analysis for our four land-use categories using the package *indicspecies* (Cáceres et al., 2022). Input for the community data matrix were species events in each land-use category (Table S8). Using the "multipatt" function, we calculated an indicator value (IndVal) of each species based on Dufrêne and Legendre (1997) with the land-use categories as groups, and we allowed the combination of site groups (as explained in Cáceres et al., 2022). We allowed either single land-use categories or neighboring land-use categories along the recovery gradient as combinations. The statistical significance of the calculated values was assessed with a permutation test with 1000 permutations.

Lastly, we compared our species community with the community derived from an assessment based on sound recorders that were placed on the same plots within the same time (Müller et al., 2023). For this, sound recordings were identified by two specialists (for details see Müller et al., 2023). Here, we identified species that were captured with both methods and counted the presence of each species in each land-use category. As the number of analyzed plots differed between studies (camera traps: $n = 57$, sound recorders: $n = 43$) and definitions for capture frequencies were different between both methods, we calculated the number of plots on which the species occurred (presence-absence) for better comparison.

3 | RESULTS

3.1 | General summary of collected data

In total, we recorded 40 species (24 mammal species and 16 bird species) in 1197 camera days in 1487 events across all land-use categories (Table 1, Table S6). According to the IUCN Red List of Threatened Species (IUCN, 2023), three species are classified as vulnerable (*Aramides wolfi* (brown wood rail), *Tayassu pecari* (white-lipped peccary), and *Cebus capucinus* (Colombian white-faced capuchin)) and one species as endangered (*Neomorphus radiolosus* (banded ground cuckoo)). Three species were classified as near threatened (*Penelope purpurascens* (crested guan), *Leopardus wiedii* (margay), and *Panthera onca* (jaguar)), whereas all other species were classified as least concern or did not have an assessment due to deficient data.

Carnivora was the most species-rich group, with nine species, followed by Rodentia with four species and Galliformes and Columbiformes with three species each. Among the 40 species, we identified 34 wild and six domestic vertebrates. Species with the most events were domestic chicken ($n = 343$), Central American agouti ($n = 258$), cattle ($n = 196$), and lowland paca ($n = 123$).

After assessing the species' prevalent foraging stratum, we excluded eight non-ground-based species (*Cebus capucinus*, *Buteogallus anthracinus*, *Phaethornis striigularis*, *Coragyps atratus*, *Penelope purpurascens*, *Aramus guarauna*, *Furnarius leucopus*, and *Sporophila nigricollis*) from our data set and continued analysis with the remaining 32 ground-based species.

3.2 | Comparison with sound recorders

A comparison of our results with published data of vertebrate communities derived from sound recorders, that were placed on the same plots at the same time, showed that there is little overlap in species detection using both methods (Table S1). From 32 wild vertebrate species identified by camera traps and 316 by sound recorders, only 11 species were detected by both methods.

3.3 | Patterns of species diversity and biomass along the forest recovery gradient

Species diversity (q0 and q1) and biomass of wild mammals each increased along the forest regeneration gradient (Figure 3a,d,g; Table S2). Wild birds showed highest values for these metrics in older regenerating forests (PRII and CRII) and old-growth forest (Figure 3b,e,h), but only a significant trend along the recovery gradient for biomass (Table S2). Domestic vertebrates showed a significant decrease from agriculture towards old-growth forests in diversity (q0 and q1) and biomass (Figure 3c,f,i; Table S2). High biomasses of domestics in agriculture were quantified due to a high number of events by domestic cattle in pastures ($n = 196$) and their high body mass.

The analysis of spatial independence of our selected plots revealed that the residuals of all nine linear models are spatially independent (Figure S3), indicating that vertebrate distributions are not explained by the longitudinal, latitudinal, or altitudinal parameters of the location of our selected plots. Our predicted values for vertebrate species diversity (q0), Shannon diversity, and biomass for all plots based on a generalized additive model are provided in Table S5. They can be used in future investigations of our study area, which consider land-use category, space (latitude, longitude), elevation, forest cover within a radius of 1 km, distance to the nearest forest and distance to the nearest forest edge.

3.4 | Species networks across land-use

Our network analysis examined the habitat preferences and specialization of vertebrate groups (Figure 4). The results showed that wild mammals are not specialized in their habitat use regarding the four land-use categories, which is reflected in a low degree of specialization not significantly different from the null model ($H_2' = 0.12$; $p > .05$). The network for wild mammals showed that most species were recorded in several land-use categories (Figure 4a). Large vertebrates (defined as >3 kg based on Cardillo et al., 2005) were found across all land-use categories. For example, *Cuniculus paca* (lowland paca) and *Dasyprocta punctata* (Central American agouti) were recorded in plots of all four land-use categories. From the two peccari species *Tayassu pecari* (white-lipped peccari) was present in all three forested categories (Recovery I, Recovery II, and Old-growth forest) and *Dicotyles tajacu* (collared peccary) was present in regenerating

TABLE 1 Independent events per species on the different land-use categories along a forest recovery gradient (PA: Pasture, CA: Cacao plantation, PR: Pasture recovery, CR: Cacao recovery, RI: 0–20 years recovery, RII: 20–38 years recovery, OG: Old-growth forest) as well as the total number of events per species, and the number of plots (*n* plots) a species was captured on.

Subcategories		PA	CA	PRI	CRI	PRII	CRII	OG	Total	*n* plots
Wild mammals										
Artiodactyla										
Mazama gualea	South American Red Brocket	0	0	1	1	0	0	3	5	4
Carnivora - Felidae										
Leopardus pardalis	Ocelot	0	1	1	0	2	1	4	9	8
Leopardus wiedii	Margay	0	0	2	1	0	0	2	5	4
Panthera onca	Jaguar	0	0	1	0	2	0	3	6	6
Puma concolor	Cougar	1	0	0	0	2	10	7	20	6
Herpailurus yagouaroundi	Jaguarundi	0	0	0	0	0	0	1	1	1
Carnivora - Mustelidae										
Eira barbara	Tayra	1	0	1	4	1	3	8	18	10
Neogale spec.		0	0	0	0	1	0	0	1	1
Carnivora - Procyonidae										
Procyon cancrivorus	Crab-eating raccoon	0	0	0	2	1	0	1	4	4
Cetartiodactyla										
Dicotyles tajacu	Collared peccary	0	0	0	1	6	17	0	24	4
Tayassu pecari	White-lipped peccary	0	0	4	2	14	6	19	45	15
Cingulata										
Dasypus novemcinctus	Nine-banded armadillo	4	6	9	12	7	7	14	59	20
Didelphimorphia										
Didelphis marsupialis	Common opossum	1	6	0	0	6	2	4	19	12
Pilosa										
Tamandua mexicana	Northern tamandua	0	0	0	0	0	1	1	2	2
Primates										
*Cebus capucinus**	Colombian white-faced capuchin	0	0	0	0	1	0	0	1	1
Rodentia										
Cuniculus paca	Lowland paca	0	8	0	61	5	12	37	123	22
Dasyprocta punctata	Central American agouti	0	7	1	92	19	15	124	258	27
Oecomys spec.		0	17	0	1	0	0	5	23	7
Sciurus granatensis	Red-tailed squirrel	0	0	0	1	8	0	10	19	7
Wild birds										
Accipitriformes										
*Buteogallus anthracinus**	Common black hawk	0	0	0	0	0	0	1	1	1
Caprimulgiformes										
*Phaethornis striigularis**	Stripe-throated hermit	0	0	0	1	0	0	0	1	1
Cathartiformes										
*Coragyps atratus**	Black vulture	14	0	0	0	0	0	0	14	1
Columbiformes										
Geotrygon montana	Ruddy quail-dove	0	0	1	0	5	0	0	6	2
Leptotila pallida	Pallid dove	0	11	0	0	4	1	0	16	4
Leptotrygon veraguensis	Olive-backed quail-dove	0	0	0	0	1	0	3	4	2
Cuculiformes										
Neomorphus radiolosus	Banded ground cuckoo	0	0	0	0	1	0	0	1	1

(Continues)

TABLE 1 (Continued)

Subcategories		PA	CA	PRI	CRI	PRII	CRII	OG	Total	*n* plots
Galliformes										
Odontophorus erythrops	Rufous-fronted wood-quail	0	0	0	0	0	0	2	2	2
*Penelope purpurascens**	Crested guan	0	0	0	0	0	1	0	1	1
Gruiformes										
Aramides wolfi	Brown wood rail	0	0	0	0	2	1	0	3	3
*Aramus guarauna**	Limpkin	0	1	0	0	0	0	0	1	1
Passeriformes										
*Furnarius leucopus**	Pale-legged hornero	1	0	0	0	0	0	0	1	1
*Sporophila nigricollis**	Yellow-bellied seedeater	0	8	0	0	0	0	0	8	1
Struthioniformes										
Crypturellus soui	Little tinamou	0	0	0	0	0	1	0	1	1
Tinamus major	Great tinamou	0	0	0	2	9	0	6	17	8
Domestics										
Bos taurus	Domestic cattle	194	0	2	0	0	0	0	196	5
Canis lupus familiaris	Domestic dog	12	13	0	1	0	5	0	31	10
Equus africanus	Domestic ass	0	0	0	1	1	0	2	4	3
Equus caballus	Domestic horse	69	1	1	3	0	0	6	80	8
Gallus gallus domesticus	Domestic chicken	337	6	0	0	0	0	0	343	6
Sus domesticus	Domestic pig	4	0	0	0	0	0	0	4	2
Homo sapiens		36	46	12	4	0	7	5	110	21
Total events per land-use category		674	131	36	186	102	90	268	1487	

Note: Species marked with asterisk were not classified as ground-based and excluded from analysis together with humans.

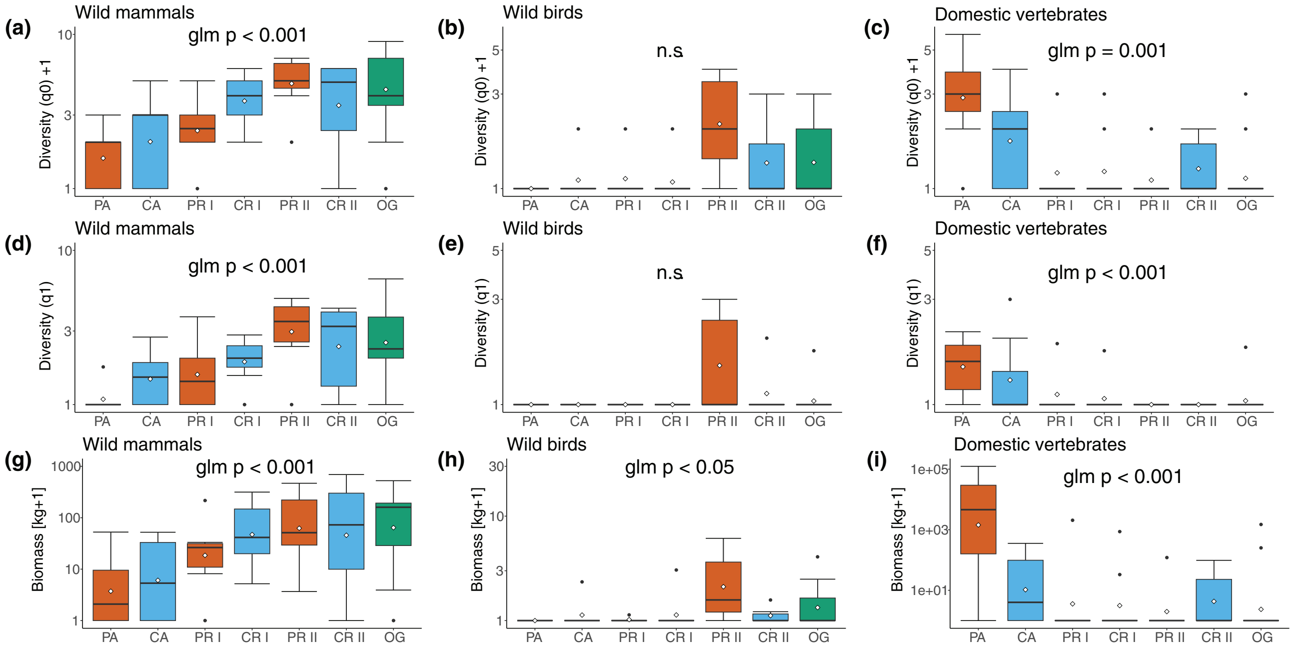

FIGURE 3 Number of observed species (diversity (q0)) (a–c), effective number of species (diversity q1) (d–f), and biomass (g–i) of wild mammals (a, d, g), wild birds (b, e, h), and domestic vertebrates (c, f, i) into seven land-use subcategories (PA: Pastures, CA: Cacao plantations), regenerating forests with different legacies and times since abandonment, and old-growth forests (OG). Recovery I (PR I, CR I) ranges from 0 to 20 years, and recovery II (PR II, CR II) from 20 to 38 years. Red color indicates active or former pastures, blue color indicates active or former cacao plantations, and green color indicates old-growth forest. Means are shown as white diamonds. The axis of the dependent variable was log-transformed for visualization. *p* values were extracted from generalized linear models (lm) using ordered categories in the order displayed. Generalized linear model results are provided in the Appendix S1.

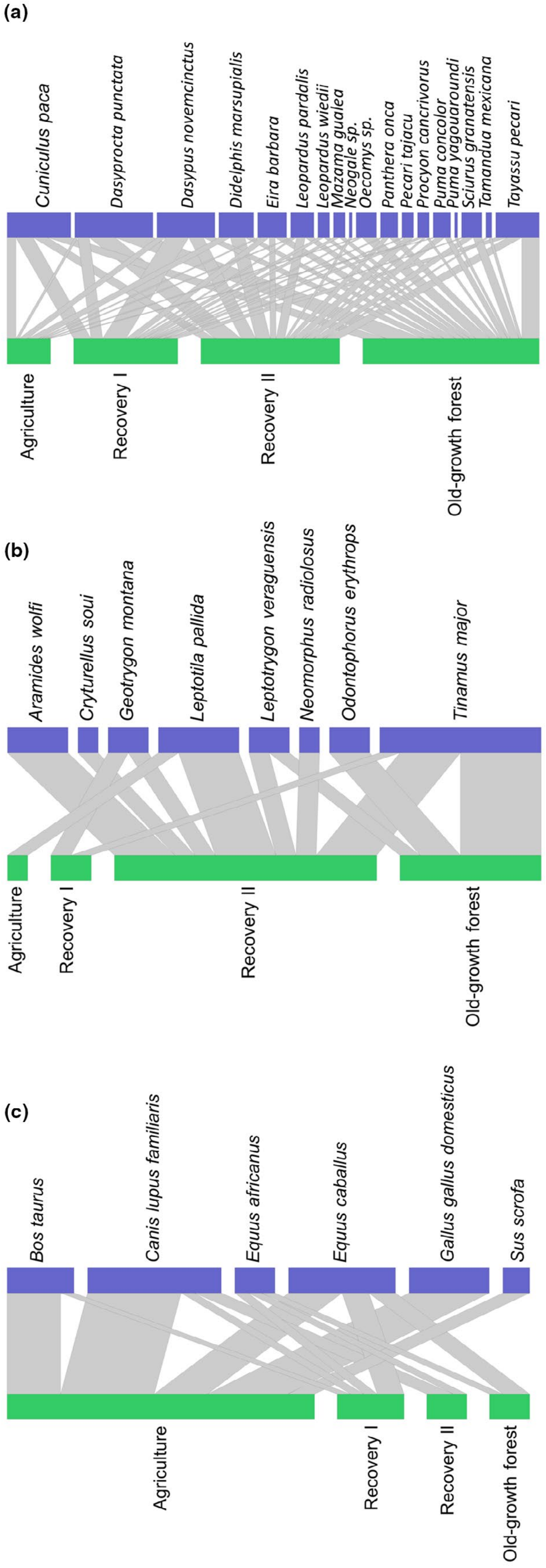

FIGURE 4 Habitat use networks of (a) wild mammals, (b) wild birds, and (c) domestic animal communities in four land-use categories. The recovery categories consist of regenerating forests with different ages since abandonment. Recovery I ranges from 0 to 20 years, and recovery II from 20 to 38 years. Agriculture consisted of pastures and cacao plantations. The thickness of the links represents the frequency of the species in the respective land-use category.

forests (Recovery I and Recovery II). Large predators like *Panthera onca* (jaguar) and *Puma concolor* (cougar) were also present in several land-use categories including forests and agricultural land (*P. onca*: Recovery I, Recovery II, Old-growth forest; *P. concolor*: Agriculture, Recovery II, Old-growth forest).

Wild birds showed a higher degree of specialization than wild mammals but also did not differ significantly from the null model (H_2'=0.36; $p>.05$). While most species were only found in a single land-use category, *Tinamus major* (great tinamou) was the only species being recorded in more than two categories (Recovery I, Recovery II, Old-growth forest) (Figure 4b).

Similar to wild vertebrates (birds and mammals), the specialization degree of domestic vertebrate species did not differ from the null model (H_2'=0.28; $p>.05$). Here, two-thirds of domestic species (cattle, domestic dogs, domestic horses, and domestic donkeys) were recorded in forests, whereas chicken and domestic pigs were found exclusively in agricultural land (Figure 4c).

3.5 | Indicator species for different land-use categories

We identified eight indicator species for different land-use categories or their combinations (Figure 5). *Bos taurus* (cattle), *Gallus gallus domesticus* (chicken), and *Canis lupus familiaris* (domestic dog) were identified as indicator species for agricultural land. *Aramides wolfi* (brown wood rail) and *D. tajacu* (collared peccary) were identified as indicator species for Recovery II. *T. pecari* and *D. punctata* were identified as indicator species for all three forested categories but not for active agricultural land. We did not identify any species that only serve as indicator species for old-growth forests.

4 | DISCUSSION

4.1 | Recovery of wild mammal diversity

Our analyses showed that wild mammalian species diversity (q0 and q1) in regenerating forests can recover to old-growth forest levels within a short recovery time of 20–38 years. This is consistent with other studies, for example, a review of faunal recovery in the tropics

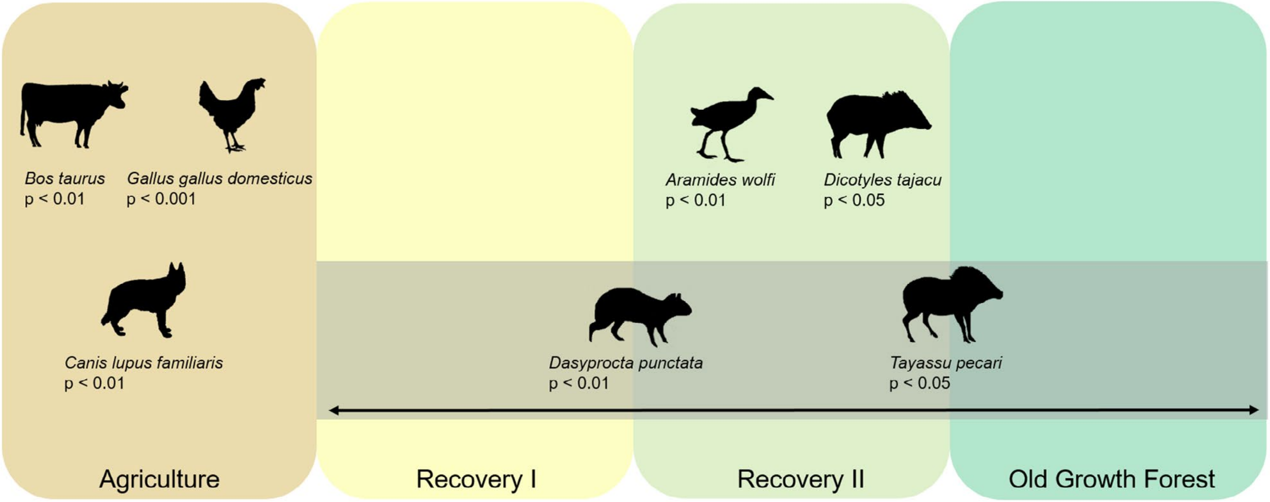

FIGURE 5 Indicator species in four land-use categories. The recovery categories consist of regenerating forests with different ages since abandonment. Recovery I ranges from 0 to 20 years, and recovery II from 20 to 38 years. Agriculture consisted of pastures and cacao plantations. In the analysis, we allowed either single land-use categories or neighboring land-use categories along the recovery gradient as a combination of site groups. Gray background indicates that the animals were identified as indicator species for several land-use categories. We determined species as indicator species when the indicator value (IndVal) had a significance level lower than .05.

has shown that animals species richness across many taxa of vertebrates and invertebrates are predicted to reach old-growth levels after 20–40 years of recovery time (Dunn, 2004), while a more recent meta-analysis has shown a recovery of tropical vertebrate species richness to old-growth levels after 40 years (Acevedo-Charry & Aide, 2019).

The mechanisms and main drivers of restoration success, that cause a return to old-growth forests conditions, are not fully understood yet. A meta-analysis by Crouzeilles et al. (2016) for example did not identify a main driver for mammal restoration. In our study area, we propose that the rapid recovery could be explained by the mosaic landscape consisting of forest fragments and agricultural patches. Our study sites are characterized by short distances to the nearest old-growth forest from each plot (mean: 59 m, ranging from 0 to 202 m), and a high old-growth forest cover (mean: 74% within a 1-km radius of each plot, CI: 68–79) (Escobar et al., 2024). The close proximity of forest fragments to one another might allow for easy access of vertebrates between regenerating forests, while the large amount of remaining old-growth forest could serve as a reservoir for vertebrate species.

Although our method does not allow to assess the time that the animals spend in the different habitats or the activities carried out, we argue that the presence of captured vertebrates represents recovery, as it indicates volitional habitat occupancy by the species. Following this, our study supports the theory that regenerating forests can mitigate the effects of deforestation in areas with large amounts of remaining old-growth and should thus be considered for conservation efforts (Chazdon et al., 2009).

4.2 | Recovery of wild bird diversity

Our analysis of ground-based wild bird species diversity (q0 and q1) did not detect significant trends along the forest recovery gradient. We explain this result by the combination of methods, that we used. Generalized linear models using ordered categories are well suited to explore trends along a trajectory of ordered categories. Using camera traps, we did not find many ground based bird species and captured species showed low frequencies of events due to methodological limitations (see below). These metrics were especially low in active agricultural land and early regenerating forests, which explains the lack of a significant trend. Other methods such as surveys by sight or vocalization might be better suited for detecting bird species and individuals (Falconí-López et al., 2024; Lennox et al., 2018; Reid et al., 2012). Although we did not detect a trend along the regeneration gradient, we showed that the measured metrics are highest in older regenerating and old-growth forests, which is consistent with other studies. Globally, bird species richness has been shown to reach old-growth levels after 40 years, similar to mammals (Acevedo-Charry & Aide, 2019). A study in Costa Rica comparing restoration methods showed that there is no difference in avian communities between active and passive restoration even within short regeneration times of 6–9 years (Reid et al., 2012) when there is enough surrounding old-growth forest. For our study we conclude, that we might not have captured the whole community of ground-based birds, but our results of the birds, that have been captured, support our hypothesis that ground-based birds can recover in older secondary forests, especially when they have a legacy as a former pasture.

4.3 | Recovery of wild mammal and bird biomass

The number of observed species does not need necessarily correlate with biomass, given the significant interspecific variation in size and biomass, that mammal and bird taxa display. In our study, the examined vertebrate groups showed different trajectories of biomass along the recovery gradient. Studies on biomass recovery of tropical forests are rare and focus mostly on plant biomass (Poorter et al., 2016; Staples et al., 2020; Wang et al., 2017). However, the amount of vertebrate biomass can give important information in addition the number of observed vertebrate species (Potapov et al., 2024; Sobral et al., 2017). It can be assumed that high biomasses have the potential for a greater physical impact on the ecosystem due to the occurrence of larger animals with greater energy requirements or high abundances. For example, similar to the influence of high vertebrate abundances on many ecosystem processes (Dirzo et al., 2014), high vertebrate biomasses could also alter processes like seed dispersal, grazing pressure, soil compaction due to trampling and nutrient cycling due to the amount of feces and carcasses. Our results showed that biomass of wild mammals and birds was highest in older regenerating forests and old-growth forests, suggesting that the biomass of wild vertebrates has the highest impact on old-growth and secondary forests with longer regeneration time.

4.4 | Land-use and biomass of domestic vertebrates

In our study area, we observed husbandry of domestics ranging from fenced and semiopen pastures to free-ranging livestock in the villages close to our study sites. Given that domestic animals are usually managed by humans, our focus regarding domestics centres on their habitat selection patterns and ecosystem impacts when they are able to roam into the forest, rather than on their recovery dynamics. So far, knowledge about the habitat preferences of domestic animals are scarce and studies focus more on pastoralist settings where animals are more mobile and free in selecting their habitat (Butt, 2010; Feldt & Schlecht, 2016; Schlecht et al., 2006, 2009). As expected, in our study, agriculture was the most frequently exploited habitat by domesticated vertebrates. However, we showed that free-ranging domestic vertebrates have access to forest environments and also choose to spend time there. This could be of importance considering their ecological impact on tropical forests by their foraging behavior, trampling on vegetation, or depositing nutrients with dung (Aarons et al., 2009; Bloor, 2015; Williams & Haynes, 1995) or urine (Clay et al., 2015). Biomass of domestic vertebrates followed a pattern opposite to wild vertebrates with the highest values in agriculture and fell into much higher range sizes. Globally, the estimated biomass of domesticated mammals is more than 30 times higher than that of terrestrial mammals, with cattle contributing most to total mammal biomass (Greenspoon et al., 2023), which is also the case in our study area with substantially higher biomasses of domestics than of wild vertebrates.

4.5 | Habitat specialization and indicator species

The species-habitat networks revealed a low degree of specialization for all three vertebrate groups which hints to a low specificity of old-growth forests along with the lack of indicator species for these. These findings support the assumption that regenerating forests may be similar habitats for vertebrates after 20–38 years. We did not identify individuals based on camera trap photos since it was not possible for all captured species, but we assume that the individuals move between the different land-use categories and use them concurrently suggesting a high habitat connectivity in our study area. The high habitat connectivity is demonstrated, for example, in detecting *Panthera onca* (Jaguar) in both forest regeneration categories and old-growth forests as well as of *Puma concolor* (Cougar) in agriculture, late recovery forest, and old-growth. Both cats have large home ranges (Nuñez-Perez & Miller, 2019) that far exceed the sizes of patches in the different land-use categories in our study area or even the whole study area. Our results show that apex predators are still present in our study area, which bears the risk of human/wildlife conflicts. *P. concolor*, for example, was captured at night on a pasture plot that has been used by humans and domestic animals the day before (Figure 2c–f). Main sources of conflicts between humans and felids are predation on livestock and attacks on people which can cause retaliatory killing of felids by humans (Inskip & Zimmermann, 2009). For example, a study based on interviews of local people in our study area about the perceived harm by *P. onca* for livestock or humans revealed a general low perception of harm (Álvarez & Zapata-Ríos, 2022). However, when attacks on livestock by *P. onca* occurred, people killed the animal in more than half of the cases.

4.6 | Limitations and outlook

While our research delivered further insights about recovery patterns and habitat selection, several methodological limitations remain that were beyond the scope of our methodologies. For example, we found a much lower number of species and little species overlap when comparing our results with data derived from sound recorders, that were placed on the same plots at the same time (Müller et al., 2023). This can be explained by methodical reasons, as our camera trap approach is suitable only for capturing animals that live or forage on the ground, explaining the absence or low frequency of flying or canopy-dwelling animals. For example, flying birds such as toucans were frequently reported in the sound data, but are underrepresented in our study as they forage in the canopy and rarely move to lower strata. This also applies to mammals frequently observed in our study area, such as canopy-dwelling primates (only one recording in this study). In addition to the limitations of camera traps, this study only covers one season neglecting intra-annual variation and our chronosequence comprises comparatively short regeneration times. Future studies in our study area covering more seasons could give better insights into the development of secondary forests when regeneration ages increase. Another remaining question is the impact of vertebrate biomasses on forests with different ages. Here, we delivered first insights into the distribution of biomass along a recovery gradient, but the consequences and possible negative implications need further investigations.

5 | CONCLUSION

The results of our analyses delivered evidence to answer our initial hypotheses. (1) We showed that wild mammals, primarily expected in old-growth forests, also use regenerating forests and agricultural land reaching old-growth levels of species diversity (q0 and q1) in late regeneration forests. The comparable short regeneration times of 20–38 years in our study area appears to be sufficient to restore habitat for many vertebrate species. Our results can be mainly explained by the high connectivity between the habitats with different restoration times and close distances to the next old-growth forest. This suggests a high regeneration potential for landscapes with comparatively low anthropogenic disturbances by patchily distributed small-scale agriculture. (2) Our results showed that the differentiation of wild mammals and birds can be useful when analyzing vertebrate communities, as demonstrated by different patterns of species diversity (q0 and q1) and biomass. (3) We did not detect indicator species for old-growth forests which indicates a low specificity of old-growth. (4) Our results delivered insights into the habitat preferences of domestic vertebrates, showing that they are not only dominant in agricultural land, but that they have access to forests, which could potentially impact these ecosystems due to their presence and often high biomasses.

We conclude that our study delivers evidence for the importance of remaining old-growth forests but also for recovering forests for the preservation and restoration of biodiversity, which should be considered in conservation efforts, for example, when prioritizing areas for the establishment of protected areas.

AUTHOR CONTRIBUTIONS

Nina Grella was involved in formal analysis, investigation, data curation, writing—original draft, and visualization. Heike Feldhaar was involved in writing—review and editing, supervision. Jörg Müller was involved in conceptualization, formal analysis, writing—review and editing, and supervision. Christian Fiederer, Marco Heurich, Felicity L. Newell, and Karen Pederson were involved in writing—review and editing and formal analysis. Nico Blüthgen, Annika Busse, Ana Falconí-López, Maria de la Hoz, Peter Kriegel, Marcel, Pühls, Dominik Rabl, Martin Schäfer, Sebastian Seibold, and Constance J. Tremlett were involved in fieldwork, writing—review and editing. David A. Donoso was involved in writing—review and editing.

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CONFLICT OF INTEREST STATEMENT

No potential conflict of interest was reported by the authors.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in the Dryad Digital Repository: 10.5061/dryad.bnzs7h4mj

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