



RESEARCH ARTICLE

Environmental correlates of richness, community composition, and functional traits of terrestrial birds and mammals in a fragmented tropical landscape

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Received: 1 December 2019 / Accepted: 15 September 2020 / Published online: 21 September 2020
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Abstract

Context Tropical forest loss and fragmentation and the associated loss in species diversity are increasing in both magnitude and scope. Much attention has been paid to how attributes of forest fragments, such as area and forest structure, impact the diversity and functional composition of vertebrate communities, while more recent work has begun to consider the importance of landscape-level variables, such as surrounding tree cover. Yet, the relative impacts of these factors on species diversity and functional composition remain unclear, particularly among under-studied taxonomic groups.

Objectives We quantified how species richness, community composition, and functional traits of terrestrial birds and mammals are associated with variation in fragment area, elevation, habitat structure and surrounding tree cover. Our goal was to determine the degree to which these diverse explanatory variables contribute to species diversity.

Methods We used motion-activated camera traps to sample terrestrial birds and mammals in 22 forest fragments in northwestern Ecuador. We used a hierarchical multi-species occupancy model accounting for imperfect species detection to estimate species richness and species composition differences among fragments, weighted multiple regression and distance matrix regression to assess covariates of richness and composition, and an RLQ ordination to assess covariation of environmental conditions and species traits.

Results Terrestrial mammals and birds exhibited similar relationships to key environmental variables, but also showed guild-specific differences. Elevation

Rachel N. Cook and Tadeo Ramirez-Parada contributed equally to this study.

Electronic supplementary material The online version of this article (<https://doi.org/10.1007/s10980-020-01123-4>) contains supplementary material, which is available to authorized users.

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was significantly associated with differences in species richness and community composition for both groups. Forest cover in the surrounding matrix was associated with higher species richness and changes in community composition in mammals, but not terrestrial birds. Canopy openness showed a positive association with mammalian species richness but no relationship with bird species richness. There was no association between density of large trees and richness for either group. We found no significant associations between environmental variation and functional composition among forest fragments.

Conclusions This work highlights the general importance of elevation and forest cover in shaping patterns of species diversity and composition in forest fragments and suggests heightened sensitivity to matrix conditions in mammals relative to terrestrial birds.

Keywords Agricultural matrix · Camera trap · Chocó biogeographic zone · Imperfect species detection · Multi-level occupancy modeling · RLQ analysis

Introduction

Habitat loss and fragmentation are among the leading causes of global species decline today (Pimm and Raven 2000; Newbold et al. 2015). These phenomena are particularly pronounced in the tropics (Brinck et al. 2017), which contain about two-thirds of all known species (Pimm and Raven 2000) but have experienced extensive habitat modification due to human activities like agriculture and timber extraction (Gibson et al. 2011). These processes have resulted in isolated patches of remnant or regenerating forest fragments separated by cleared land. Resolving the ways in which features of these modified landscapes influence patterns of terrestrial vertebrate diversity, community composition, and functional traits remains a priority of landscape ecology and conservation biology.

Studies that focus solely on patch-level attributes of fragments such as habitat structure or area often fail to predict diversity (Brady et al. 2011) because they do not include properties of the surrounding matrix (Dunning et al. 1992; Şekercioğlu et al. 2002; Pardini 2004; Harvey et al. 2006; Hawes et al. 2008;

Tscharntke et al. 2008; Mendenhall et al. 2014). Increased forest cover in the matrix may provide more resources and habitat, serving to increase functional connectivity between forest fragments (Uezu et al. 2005; Harvey et al. 2008) by decreasing habitat isolation and enabling greater mobility (Taylor et al. 1993; D'Eon et al. 2002; Newbold et al. 2014). At the same time, however, species' occurrences are also likely to be shaped by pre-existing environmental factors such as elevational gradients (Montaño-Centellas and Garitano-Zavala 2015). Reconciling the relative importance of these various factors requires simultaneous evaluation of the effects of area, habitat structure, surrounding forest cover and elevation while accounting for imperfect species detection—the inability to detect a species even if it is truly present in a habitat (Lasky et al. 2016; Zimbres et al. 2018).

Most research to date has focused on a few particularly well-studied taxonomic groups such as understory birds (Daily et al. 2001; Şekercioğlu et al. 2002; Hawes et al. 2008; Vetter et al. 2010; Powell et al. 2015), warranting further research on these relationships among relatively understudied groups, including terrestrial vertebrates. Terrestrial vertebrates may be particularly sensitive to habitat loss and fragmentation due to heightened predation risk, loss of critical microhabitat niches and limited dispersal from source to sink populations (Şekercioğlu et al. 2002; Cleary et al. 2007; Stratford and Stouffer 2015). Still, the impacts of fragmentation may vary among guilds of terrestrial vertebrates due to differences in species functional traits such as body size and diet (Vetter et al. 2010). For example, studies suggest that terrestrial birds, especially insectivores, may be highly sensitive to fragment area (Şekercioğlu et al. 2002) and habitat structure (Cleary et al. 2007). Terrestrial mammals, on the other hand, may frequently venture into the matrix and thus may be more influenced by tree cover surrounding fragments (Pardini 2004; Garmendia et al. 2013, but see Zimbres et al. 2018). However, the small number of studies on terrestrial taxa to date make it difficult to draw broad inferences about predictors of terrestrial vertebrate persistence in fragmented tropical landscapes.

Along with better-studied indices of diversity, there is a strong need to resolve how terrestrial vertebrate functional traits influence their response to environmental changes such as landscape fragmentation. Simultaneously evaluating the effects of

fragmentation on community-level metrics, such as richness and composition, with functional trait analyses may increase our understanding of how terrestrial vertebrate species are likely to respond to changing environmental conditions (Henle et al. 2004). Furthermore, doing so may increase our understanding of the consequences of biodiversity change for ecosystem functioning (Larsen et al. 2005; Soliveres et al., 2016; Carlucci et al. 2020). RLQ analysis is an ordination technique that can help researchers gain a deeper understanding of the relationship between variation in functional composition of animal communities and environmental conditions across the landscape (Dolédec et al. 1996). Nevertheless, this is still a relatively underutilized technique (Dray and Legendre 2008), and there is a need for more studies exploring how species traits influence their responses to environmental change (Lasky et al. 2016), particularly in human-modified landscapes (Bregman et al. 2014).

In this study, we employed motion-activated camera traps in a fragmented landscape to characterize how species richness, community composition and functional traits (i.e., body length, diet specialization, and habitat specialization) of terrestrial birds and mammals vary in response to area, elevation, habitat structure (i.e., density of large trees and canopy openness) and surrounding forest cover. Our *a priori* hypothesis was that elevation, a common determinant of species richness and composition across a wide range of taxa (McCain 2004; Montaña-Centellas and Garitano-Zavala 2015; Walter et al. 2017b;) would be negatively associated with both mammal (McCain 2004) and bird species richness and composition (Montaña-Centellas and Garitano-Zavala 2015; Walter et al. 2017b). Based on patterns from other studies, we predicted that richness and community composition of birds (Walter et al. 2017a) and mammals (Pardini 2004) would be positively correlated with surrounding forest cover. To the extent that body size reflects dispersal ability (Şekercioğlu et al. 2002; Garmendia et al. 2013), we predicted that the relationship between forest cover and median body length would be negative for both birds and mammals, as small-bodied mammal and bird species might be more dispersal-limited and might increase in frequency in areas with greater connectivity among fragments. We also predicted that terrestrial birds would respond positively to fragment area, due to

more limited dispersal capacity through the matrix (Şekercioğlu et al. 2002) compared to mammals (Garmendia et al. 2013). On the other hand, a negative association was projected for presence of larger trees and canopy openness among terrestrial birds, especially those with specialized diets due to their greater sensitivity to microhabitat features (Harvey et al. 2006; Cleary et al. 2007; Gibson et al. 2011; Stratford and Stouffer 2015).

Materials and methods

Study site and sampling design

We conducted our study in and around the 120,000 ha Mache-Chindul Ecological Reserve (REMACH) in Esmeraldas Province, Ecuador from August to December 2014. The area is part of the relatively poorly studied Chocó Biogeographic zone—an area of global conservation priority that has experienced intense habitat modification in recent decades (CEPF 2018). REMACH contains a coastal mountain range separated from the Andes by a coastal plain; elevations range from sea level to 700 m a.s.l. Rainfall varies from 2500–3500 mm annually, with the rainy season typically occurring between January and June (Clark et al. 2006). The site has and continues to experience high deforestation rates; 10% of the remaining forest was cleared between 2000 and 2008 (Van Der Hoek 2017). Within REMACH, the 3500 ha Bilsa Biological Station (BBS) represents the largest continuous patch of intact forest. The matrix surrounding our study fragments is composed primarily of pasture, cacao and other crops.

Camera traps were used to sample terrestrial birds and mammals across 22 forest fragments ranging in size from 2.67 to 46.42 ha (Fig. 1). Motion-activated camera traps, when combined with hierarchical multi-species occupancy models that account for imperfect detection, offer a powerful and robust sampling method for studies on faunal diversity, especially secretive and nocturnal species (Rovero et al. 2014). We considered a species to be present or absent within a fragment based on camera footage. Though this approach does not reflect relative abundances within each fragment, it does circumvent the potential bias of double counting individuals within a fragment. Fragments were chosen to minimize the correlation

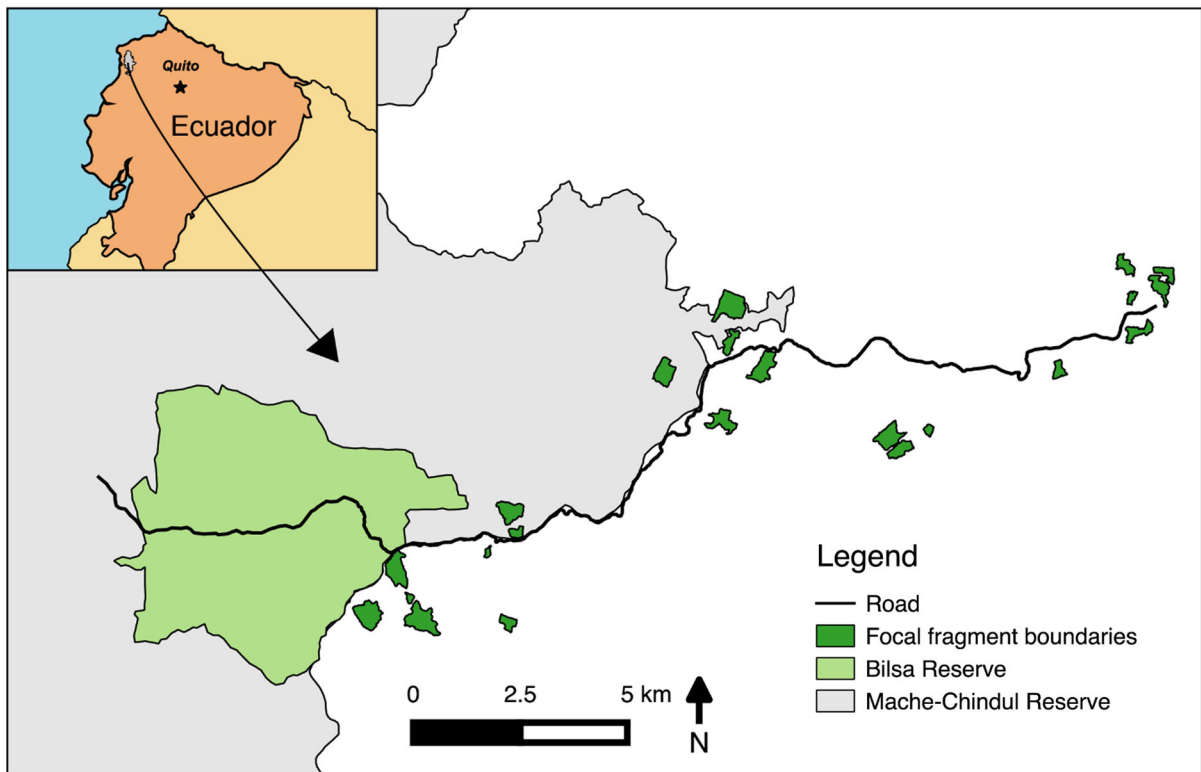


Fig. 1 Overview of study area and sampled forest fragments in northwest Ecuador. Inset shows location of Mache-Chindul Reserve within Ecuador. Dark green area shows the 22 focal forest fragments sampled for terrestrial mammals and avifauna

in this study. Light green shows the area of Bilsa, the largest tract of continuous forest in our study area. The map does not depict unsampled forest fragments in the study area

between elevation and fragment size. We defined terrestrial avian species as those known to be obligate ground foragers following Ridgley and Greenfield (2001); for example, all members of the genus *Sclerurus*. Nesting behavior for many species in this study is unknown. For mammals, we included species known to spend a substantial portion of their time on the ground following Tirira (2017); for example, the central American agouti (*Dasyprocta Punctata*).

Camera placement

Within each fragment, we established a 500 m \times 5 m linear transect following the protocol described in Browne and Karubian (2016). Transects began at the edge of each forest fragment and continued inward towards the center, which permitted sampling of both edge and core habitats. For a few smaller fragments where a 500 m transect would not fit within the fragment ($n = 5$), we divided sampling into parallel

transects separated by at least 50 m ($n = 2$) or reflected the transect back towards the center upon reaching the opposite edge ($n = 3$). Along each transect, we placed 9 motion-activated camera traps (either Browning Strike Force Trail Camera or Bushnell Trophy Cam HD) at roughly 60 m increments (0, 60, 120, 180, 240, 300, 360, 420, 480 m), with the first camera located near the edge of the fragment. There was some variation in camera placement (± 10 m) because there was not always an ideal location to attach the camera at the 60 m mark along the transect. Ideal locations were those that provided an appropriate field of view and appeared to be potentially frequented by animals (Rovero et al. 2013). Cameras were placed 10–50 cm above the ground and were typically attached to trees. We removed small amounts of vegetation directly obstructing the camera view, taking care to minimize disturbance to the site. We set the cameras to take video footage ranging in duration from 10 to 30 s depending on camera model

and whether footage was taken during the day or night. We left the cameras in each fragment for an average of 15.4 days (range: 1.36–21.99), with 4–5 fragments concurrently sampled at any given time. Cameras occasionally malfunctioned or stopped recording, so we truncated sampling periods from these cameras to the time when the last video was taken. These methods yielded a total of 1783 videos of our target species across 2972 camera trap sampling days. For each video, we identified each animal to the lowest taxonomic level possible following Tirira (2017) and Ridgley and Greenfield (2001), achieving species-level identification in most instances. We excluded detections of rat and mice species from analyses ($n = 794$ videos excluded) because video quality was insufficient for species-level identification for these groups (Srbek-Araujo and Chiarello 2005, Ahumada et al. 2013). A distribution of cumulative sampling effort across fragments in our study is provided in Figure S1.

Habitat sampling

Patch area and elevation

We estimated fragment area by manually walking the borders of each fragment and mapping the boundaries in QGIS (QGIS Development Team 2012). We estimated fragment elevation as the average of elevation measurements taken with a handheld GPS within each transect sub-plot (see below). Importantly, among our sampled fragments, elevation was strongly correlated with distance to Bilsa Biological Station (BBS) ($r = -0.94$) the largest expanse of contiguous forest within REMACH. We prioritize elevation over distance to BBS in all analyses due to the vast body of work supporting the role of elevation in driving patterns of species richness (McCain 2004; Walter et al. 2017b) and community composition (Montaño-Centellas and Garitano-Zavala 2015).

Habitat structure

Within each fragment, we quantified canopy openness and density of large trees. We chose to include these measures because they have proven important for other species in this system (Walter et al. 2017b) and are known to influence patterns of diversity for our target species. We visually estimated canopy openness

in each of $n = 100$, 5×5 m subunits along each 500 m transect. At each subunit, we categorized the canopy above it as open ($> 66\%$ open), partially open (33–66% open), or closed (0–33% open), and assigned it a corresponding score of 1, 0.5 or 0 respectively. All 100 subunits along the transect in each fragment were then averaged to obtain a continuous canopy openness index across the entire fragment ranging from 0 (all plots within a fragment categorized as closed) to 1 (all plots within a fragment categorized as open). We estimated the density of large trees by counting the number of trees with a diameter at breast height (DBH) greater than 50 cm within each 5×5 m subunit along each transect and again averaged across all 100 subunits within each fragment to obtain a fragment-level estimate.

Surrounding forest cover

To estimate tree cover surrounding each fragment, we quantified total available forest habitat in 2013 using the Global Forest Change dataset (Hansen et al. 2013), which is the best available map of contemporary forest cover in our study area, following the methods detailed in Browne and Karubian (2016). The most recent baseline information of forest cover in our area by Global Forest Change dataset is from 2000, after which only information on forest loss through 2013 is available. Across our study area, we classified each 30×30 m grid cell as forest if the estimated proportion of tree canopy cover in 2000 was $> 95\%$, or else the grid cell was classified as non-forest. We then used the Global Forest Change dataset on forest loss in the 2000–2013 period to convert grid cells that experienced forest loss during this time period to non-forest. From there we calculated the proportion of grid cells classified as forest within circular plots of varying radii extending from the center of each study fragment.

Because we had no a priori information to know the spatial scales at which surrounding forest cover was more likely to affect species richness and composition, we selected the spatial scale for analysis by comparing the magnitude of the variance inflation factors (VIFs) and AIC scores from species richness GLM models including forest cover at different radii of 500, 1000, 1500, 2000, and 2500 m and multiple matrix regressions for community composition. These models accounted for fragment area, elevation, mean canopy

openness, and the density of large trees in each fragment. For mammals, we selected the forest cover radii yielding the model with lowest AIC score among models with maximum VIFs equal to or less than 3 (following Zuur et al. 2010). For birds, all forest cover radii generated nearly identical AIC scores (i.e. Table S1), so we selected the radius that minimized collinearity among predictors (i.e., minimized the maximum VIF in the model). This scheme selected a radius of 2 km for mammals and 0.5 km for birds. These forest cover radii were preserved in all subsequent analyses.

Species traits

We derived a species traits table by using current information from Birds of the World (Billerman et al. 2020), Encyclopedia Britannica (2020) and the IUCN Red List (Version 2019-2). We focused on diet, body size and forest specialization. For diet, we classified species as either omnivore or not (i.e. to account for species with specialized diets). For body size, we categorize each species as having small, medium, or large body size based on the distribution of recorded body sizes among species of their corresponding guild within our sample. For forest specialization, we indicated whether a species was known to occur only in forest sites or in other types of habitat (such as pastures, plantations, wetlands, and shrublands).

Analysis

Estimation of species richness and compositional similarity

We derived estimates of species richness and compositional similarity for ground mammals and ground-foraging birds separately using a hierarchical multi-species occupancy model (Zipkin et al. 2010). This modeling framework overcomes the problematic assumption of perfect species detection by treating the occurrence of a species as an imperfectly observed latent variable determined by its probability of occurrence in a site (MacKenzie et al. 2002). Consequently, observed data are assumed to be generated by a Bernoulli process governed by the probability of detection of a given species in a site and its true, latent occupancy status. The multi-species occupancy model expands the single-species approach by incorporating

additional information generated by the detection record of multiple species in a community, providing simultaneous estimates of both occurrence and detection probabilities across species. Consequently, species-specific parameters are treated as random effects stemming from community-level ‘hyper-parameters’. In this way, the aggregate data of the entire community can be used to generate species-specific occurrence estimates, which is especially beneficial for rare species that ‘borrow strength’ from more abundant ones (model formulation detailed in Appendix S1; Zipkin et al. 2009, 2010; Burton et al. 2012). We used a Bayesian framework for statistical inference, and implemented the model using JAGS (Plummer 2003).

We treated each camera deployment in a fragment as a replicated survey and modeled the occurrence and detection probability components of the model using logistic regression. For each camera, a species was noted as detected if it appeared in the camera trap footage at least once during the camera’s deployment and noted as non-detected if it did not, which circumvents the chance of double-counting individuals. We originally aimed to model occurrence using covariates from all variables to be able to identify species-specific relationships. However, the relatively low number of species detected for both mammals and birds and their low detection probabilities yielded wide credible intervals for all predictor parameters. Consequently, we modeled occurrence using only species-level random intercepts, and detection probabilities using species-level random intercepts, as well as the start date and duration of each survey to control for temporal differences in sampling effort (see Appendix S1 for full model specification). Occupancy models assume ‘closed’ occupancy states (no patches become occupied or unoccupied by a species during the study period), independent probabilities of occupancy among sites, and homogenous detectability of species among sites (MacKenzie et al. 2002), assumptions rarely met fully by camera trap studies. In the case of our study, the relatively short period of sampling, the long distances between many of the fragments sampled, and the consistent criteria for camera trap placement among fragments should allow our design to approximate these assumptions reasonably well.

To obtain posterior distributions of species richness and composition similarity (see below), we extracted a total of 15,000 samples from 3 Monte Carlo Markov

Chains (MCMC) after a burn in period of 15,000 iterations. Finally, we verified chain convergence by assessing mixing in the chain traceplots, and by ensuring the Gelman-Rubin statistic ('R-hat') was < 1.1 for all estimated parameters (Kéry and Schaub 2011). All prior parameter distributions used in the model were weakly or non-informative (Appendix S1; see Tables S2–3 for detection probabilities).

Species richness analysis

For both mammals and ground-foraging birds, we assessed the relationship between species richness and our predictor variables using weighted multiple regression. We used the latent occupancy matrix estimated in each iteration of the occupancy model to generate a posterior distribution of richness estimates. We then set the mean of the posterior distributions for each fragment as a response. We regressed these richness estimates against area, elevation, canopy openness, surrounding forest cover, and density of large trees ($\text{DBH} \geq 50$), which were standardized to aid comparison of effect sizes (Schiezeth 2010) (mean = 0, SD = 1). To account for differences in the uncertainty of richness estimates across fragments, we used a weighted least squares (WLS) regression following the approach outlined by Tingley and Beissinger (2013), using the precision of the richness estimate produced by the occupancy model (the inverse of its variance) as a weight for each observation. Prior to conducting this analysis, we checked for collinearity among predictor variables and calculated variance inflation factors (VIFs) among all predictors included in the analyses, which were all < 2.4, well below the threshold of 3 suggested by Zuur et al. (2010). We tested for spatial autocorrelation in regression residuals using the Mantel test (Mantel 1967), finding no evidence of spatial autocorrelation for mammals nor birds (Mammals: Mantel $r = 0.04$, $p = 0.27$; Birds: Mantel $r = -0.05$, $p = 0.72$). Summary statistics and pairwise correlations for all environmental predictors are presented in Table S4 and Table S5 respectively.

Species composition

To assess the relationship between species composition of a fragment and our environmental covariates, we used a distance matrix regression approach

(Smouse et al. 1986), in which differences between fragments for all variables (ecological distances) are used as predictors of differences or similarities in species composition. To account for imperfect species detection in calculating patch similarities, we used the latent occupancy matrix derived from the multi-species occupancy model to calculate the Sørensen-Dice species similarity index (Sørensen 1948) in each iteration of the model. We then used the mean of the posterior Sørensen-Dice index distribution as the response in our analysis. Ecological distances for all predictors were centered and standardized to ease comparison of effect sizes.

Environmental variation and functional trait analysis

We examined patterns of co-variation between environmental variables and species traits through RLQ analysis (Dolédéc et al. 1996), a three-table ordination method that quantifies the common structure between a site \times environment dataset (R table) and a species \times traits dataset (Q table) using the abundance or presence/absence (as in this study) of species across sites as a link (L table). RLQ analysis yields an ordination plot whose first axis represents the dominant vector of the co-inertia between environmental variables and species traits, with successive axes summarizing the remaining co-correlation. This method enables the projection of sites, species, environmental vectors, and trait vectors into a common ordination space, allowing a qualitative assessment of patterns of co-variation between environmental factors and functional community composition (Dolédéc et al. 1996; Dray and Legendre 2008; Dray et al. 2014).

We included area, elevation, surrounding forest cover, canopy openness, and density of large trees as environmental variables. For birds, we considered body length, diet specialization, and forest specialization as species traits. For mammals, we included the same traits but excluded forest specialization, as only one of the mammal species detected in our survey was considered a forest specialist. Our sample resulted in few species in each category of forest specialization and diet specialization (Table 1). Therefore, in order to include these variables in the RLQ ordination, we transformed forest specialization into a binary variable indicating whether a species could only occupy forest or other habitats as well, and diet into a binary variable

Table 1 Species information for all terrestrial birds and mammals recorded in 22 forest fragments in northwest Ecuador

Species	Class	Diet	Body size	Forest specialization
<i>Lowland paca</i> (<i>Cuniculus paca</i>)	Mammal	Frugivore (specialist)	Medium (60–82 cm)	Forest only
<i>Central American agouti</i> (<i>Dasyprocta punctata</i>)	Mammal	Granivore	Small (41.5–62 cm)	Forests and gardens/plantations
<i>Nine-banded armadillo</i> (<i>Dasyprocta novemcinctus</i>)	Mammal	Omnivore (generalist)	Medium (76.2)	Forest, savanna, shrubland, grassland, gardens/plantations
<i>Common opossum</i> (<i>Didelphis marsupialis</i>)	Mammal	Omnivore (generalist)	Small (26–43 cm)	Forest, shrubland and gardens/plantations
<i>Tayra</i> (<i>Eira barbara</i>)	Mammal	Carnivore (opportunistic)	Medium (60–68 cm)	Forest and savanna
<i>Jaguarundi</i> (<i>Herpailurus yagouaroundi</i>)	Mammal	Carnivore	Medium (60–70)	Forest, savanna, shrubland, grassland
<i>Ocelot</i> (<i>Leopardus pardalis</i>)	Mammal	Carnivore (opportunistic)	Medium (70–90 cm)	Forest, savanna and shrubland
<i>White-nosed coati</i> (<i>Nasua narica</i>)	Mammal	Omnivore (generalist)	Large (73–136 cm with tail)	Mainly forest, some grassland
<i>Gray and black four-eyed opossum</i> (<i>Philander</i> sp.)	Mammal	Omnivore (generalist)	Medium (40–80 cm)	Forest, shrubland and gardens/plantations
<i>Crab-eating raccoon</i> (<i>Procyon cancrivorus</i>)	Mammal	Carnivore (specialist)	Medium (50–65 cm)	Forest and wetlands
<i>Red-tailed and western dwarf squirrels</i> (<i>Sciuridae</i> sp.)	Mammal	Granivore (specialist)	Small (12–16 cm)	Forest and urban areas
<i>Northern tamandua</i> (<i>Tamandua mexicana</i>)	Mammal	Insectivore (generalist)	Large (121.92 cm)	Forest and savanna
<i>Brown wood-rail</i> (<i>Aramides wolfi</i>)	Bird	Omnivore (fruits, seeds, insects)	Large (33–36 cm)	Forest only
<i>Orange-billed sparrow</i> (<i>Arremon aurantirostris</i>)	Bird	Omnivore (generalist)	Small (14.5–16.5 cm)	Forest and shrubland
<i>Bertelsch's tinamou</i> (<i>Crypturellus bertelschi</i>)	Bird	Omnivore (generalist)	Medium (28 cm)	Forest and heavily degraded former forest
<i>Little tinamou</i> (<i>Crypturellus soui</i>)	Bird	Omnivore (generalist)	Medium (20–24 cm)	Forest, shrubland and plantations
<i>Black-headed anthrush</i> (<i>Formicarius nigricapillus</i>)	Bird	Insectivore	Small (18 cm)	Forest only
<i>Ruddy quail-dove</i> (<i>Geotrygon montana</i>)	Bird	Omnivore (fruits, seeds, insects)	Medium (23–25 cm)	Forest and plantations
<i>Indigo-crowned quail-dove</i> (<i>Geotrygon purpurata</i>)	Bird	Omnivore (fruits, seeds, insects)	Medium (23–25 cm)	Forest only
<i>Olive-backed quail-dove</i> (<i>Geotrygon veraguensis</i>)	Bird	Omnivore (fruits, seeds, insects)	Medium (23–25 cm)	Forest only
<i>Scaled antpitta</i> (<i>Grallaria guatemalensis</i>)	Bird	Insectivore (Opportunistic)	Small (15–20.3 cm)	Forest and plantations
<i>Pallid/white-tipped dove</i> (<i>Leptotila</i> sp.)	Bird	Omnivore (seeds, fruits, insects)	Medium (23–31 cm)	Forest, shrubland, pastureland, heavily degraded former forest
<i>Scaly-breasted wren</i> (<i>Microcerculus marginatus</i>)	Bird	Insectivore	Small (11 cm)	Forest only
<i>Buff-rumped warbler</i> (<i>Myiothlypis fulvicauda</i>)	Bird	Insectivore	Small (12.7–15.3 cm)	Forest and wetlands
<i>Rufous-fronted wood-quail</i> (<i>Odontophorus erythrops</i>)	Bird	Omnivore (fruits, seeds, insects)	Medium (23–28 cm)	Forest only
<i>Scaly/thawny-throated leafhoppers</i> (<i>Sclerurus</i> sp.)	Bird	Insectivore (Opportunistic)	Medium (16.5)	Forest only
<i>Great tinamou</i> (<i>Tinamus major</i>)	Bird	Omnivore (fruits, seeds, some insects)	Large (43 cm)	Forest and heavily degraded former forest

indicating whether a species was omnivorous or specialized on plant or animal feeding. We include body length as a continuous variable, assigning the median value from the body size ranges for each species reported by the Cornell Lab of Ornithology's Birds of the World (Billerman et al. 2020).

Implementation of RLQ analysis requires preliminary ordination analysis of each component dataset. Accordingly, we performed Correspondence Analysis (CA) on the L table, and used the site and species weights of the CA to conduct Principal Component Analysis (PCA) on the R table and a Hill-Smith analysis for the Q table (Hill & Smith 1976), which contained both categorical and continuous species traits (Tables S6–8). Separate RLQ analyses were carried out for mammals and birds. Following Dray et al. (2014), we used the fourth corner statistic (Legendre et al. 1997) and two permutation models to assess global significance of the RLQ analysis and of the correlations of both environmental variables and traits with the axes of the RLQ ordination. Permutation model 2 tests the null hypothesis that the presence/absence of species (with fixed traits) is not affected by environmental variables (permutation of fragments: rows of R or L). Permutation model 4 tests the null hypothesis that species composition of fragments (with fixed environmental conditions) does not depend on species traits (permutation of species: rows of Q or columns of L). Simultaneously assessing significance of both these models (i.e., the null hypothesis that R or Q are not linked to L) has been shown to minimize the probability of type I errors (Dray and Legendre 2008, Ter Braak et al. 2012). We corrected for multiple hypothesis testing using the Holm-Bonferroni method (Holm 1979). RLQ, fourth corner, CA, PCA, and Hill-Smith analyses were implemented through the 'ade4' package version 1.7-15 in R (Dray and Dufour 2007; R Core Team 2020).

Results

Species richness

We detected a total of 12 terrestrial mammal species and 15 terrestrial bird species across the 22 sampled forest fragments, with a median estimated richness of 9 mammal and 7 bird species per fragment after accounting for imperfect detection (see Table 1 for a

full list of species). Our models accounted for a significant amount of variation in estimated species richness across fragments for both mammals (adjusted $R^2 = 0.75$, $p < 0.001$) and bird species (adjusted $R^2 = 0.41$, $p = 0.016$ for birds).

Elevation had significant positive effects on both mammal and bird species richness (Fig. 2a). An increase in elevation of 160 m (equal to 1SD) was associated with an average increase of 0.85 species for mammals and 1.05 species for birds. Fragment area showed a marginally significant positive relationship with avian species richness, with increases of 9.9 ha (1SD) resulting in an increase of 0.77 species in a fragment (Fig. 2b), while mammalian richness showed no significant associations.

Surrounding forest cover was significantly associated with increases in mammal species richness but did not have a significant effect on bird species richness across fragments for any available forest cover radius (Fig. 2c, Table S1). For mammals, an increase of 16% in surrounding forest cover at a 2 km radius (1SD) was associated with an average increase of 0.60 species per fragment (Fig. 2c). Canopy openness showed a positive relationship with mammalian species richness, with an increase of 0.04 in canopy openness index (1SD, on a unitless scale from 0–1) associated to average increases of 0.44 species, but we detected no significant associations with avian species richness (Fig. 2d). We did not detect significant effects of density of large trees on species richness for either group (Fig. 2e).

Community composition

The multiple matrix regression on habitat characteristics explained a significant amount of variation in terrestrial mammal and bird community composition (Table 2, Mammals: $R^2 = 0.27$, $p = 0.001$; Birds: $R^2 = 0.19$, $p = 0.003$). Differences in elevation predicted changes in community composition among fragments for both mammal and bird communities but with an effect size of twice the magnitude for birds within the range of our data (Table 2). Differences in surrounding forest cover were associated with significant differences in community composition for mammals, but not birds. For mammals, differences in forest cover were associated with changes in community composition of nearly twice the magnitude of those associated with differences in elevation.

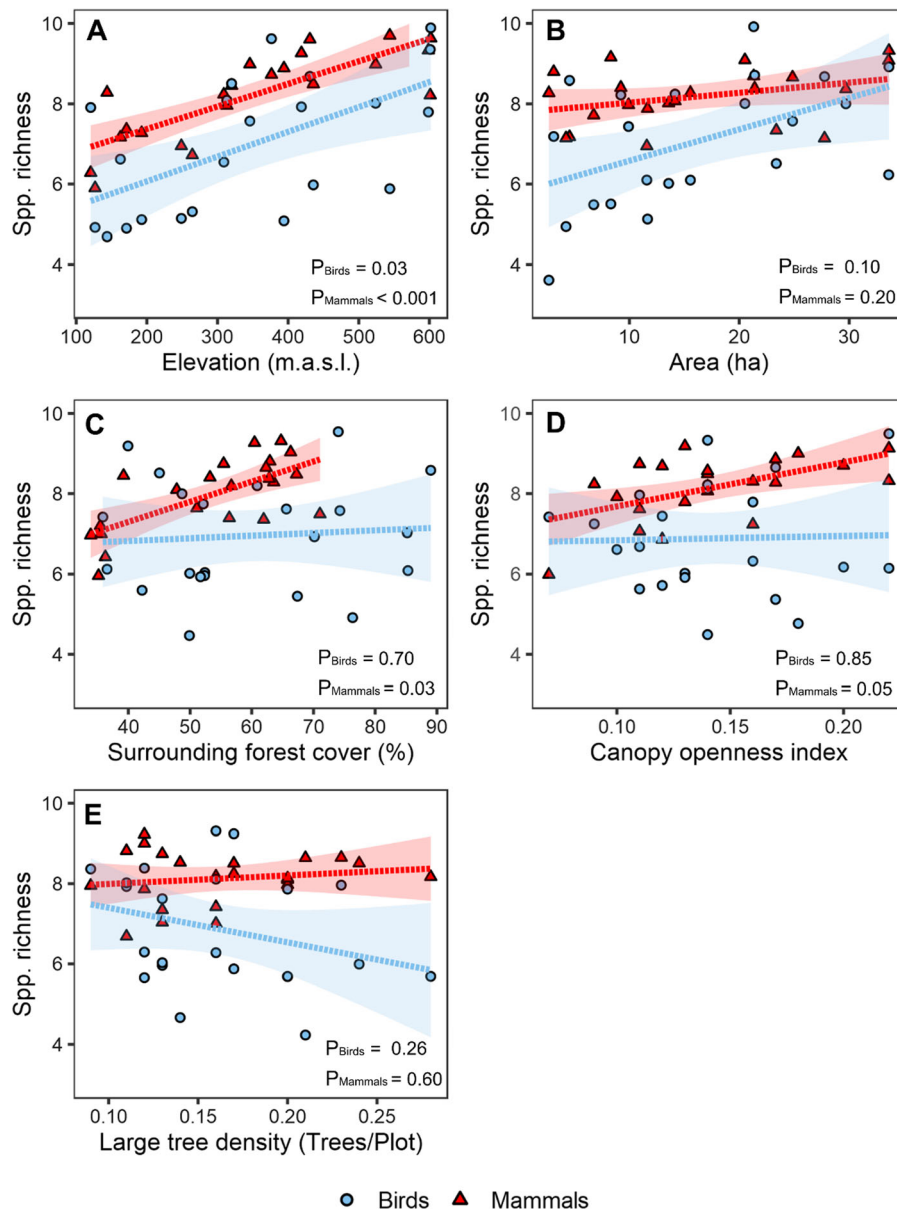


Fig. 2 Conditional plots from a multiple regression model of terrestrial bird and terrestrial mammal spp. richness (blue and red respectively) vs environmental variables in 22 rainforest fragments in the Chocó biogeographic zone, northwestern Ecuador (Mammals: Intercept = 8.21, adjusted $R^2 = 0.75$,

$F = 13.42$, $p < 0.001$; Birds: Intercept = 7.79, adjusted $R^2 = 0.41$, $F = 3.91$, $p = 0.017$). The forest cover radius used for mammals was 2 km, whereas that used for birds was 0.5 km (see “Materials and Methods” section)

Environmental conditions and functional community structure

For mammals, the first axis of the RLQ ordination identified a negative relationship between forest cover, area, and body length, indicating that increases in

surrounding forest cover and fragment area are associated with increases in the relative frequency of small-bodied species (Fig. 3a–c, Table 3). For birds, the first axis of the RLQ ordination was related to a similar degree to elevation, forest cover, fragment area, and elevation gradients and to shifts from

Table 2 Multiple matrix regression of similarities in terrestrial mammal and bird community compositions vs. environmental characteristics across forest fragments

The forest cover radius used for mammals was 2 km, whereas that used for birds was 0.5 km (see “Materials and Methods” section). Values in boldface are statistically significant at the $p < 0.05$ level

	Mammals		Ground foraging birds	
	Coefficient	p	Coefficient	P
Intercept	0.721	0.002	0.59	0.003
Canopy openness	0.011	0.32	− 0.006	0.63
Large trees	0.011	0.28	0.016	0.17
Surrounding forest cover	− 0.039	0.001	0.005	0.66
Area	0.009	0.294	0.004	0.71
Elevation	− 0.021	0.03	− 0.040	< 0.001
R^2	0.27		0.19	
F -stat	16.7		10.34	
p	0.002		0.004	

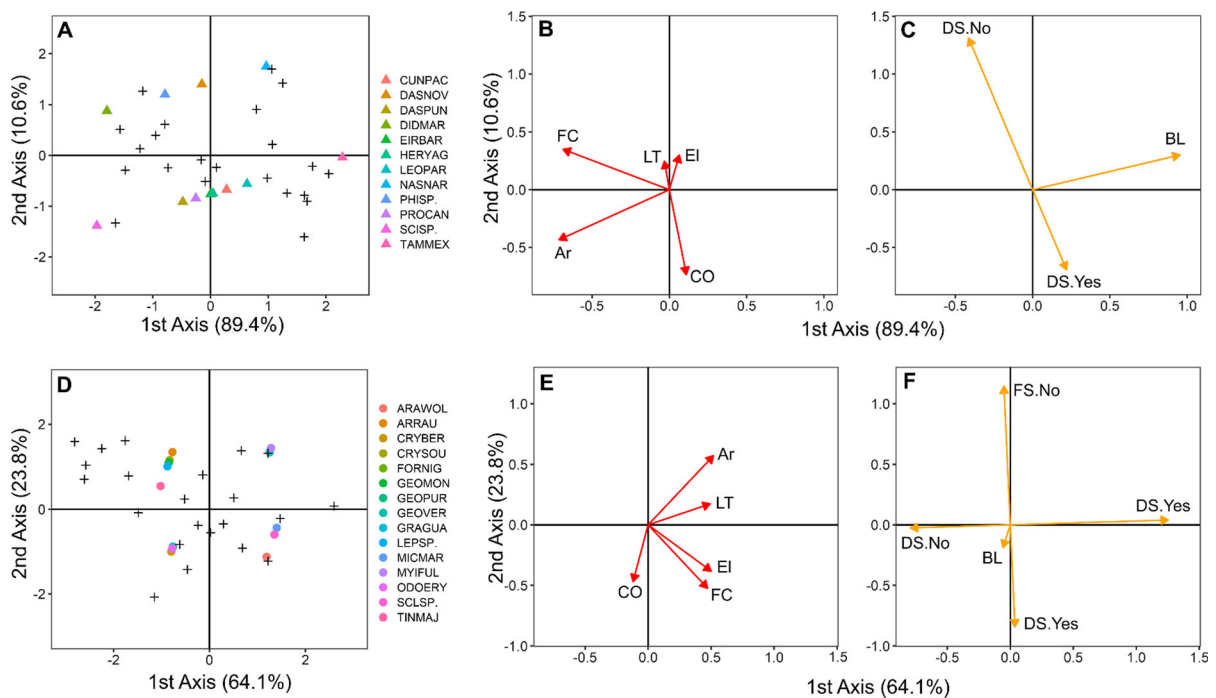


Fig. 3 RLQ ordination analyses of the relationship between environmental variables and species traits for 12 mammal and 15 ground foraging bird species (mammals: **a**, **b**, **c**; birds: **d**, **e**, **f**) across 22 rainforest fragments of the Chocó biogeographic zone, northwestern Ecuador. **a** and **d** show the projection of species (colored shapes) and fragments (+) along the first two axes of the RLQ ordination. **b** and **e** show the projection of elevation (*El*), forest cover (*FC*; 2 km radius for mammals, 0.5 km radius

for birds), area (*Ar*), density of large trees (*LT*), and canopy openness (*CO*) across forest fragments as vectors of environmental variation. **c** and **f** display vectors of trait variation among species corresponding to body length (*BL*), and diet specialization (omnivorous or plant/animal feeding only: *DS.Yes*, *DS.No*). The RLQ ordination for birds also included a binary forest specialization trait (*FS.Yes*, *FS.No*) indicating whether a species can occupy habitats other than rainforest

omnivory to greater diet specialization (Fig. 3d–f, Table 3). However, no relationships remained significant after accounting for multiple hypothesis testing for mammals or birds (Table 3). Accordingly, global significance tests for the RLQ ordination did not

support a general link between the environmental variables and species functional traits (Table 3).

Table 3 Fourth corner statistical tests of associations between environmental variables and species traits and RLQ ordination axes

Fourth corner statistical tests of associations between environmental variables and species traits and RLQ ordination axes	Stat	1st RLQ axis			2nd RLQ axis		
		Obs	P ₂	P ₄	Obs	P ₂	P ₄
Mammals							
<i>Environmental variables</i>							
Canopy openness	r	0.02	1.0	1.0	− 0.04	1.0	1.0
Large trees	r	− 0.01	1.0	1.0	0.01	1.0	1.0
Area	r	− 0.13	0.20	0.58	− 0.02	1.0	1.0
Forest cover	r	− 0.12	0.21	1.0	0.02	1.0	1.0
Elevation	r	0.01	1.0	1.0	0.02	1.0	1.0
<i>Traits</i>							
Body length (cm)	r	0.14	0.03	0.38	0.02	0.71	1.0
Diet specialization	F	0.25	0.60	1.0	0.60	0.30	1.0
		P ₂			P ₄		
Global significance		0.19			0.71		
Ground foraging birds							
<i>Environmental variables</i>							
Canopy openness	r	− 0.02	1.0	1.0	− 0.05	1.0	1.0
Large trees	r	0.09	1.0	1.0	0.02	1.0	1.0
Area	r	0.10	1.0	1.0	0.06	1.0	1.0
Forest cover	r	0.09	1.0	1.0	− 0.06	1.0	1.0
Elevation	r	0.10	1.0	1.0	− 0.04	1.0	1.0
<i>Traits</i>							
Body length (cm)	r	− 0.01	1.0	1.0	− 0.02	1.0	1.0
Diet specialization	F	2.24	0.11	1.0	0.00	1.0	1.0
Forest specialization	F	0.00	1.0	1.0	1.40	0.11	1.0
		P ₂			P ₄		
Global significance		0.37			0.83		

P values from permutation models 2 (permutations of fragments across environmental variables: P₂) and 4 (permutation of species across traits: P₄) are presented for both environmental/trait correlations with RLQ ordination axes and global significance tests. P values were corrected for multiple hypothesis testing using the Holm–Bonferroni method

Discussion

Forest cover and elevation were the strongest overall predictors of diversity and composition of terrestrial birds and mammals in a fragmented landscape in northwest Ecuador. In contrast, we found no significant associations between environmental and trait variation for mammal nor bird communities across fragments. Elevation showed a strong positive relationship with species richness and community composition in both mammals and birds. Surrounding forest cover had a strong positive relationship with species richness and was associated with changes in community composition among mammals, but not terrestrial birds, while fragment area was positively associated with species richness for terrestrial birds, but not mammals. In broad terms, these findings corroborate the widespread importance of elevation in

determining patterns of species richness and composition, and highlight how the effects of different environmental attributes such as surrounding forest cover and fragment area may vary among terrestrial birds and mammals.

Elevation has been found to be a strong driver of species richness in tropical regions (e.g., Montañó-Centellas and Garitano-Zavala 2015; Walter et al. 2017b; Quintero and Jetz 2018). Along our 480 m elevational gradient (from 120 to 600 m), species richness is positively correlated with elevation, which deviates from other studies reporting the opposite pattern (e.g., Visco et al. 2015) but may be consistent with a mid-elevation peak observed in other systems (McCain 2004; Quintero and Jetz 2018). Alternatively, higher rates of land conversion for agriculture at lower elevations in our study area may have pushed some ‘lowland’ species to shift their ranges upward.

Previous work in the same fragments studied here has documented heterogeneous relationships with elevation across guilds in this study area. As with terrestrial mammals and birds, palm tree (*Arecaceae*) richness and abundance increase with elevation, which also predicts palm tree community composition (Browne and Karubian 2016). Because palm fruits are an important food source for terrestrial mammals and birds (e.g., Smythe 1986; Zona and Henderson 1989; Peres 1994; Campos et al. 2012), increased numbers and diversity of these trees at higher elevations may contribute to the patterns we observe in the current study. In contrast, nocturnal birds exhibit the opposite relationship with elevation (Walter et al. 2017b), while large-bodied frugivorous birds (Walter et al. 2017a), understory birds (Durães et al. 2013), and orchid bees (Botsch et al. 2017) show no or weak relationships.

An important caveat when interpreting these findings is that, in our study system, elevation is highly correlated with distance to Bilsa Biological Station. At 3500 ha, Bilsa is by far the largest contiguous patch of forest in the area and has the potential to serve as a source population for many of the species included in the current study. In this case, proximity to Bilsa may help to offset some of the negative consequences of fragmentation by allowing establishment of diverse communities in otherwise inhospitable patches of remnant forest (Hanski and Gaggiotti 2004). We elected to focus on elevation for the current study because of its widespread importance but highlight that distance from this potential source population may also be playing an important role in the patterns we document here. Given the tight correlation between these two factors in our current data set, we were unable to ascertain the degree to which elevation vs. degree of isolation may be driving observed patterns. As such, a priority for future work in disentangling the effects of these two parameters by employing a study design capable of independently assessing elevation and distance to contiguous forest.

The significant effect of surrounding forest cover on community composition for mammals may be related to the fact that higher cover in the matrix can increase connectivity between forest patches (Uezu et al. 2005). Consistent with this idea, the RLQ ordination identified a positive, although not statistically significant, relationship between surrounding forest cover and the frequency of small-bodied mammal species. Moreover, trees in the surrounding

matrix might also provide important resources like food and shelter (Brady et al. 2011). Interestingly, we did not find the same relationship among terrestrial birds, although previous studies in the same fragments found a positive relationship between richness and surrounding forest cover among large (volant) frugivorous birds (Walter et al. 2017a).

Beyond these dominant relationships, patch area was associated with increases in richness in birds. Numerous studies since MacArthur and Wilson (1967) demonstrated an effect of increased patch size on species richness, particularly among species that are poor dispersers (Şekercioğlu et al. 2002; Bregman et al. 2014). The relationship between terrestrial bird richness and patch area might stem from relatively limited dispersal capacity in this guild, although this is not reflected in analyses of potentially dispersal-related functional traits (e.g. body length). Alternatively, it may also reflect differences in “habitat amount” between terrestrial birds and mammals (Fahrig 2013), given a forested matrix may be a suitable habitat for mammals (Garmendia et al. 2013) and rather inhospitable for dispersal-limited birds (Şekercioğlu et al. 2002). Resolving the movement and dispersal capacity of both terrestrial birds and mammals could help elucidate the mechanistic basis of these relationships, as well as the potential conservation trajectories of these taxa.

Canopy openness had a significant positive effect on mammal species richness, a pattern also exhibited by nocturnal birds (Walter et al. 2017a, b) and understory birds (Durães et al. 2013). In contrast, terrestrial birds exhibited no relationship, perhaps because any positive effect of increased solar radiation on resource availability may be balanced by negative effects on microenvironment. For example, Stratford and Stouffer (2015) found that increased canopy openness was associated with increased mid-story vegetation, which may contribute to food resource availability but may also serve as an impediment for terrestrial avian species due to an associated increase in leaf litter. Furthermore, increases in light intensity (Visco et al. 2015) and understory temperatures (Zellweger et al. 2020) associated with more open canopies may disproportionately impact terrestrial birds. More detailed work on the ecological and microenvironmental correlates of canopy openness would help to resolve between these alternatives.

Environmental variation among fragments was not associated with detectable changes in functional traits among bird nor mammal species. For variables that affected species richness and community composition across fragments, the lack of significant trait-environment relationships could indicate that species that are gained, lost, or turnover along environmental gradients might not significantly differ in the functional traits we assessed. However, considering the number of studies that have detected strong associations with environmental variables and species traits (Henle et al. 2004; Cleary et al. 2007; Bregman 2014), the lack of statistically significant associations in this study is more likely due to the relatively small number of species detected in our sample (12 mammals, 15 birds), the presence-absence nature of our occurrence data, and the use of coarse categorical traits that may have hindered our ability to detect significant signals in the data using RLQ ordination. Further studies analyzing a broader array of species and quantifying species abundance across fragments might be necessary to conclusively assess whether patterns of species gain, loss, and turnover among forest fragments are associated to non-random patterns of functional trait variation among mammals and terrestrial bird species.

Conclusion

This study contributes to our general understanding of the environmental correlates of diversity among terrestrial vertebrates while providing an important baseline for two understudied guilds in the Chocó biogeographic zone, a poorly known ‘hotspot’ for the conservation of biodiversity. Our results corroborate the importance of elevation in shaping species richness and composition and highlight the importance of maintaining sufficient tree cover in the matrix that surrounds fragments for the conservation of mammals, and potentially birds, in our system. We did not detect significant associations between functional traits and environmental variables among fragments, though further studies employing abundance data for each species and analyzing a broader range of taxa might produce meaningful associations. Overall, this study highlights the need for further work on understudied tropical taxa to better resolve how biogeographic factors such as elevation may intersect with

anthropogenic factors such as fragmented forest cover to shape contemporary patterns of diversity.

Acknowledgements We thank the Ecuadorian Ministry of the Environment and landowners in and around the Mache-Chindul Reserve for maintaining these forests and granting access. We also thank the Fundación para la Conservación de los Andes Tropicales (FCAT), particularly Domingo Cabrera, Luis Carrasco, Nelson Gonzalez, Monica Gonzalez and Jorge Olivo, and Scott T. Walter for logistical support. Funding was provided by the Conservation Food and Health Foundation; Conservation, Research and Education Opportunities International; Disney Conservation Fund; National Science Foundation (EAGER #1548548, DDIG #1501514, L.B. Graduate Research Fellowship); Ornithological Council; Tulane University; and the United States Fish and Wildlife Service Neotropical Migratory Bird Act (NMBCA #5605). We conducted work under permits from the Ecuadorian Ministry of the Environment (#010-2014-IC-FLO-FAU-DPE-MA).

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