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Sensitivity of tropical montane birds to anthropogenic disturbance and management strategies for their conservation in agricultural landscapes

Ian J. Ausprey^{1,2,3}  | Felicity L. Newell^{1,2,3}  | Scott K. Robinson^{1,2}

¹Florida Museum of Natural History, University of Florida, Gainesville, Florida, USA

²Department of Biology, University of Florida, Gainesville, Florida, USA

³Division of Conservation Biology, Institute of Ecology & Evolution, University of Bern, Bern, Switzerland

Correspondence

Ian J. Ausprey, Florida Museum of Natural History, University of Florida, 3215 Hull Rd, Gainesville, FL 32611, USA.

Email: iausprey@ufl.edu

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Abstract

Tropical montane bird communities are hypothesized to be highly sensitive to anthropogenic disturbance because species are adapted to a narrow range of environmental conditions and display high rates of endemism. We assessed avian sensitivity at regional and continental scales for a global epicenter of montane bird biodiversity, the tropical Andes. Using data from an intensive field study of cloud forest bird communities across 7 landscapes undergoing agricultural conversion in northern Peru (1800–3100 m, 2016–2017) and a pan-Andean synthesis of forest bird sensitivity, we developed management strategies for maintaining avian biodiversity in tropical countrysides and examined how environmental specialization predicts species-specific sensitivity to disturbance. In Peru, bird communities occupying countryside habitats contained 29–93% fewer species compared with those in forests and were compositionally distinct due to high levels of species turnover. Fragments of mature forest acted as reservoirs for forest bird diversity, especially when large or surrounded by mixed successional vegetation. In high-intensity agricultural plots, an addition of 10 silvopasture trees or 10% more fencerows per hectare increased species richness by 18–20%. Insectivores and frugivores were most sensitive to disturbance: abundance of 40–70% of species declined in early successional vegetation and silvopasture. These results were supported by our synthesis of 816 montane bird species studied across the Andes. At least 25% of the species declined due to all forms of disturbance, and the percentage rose to 60% in agricultural landscapes. The most sensitive species were those with narrow elevational ranges and small global range sizes, insectivores and carnivores, and species with specialized trophic niches. We recommend protecting forest fragments, especially large ones, and increasing connectivity through the maintenance of early successional vegetation and silvopastoral trees that increase avian diversity in pastures. We provide lists of species-specific sensitivities to anthropogenic disturbance to inform conservation status assessments of Andean birds.

KEYWORDS

agriculture, Andes, bird, countrysides, fragmentation, montane, sensitivity, tropical

Sensibilidad de aves montanas a perturbaciones antropogénicas y estrategias de manejo para su conservación en paisajes agrícolas

Resumen: Se ha hipotetizado que las comunidades de aves tropicales montanas son sumamente sensibles a la perturbación antropogénica porque las especies están adaptadas a una reducida gama de condiciones ambientales y tienen altas tasas de endemismo. Evaluamos

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la sensibilidad aviar a escalas regional y continental para un epicentro global de biodiversidad de aves montanas, los Andes tropicales. Utilizando datos de un estudio intensivo de campo de comunidades de aves de bosques nublados en 7 paisajes bajo conversión agrícola en el norte de Perú (1800 – 3100 m, 2016–2017) y una síntesis pan-Andina de sensibilidad de aves de bosque, desarrollamos estrategias de manejo para el mantenimiento de la biodiversidad de aves en campañas tropicales y examinamos cómo la especialización ambiental predice la sensibilidad de cada especie a la perturbación. Las comunidades de aves ocupando hábitats campestres tropicales en Perú contenían 29 – 93% menos especies en comparación con las de bosques y tuvieron una composición distinta debido a los altos niveles de recambio de especies. Los fragmentos de bosque maduro fungieron como reservorios para la diversidad de aves de bosque, especialmente cuando eran extensos y estaban rodeados por vegetación secundaria mixta. En las parcelas con actividad agrícola intensiva, la adición de 10 árboles silvopastoriles o 10% más de cercos por hectárea incrementó la riqueza de especies en 18 – 20%. Las insectívoras y frugívoras fueron más sensibles a la perturbación: la abundancia de 40 – 70% de especies declinó en la vegetación secundaria temprana y en la silvopastura. Estos resultados fueron sustentados por nuestra síntesis de 816 especies de aves montanas estudiadas en los Andes. Por lo menos 25% de estas especies declinaron debido a todas las formas de perturbación, y el porcentaje incrementó a 60% en paisajes agrícolas. Las especies más sensibles fueron aquellas con rangos altitudinales estrechos y extensiones de distribución pequeñas, las insectívoras y carnívoras y las especies con nichos tróficos especializados. Recomendamos la protección de fragmentos de bosque, especialmente los extensos, y el incremento de la conectividad mediante el mantenimiento de vegetación secundaria temprana y árboles silvopastoriles que incrementan la diversidad de aves en los pastizales. Proporcionamos listas de la sensibilidad de cada especie a la perturbación antropogénica para contribuir a las evaluaciones del estatus de conservación de aves Andinas.

PALABRAS CLAVE

Agricultura, Andes, aves, campo, fragmentación, sensibilidad, trópico

INTRODUCTION

Tropical montane forests lie at the frontlines of the global biodiversity crisis given that they are globally significant biodiversity hotspots and are under pressure from rapid human demographic expansion (Myers et al., 2000). The loss and fragmentation of forests coupled with human-induced climate change mean that montane biota face a future dominated by novel environmental constraints (Beniston, 2003). In the tropical mountains of Latin America, smallholder farmers are driving deforestation through shifting agriculture, in which large tracts of primary forest are converted to heterogeneous mosaics of disturbed remnant vegetation (Curtis et al., 2018). Determining the sensitivity of montane species to anthropogenic disturbance and identifying opportunities to maintain or restore key ecosystem features that promote biodiversity can inform management strategies to maintain biodiversity and human well-being throughout the tropics.

Neotropical montane birds are thought to be sensitive to anthropogenic disturbance because of their high rates of endemism, narrow elevational ranges, and specialized habitat requirements (Jankowski & Rabenold, 2007; Jankowski et al., 2013; Palacio et al., 2020). However, comprehensive assessments of species-specific sensitivity are lacking for the Tropical Andes Biodiversity Hotspot at local and continental scales. Such

assessments are needed to develop conservation assessment databases, such as those developed for North American avifauna (Partners in Flight, 2022), and to identify major predictors of disturbance sensitivity (Ausprey et al., 2022; Karp et al., 2019).

Maintaining forest bird diversity across tropical mountains requires identifying management strategies that embrace the mixture of biophysical gradients and anthropogenic disturbance regimes contributing to landscape heterogeneity in tropical montane ecosystems (Rahbek et al., 2019; Sarmiento, 2000). In particular, anthropogenic habitat conversion produces novel habitat configurations that reflect historical and contemporary socioeconomics (Fernandez et al., 2015). The Andes hosted advanced human civilizations for millennia preceding European contact and contain cultural landscapes reflecting the historical human footprint (Bush et al., 2015; Sarmiento, 2000; Sarmiento & Frolich, 2002; Valencia et al., 2010). Current policies encourage forest destruction as part of economic development (Saleth, 1991), producing a wide diversity of habitat elements common to agricultural landscapes or “countrysides,” such as forest fragments, early successional growth, and silvopasture (Hughes et al., 2002). Identifying management approaches that maintain or restore key habitat structures is critical for retaining biodiversity in tropical countrysides.

Understanding how tropical montane bird communities respond to anthropogenic disturbance is hampered by a lack of studies that survey communities over a full gradient of disturbance, report species-specific sensitivities to different types of disturbance, and synthesize species responses to disturbance across the Andes. We used intensive field surveys of cloud forest bird communities across 7 replicate cloud forest landscapes undergoing agricultural conversion in northern Peru to examine how remnant habitat elements associated with agricultural disturbance (forest fragments, early successional vegetation, fencerows, and silvopasture trees) contribute to the retention of avian diversity in tropical countrysides. We also determined species-specific sensitivities to different forms of agricultural disturbance and provide simple management recommendations for smallholder farmers and conservation practitioners interested in conserving avian biodiversity in agricultural landscapes. Second, we synthesized the literature on Andean forest bird communities inhabiting disturbed landscapes to develop species-specific sensitivities to different forms of anthropogenic disturbance for 816 species and test whether sensitivity is predicted by intrinsic factors indicative of environmental specialization, including range size, elevational range breadth, and dietary and foraging specialization.

METHODS

Field study design

We studied cloud forest bird communities along the forest–agricultural frontier of the Peruvian Andes in the department of Amazonas (5–7°S, 77–79°W) (Appendix S1.1). Although forest fragmentation has occurred since the agrarian reform of the 1970s (Saleth, 1991), contemporary deforestation remains high, with 3–6% forest lost since 2000 (Global Forest Watch 2019) (Appendix S1.2). Deforestation is driven by an elevated population growth rate ($\lambda > 1$) across the region (Peruvian National Institute of Statistics 2019) (Appendix S1.3) and the production of agricultural commodities, such as potatoes, vegetables, sugar cane, dairy products, and beef.

In this region, the cloud forest bird community changes compositionally along interacting elevational and agricultural land-use gradients. We selected landscapes of sufficient size and geographic position to act as independent replicates of agricultural land-use change spanning an elevational range of 1800–3100 m (mean annual temperature: 10–17°C; mean annual rainfall: 1000–1500 mm) (Newell et al., 2022). Specifically, in 2016–2017 we studied 7 landscapes (10-km² blocks >10 km apart) at approximately 200-m elevational intervals (Ausprey et al., 2022). We implemented a block impact–reference design to avoid confounding changes in species composition due to agriculture with rapid species turnover due to elevation (Morrison et al., 2008). Within each landscape, we stratified sampling among 4 habitat types in the same 300-m elevation band: contiguous mature forest connected to the Andean cordillera, isolated forest fragments, regenerating early successional forest, and agricultural matrix (silvopasture). Fragments

contained mature forest with little disturbance by humans or cattle and had been isolated for 15 to over 30 years based on analysis of Landsat imagery and conversations with local landholders. They were surrounded by a mix of shrubs, crop fields, and pasture and were generally within 2 km of contiguous forest (mean distance 972 m; range 90–2500 m). Early successional forests were regenerating pastures (15–30 years after abandonment) with dense stands of 2- to 3-m-tall saplings and few to no residual trees. Silvopasture was cattle pasture and crop fields that contained fencerows (1- to 2-m-wide belts of shrubby vegetation demarcating pasture boundaries) and relictual trees >10 cm DBH. In total, we sampled 46 sites: 7 contiguous forests and 29 forest fragments in all 7 landscapes, and 5 early successional forests and 5 silvopastures in 5 landscapes.

We quantified the bird community with 3 survey techniques to reduce detection error based on species-specific behavior: point counts, flock surveys, and mist netting. Our surveys were collectively designed to produce a near-complete inventory of the bird community in each target habitat type in the specified elevation band. We treated each forest fragment as a separate site because we were interested in examining the functioning of fragments as isolated habitat patches in an agricultural matrix. We further subdivided our analyses of silvopasture into 3 vegetation components in which bird detections were noted in the field: fencerows, pasture trees, and pasture. These represent pervasive and easily managed features of tropical countrysides. Surveys were conducted under University of Florida Institutional Animal Care and Use Committee protocol 201508764.

Bird surveys

We placed point-count survey points along transects at 100-m intervals in each site to maximize the number of points sampled in a given morning and increase detections of rare or infrequently vocalizing species. We randomly placed transects along existing trails because the terrain was steep and the understory was often dense and impenetrable. We surveyed 12 points along transects at all nonfragment sites, except, due to logistical constraints, for 1 forest site (9 points) and 1 early successional site (6 points). In fragments, the number of points was proportional to patch size (range 1–9) to maintain the same sampling effort per unit area and time as in other habitat types.

One experienced observer (I.J.A.) surveyed bird communities after spending 6 months in the region learning and practicing bird song identification. Additionally, we scanned audio recordings of surveys for any vocalizations missed in the field (recordings are deposited at the Florida Museum of Natural History). We surveyed each point 3 times during 1 of the 2 years and spaced surveys approximately 2 months apart to account for seasonal changes in vocalizations. Each count lasted 10 min and occurred during mornings with minimal rain or wind. We recorded all birds seen or heard, estimated distance in meters, and noted whether the detection was in the target habitat type. Singing activity declined precipitously or stopped altogether 2–2.5 h after dawn, and surveys were restricted to that

period to minimize variation in detectability. For point counts, we surveyed 323 points and amassed 17,989 detections of 194 species.

Following the conclusion of a point-count survey, we searched for flocks systematically along the same survey transect for an additional 2 h, recording all individuals in flocks. We recorded 105 flocks and detected 2877 individuals of 138 species.

We conducted mist netting surveys of understory species in the same area as the point-count routes for approximately 500 net hours in forest and early successional sites, and 250 net hours in fragments. Given the substantial logistical requirements of incorporating canopy nets at all sites, we restricted our sampling to the forest understory with standard 2-m-tall nets. Although data were collected as part of a long-term mark-recapture study, we only used data from 2016 to 2017. Forest and early successional sites were sampled using 2 arrays of 18 12-m nets, with each array sampled over separate 2-day visits in different locations. Fragments were sampled with 1 array over 2 days. We operated nets from dawn until 13:00. It was not logistically possible to mist net in silvopasture given active use by local communities (e.g., public trails, cows, horses, crops), and the simplified nature of vegetation in agricultural landscapes meant that we were unlikely to miss species during point-count and flock surveys. In 13,250 mist-net hours, we captured 2196 individuals of 173 species.

We conducted surveys from May to December in 2016 and 2017, which corresponded with the regional dry season and wet-dry seasonal transitions. We completed approximately half of the sampling in each year because the large-scale sampling effort across 7 replicate landscapes and multiple habitat types made it impossible for us to complete surveys in a single year. Although we recognize that species-specific abundance can vary interannually, the extreme shifts in community composition and species abundances we observed between forested and disturbed habitat types likely masked more subtle forms of temporal variation.

We assessed the effectiveness of our effort by calculating the sample coverage (SC) of each site. We used each point visit, flock encounter, and net day as repeated sampling efforts. SC was $\geq 90\%$ for all sites except 6 small fragments in which SC was $> 75\%$ (Appendix S1.4) (package iNEXT [Chao et al., 2014; Hsieh et al., 2022]). All analyses were conducted in R 4.2.1 (R Core Team, 2022).

Abundance modeling

We used multispecies hierarchical distance sampling models to estimate species-specific densities while accounting for imperfect detection based on the point-count data (Kery & Royle, 2015; Sollmann et al., 2016; Yamaura & Royle, 2017). As part of the model, the abundance of species i at site j (λ_{ij}) was modeled as a log-linear function incorporating covariates for habitat type (HAB), fragment size in log hectares (HA), and elevation (ELEV). We also included an offset to control for the number of points surveyed at each site (PTS). Forest was used as the

baseline (intercept; $\beta_{0,i}$) against which to compare abundances of species for all other habitat types ($\beta_{1,i}$):

$$\log(\lambda_j) = \beta_{0,i} + \beta_{1,i}\text{HAB}_j + \beta_{2,i}\text{HA}_j + \beta_{3,i}\text{ELEV}_j + \log(\text{PTS}_j). \quad (1)$$

We ran the model twice. Detections in silvopasture were pooled as 1 habitat category or separated into 3 components (fencerows, trees, and pasture), for a total of 4 and 7 habitat levels, respectively, for each model run. We implemented the model in a Bayesian framework with the function jagsUI (Plummer, 2003). See Appendix S5 for model details.

We ran single-species linear Poisson models for numbers of mist net captures or individuals in flocks. Forest was coded as the intercept, and habitat type, log fragment size, and elevation were included as covariates. We used log net hours or log number of points surveyed as offsets to correct for varying sampling effort (function stan_glm in package rstanarm [Goodrich et al., 2022]).

Species richness, diversity, composition, and beta diversity

We created regional species pools for each landscape by combining species lists generated across the 3 sampling methodologies. For each landscape, we calculated the proportion of species in each countryside habitat type relative to the forest site. We used species-specific densities based on the modeled point-count data to calculate diversity profile curves (i.e., Hill numbers) across the land-use gradient with the function div_profile in package hilldiv (Alberdi & Gilbert, 2019 [preprint]). We used only point-count data for diversity analyses requiring abundances because our hierarchical distance sampling model allowed us to interpret our results as densities rather than arbitrary indices of abundance (Gale et al., 2009).

We used nonmetric multidimensional scaling to visually inspect differences in species composition in ordination space based on Jaccard distance (stress = 0.12, function metaMDS in package vegan) (Oksanen et al., 2019). To quantify changes in species composition between mature contiguous forest and each countryside habitat type, we calculated Jaccard's index of dissimilarity and partitioned it into the 2 mechanistic processes of nestedness and species turnover (function beta.pair in package betapart [Baselga, 2010; Baselga & Orme, 2012]). We quantified species compositional changes based on occurrences across all sampling methodologies and for modeled densities from the point-count data.

Linear models

We calculated differences in alpha and beta diversity among countryside habitat types with linear mixed-effects models with habitat as a single categorical explanatory variable and landscape block as a random intercept to control for spatial autocorrelation within each landscape (function lmer in package lme4) (Bates et al., 2015). For analyses of fragments, we ran

additive models containing log fragment size and the combined log amount of forest and shrub cover within a 300-m radius of each fragment. This width was selected by ranking 20 linear models containing log patch size and log forest and shrub cover at increasing 50-m widths up to 1 km. The widest width best explained total species richness and Jaccard's dissimilarity between each fragment and forest when patch size in the top model set ($<2 \Delta AIC$) was 300 m (Appendix S1.5). Matrix forest and shrub cover was calculated via a supervised image classification analysis in ArcMap based on Sentinel-2 imagery from 2017 and our extensive experience with land-use practices at the study sites. We conducted all analyses of species richness for the full bird community and 5 dietary groups (insectivores, frugivores, nectarivores, granivores, and omnivores) and used R^2 values to assess the fit of all linear models.

Silvopasture microhabitats

We used data from the point-count surveys to examine fine-scale relationships between species richness and 2 forms of relictual vegetation commonly found in tropical countrysides: shrubby remnants, such as fencerows, and relict trees. Because species occurrence was likely spatially autocorrelated among consecutive points, we used multispecies spatial occupancy models to estimate species richness at each point-count location with the function `spMsPGOcc` in the package `SpOccupancy` (Doser et al., 2022). We ran 2 models: the shrub model included a covariate for the amount of shrub cover within a 50-m radius of the point-count location (digitized from high-resolution aerial photos taken the same year as the surveys) and the tree model included a covariate for the number of trees >10 m DBH counted in the field at each point-count location. Both models included elevation as a covariate to control for distributional changes related to elevation. We restricted the analysis to birds observed within a 50-m radius of the point-count center and used a full Gaussian process to account for spatial autocorrelation. We ran the models with default priors for 10,000 iterations across 3 chains with a thinning rate of 20. All parameters converged at $R\text{-hat} < 1.1$.

Species sensitivities

We categorized species-specific sensitivity to disturbance based on the results from the point count, mist-netting, and flock survey abundance models. We used habitat type beta estimates from Equation (1) to categorize sensitivity as negative (90% of posterior distribution <0), negative tendency (80% <0), positive (90% >0), or positive tendency (80% >0) (Appendices S2–S4). Remaining species were classified as having no sensitivity to disturbance or as having too few observations to make a determination ($n < 3$ total observations). We then compared sensitivity categorizations across the 3 sampling methods and

selected the categorization from the method with the largest sample size.

Andean synthesis

We systematically searched for publications on Andean forest bird communities in disturbed landscapes in Web of Science. We included only studies that reported species-specific occurrences in unfragmented mature forest and at least 1 type of anthropogenic disturbance at similar elevations or species-specific changes in abundance, occupancy, or occurrence between unfragmented mature forest and sites with anthropogenic disturbance based on statistical tests. We excluded studies from high-elevation *Pohlylepis* woodland, which is naturally patchy. We found 14 studies representing 816 species from Colombia, Ecuador, Peru (this study), Bolivia, and Argentina. Twelve studies provided occurrence data (797 species) and 8 reported statistical sensitivities (602 species) (Appendix S1.6) (Aben et al., 2008; Becker et al., 2008; Cresswell et al., 1999; Duraes et al., 2013; Edwards et al., 2017; Jones et al., 2021; Latta et al., 2011; O'Dea & Whittaker, 2007; Ramírez-Mejía et al., 2021; Renjifo, 2001; Santillan et al., 2019; Tallei et al., 2021; Valente et al., 2022). Search details and data treatment are in Appendix S5.

We compared species-specific occurrences and statistical sensitivities among studies and grouped species into 4 categories that reflected their sensitivity to disturbance: negative (species occurring only in forest in at least 1 study), positive (species occurring only in disturbed landscapes in at least 1 study), equal (species consistently found in forests and disturbed landscapes or showing no significant changes in abundance or occupancy), and uncertain (species showing negative or positive associations with disturbance across studies). We organized species into dietary groups (Wilman et al., 2014) and summarized sensitivities across all disturbance levels and for 3 habitat types (mature forest fragments, regenerating forest [early successional vegetation], and agriculture). We used logistic regression to test how 6 variables that quantify behavioral and environmental specialization predicted species-specific sensitivities (Ausprey et al., 2022; Soto-Saravia et al., 2021): global range size (Tobias et al., 2022), elevational range breadth (Quintero & Jetz, 2018), extent of insectivorous and carnivorous diets, and breadth of foraging strata and diet (Wilman et al., 2014) (function `glm` [R Core Team, 2022]). Because global range size and elevation range breadth were partially correlated ($r = 0.41$), we extracted the residuals from the regression of $\log(\text{elevation}) \sim \log(\text{range}) + \log(\text{range})^2$. These represented the extent that species had wider or thinner elevational ranges than expected given their global range and reflected the relative influence of environmental factors associated with elevation, such as rapid changes in temperature and habitat structure (Appendix S1.7). We used Bird Life International's definition of *endemism* (global range size $<50,000 \text{ km}^2$) to identify geographically range-restricted species.

All datasets are available at Figshare (Ausprey & Newell, 2023).

RESULTS

Species richness and diversity

Species richness declined on average by 20–93% across the agricultural land-use gradient. Forests had the largest number of species across taxa (mean richness = 89), followed by early successional forests (mean richness = 71), fragments (mean richness = 50), silvopasture (mean richness = 48), fencerows (mean richness = 27), pasture trees (mean richness = 33), and pasture (mean richness = 6) ($R^2 = 0.84$) (Figure 1a; Appendix S1.8). This pattern largely held for insectivores, frugivores, and omnivores (Appendix S1.9). Nectarivores were equally rich in forests and successional vegetation, and all human-modified habitats apart from fragments contained significantly more granivores than forests. Using species-specific densities derived from point-count data, forests were the most diverse and uneven among all habitat types (Figure 1b). Diversity profiles based on Hill numbers were most distinct among habitats at low values of q (species richness), reflecting the influence of rare species, and rapidly converged at high values of q that weight dominant species (inverse Simpson diversity). Fragments and early successional vegetation maintained intermediate positions between forests and silvopasture habitat types throughout the profile curve.

Species composition and beta diversity

Ordinations showed significant clustering of the different habitat types in species space, and species composition became increasingly distinct from forests in the countryside habitat types (Figure 1c). Bird communities in fragments contained a range of species from forests and the surrounding matrix and occupied a relatively large amount of species space that extended across contiguous and early successional forest communities. When using modeled densities from point-count data, habitat types were more defined and separated in species space and occupied roughly the same positions as observed with the occurrence data (Appendix S1.10).

Total pairwise dissimilarity increased as land-use intensification increased. Dissimilarity was relatively intermediate for fragments and early successional vegetation and extremely high for silvopasture ($R^2 = 0.80$) (Figure 1d; Appendix S1.11). Turnover explained the majority of total dissimilarity between forests and all habitat types except fragments, for which nestedness was more important. Turnover proportion was significantly higher in early successional vegetation and silvopasture than in fragments ($R^2 = 0.66$). All habitat types occupied distinct combinations of nestedness versus turnover values, as shown in ternary plots (Appendix S1.12). Results were similar when incorporating densities from point-count surveys, although turnover

among individuals was more prominent across all habitat types (Appendix S1.13).

Fragment size and matrix effects

Species richness increased as fragment size increased across all species and for all trophic groups except granivores ($R^2 = 0.83$ for full community) (Figure 2a; Appendix S1.14). In our system, a 1-ha fragment contained approximately 36 species on average, and richness increased by roughly 7 species per log hectare. The proportion of forest and shrub habitat within the 300-m radius was also positively related to fragment richness for the full bird community, insectivores, and frugivores (Appendix S1.14), and the contribution of matrix habitat was largest in small patches. For example, a shift from 0% to 50% forest and shrub matrix increased richness of the full community by 125% for a 1-ha fragment, 65% for a 10-ha fragment, and 45% for a 100-ha fragment (Figure 2b). For this reason, the effect of relatively small patches could be partially offset by increased amounts of matrix habitat (Figure 2c).

Jaccard's dissimilarity between fragments and contiguous forest also decreased as fragment size increased ($R^2 = 0.86$), and communities within fragments on average became 6% more similar to forests per log hectare (Figure 2d; Appendix S1.14). Smaller fragments were dissimilar from forests largely due to nestedness associated with the loss of forest species, whereas turnover was important in large fragments that hosted large numbers of species, including ones from the surrounding matrix. The extent of the matrix had a pronounced additive effect on small patches: a shift from 0% to 50% forest and shrub matrix increased similarity with forest communities by 226% for a 1-ha fragment, 111% for a 10-ha fragment, and 73% for a 100-ha fragment (Figure 2e). For this reason, similarity values of small patches with large amounts of matrix could be equivalent to large patches surrounded by less matrix (Figure 2f).

Silvopasture microhabitats

In silvopasture, species richness increased as area of shrub cover per hectare ($\beta = 32.3$, 95% CI 25.3–38.6) and number of relict trees per hectare ($\beta = 0.18$, 95% CI 0.15–0.21) increased (Figure 3). On average, an increase of 10% shrub cover per hectare increased species richness by 20% (3 species), and 10 pasture trees per hectare increased richness by 18% (5 species).

Species-specific sensitivities

The most sensitive trophic group was canopy insectivores, the majority of which declined significantly in fragments (57%), early successional vegetation (71%), and silvopasture (71%) (Figure 4; Appendix S1.15). Examples of species that declined across all agricultural habitats included *Campephilus pollens*, *Xiphocolaptes promeropyrhynechus*, *Mecocerculus stictopterus*,

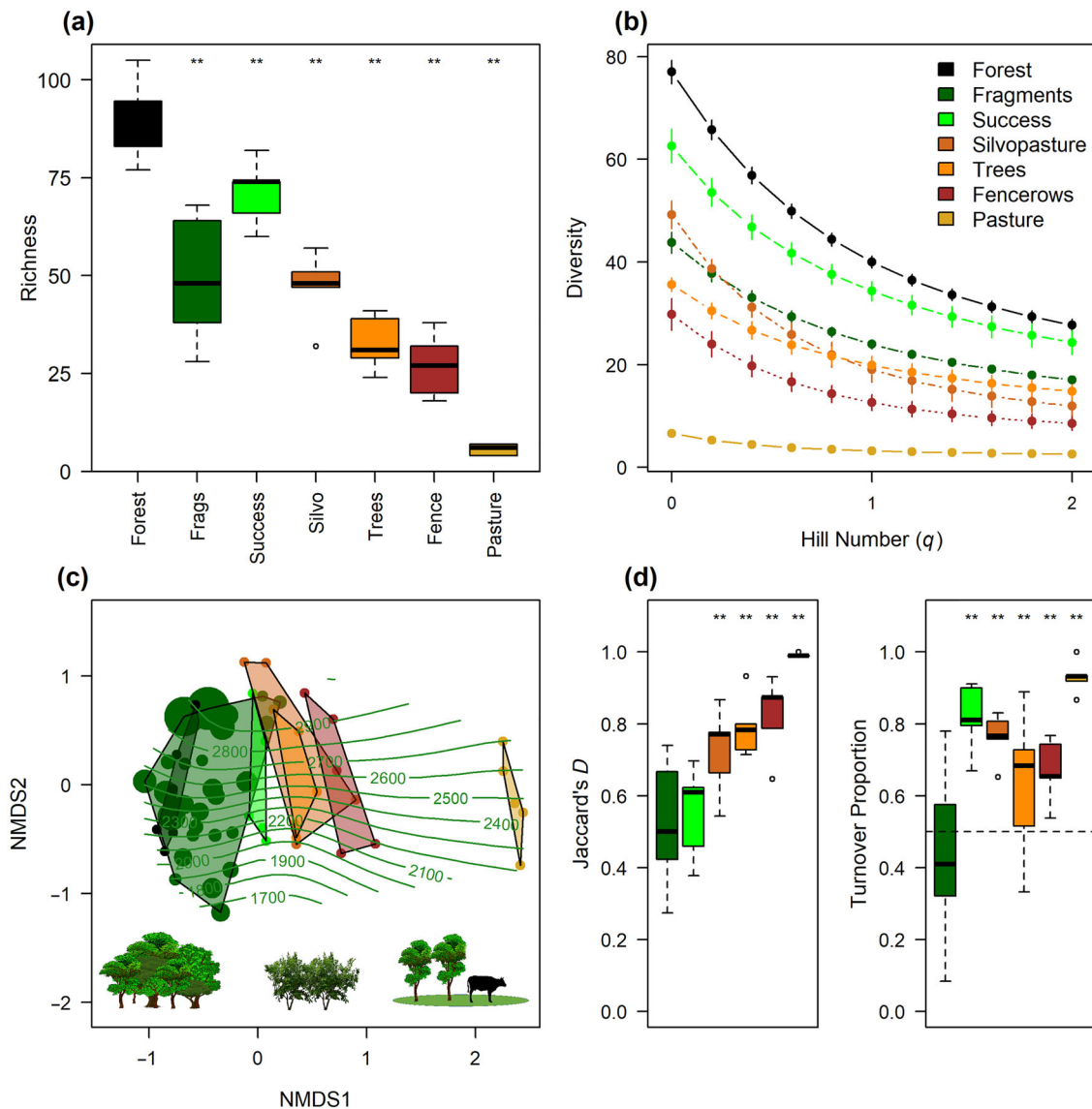


FIGURE 1 Changes in the structure of cloud forest bird communities across an agricultural land-use gradient that included contiguous mature forest ($n = 7$), mature forest fragments ($n = 29$), early successional vegetation ($n = 5$), and silvopasture and associated relict trees, fencerows, and pasture ($n = 5$) in Amazonas, Peru (data collected 2016–2017): (a) species richness for the entire bird community, (b) diversity profile curves (Hill numbers) based on densities from point-count data (mean and SE) ($q(0)$, species richness; $q(1)$, Shannon entropy; $q(2)$, inverse Simpson index), (c) ordination based on nonmetric multidimensional scaling (contours are elevation), and (d) dissimilarity between forest and countryside habitat types and proportion explained by species turnover (dashed line 50%; asterisks, significant difference [$p \leq 0.05$] relative to forests in panel [a] and fragments in panel [d]).

Sericossypha albocristata, and *Diglossa cyanea*. Other sensitive guilds were understory insectivores (35%, 44%, and 68%) (e.g., *Grallaria squamigera*, *Synallaxis unirufa*, *Cyborhinus thoracicus*, *Catharus fuscater*, and *Sphenopsis frontalis*) and frugivores (45%, 51%, and 62%) (e.g., *Pipreola arcuata*, *Butorhinus montana*, *Tangara parzudakii*, *Penelope montagnii*, and *Pharomachrus auriceps*). Declines were even more pronounced in the 3 silvopasture components, ranging from 64% to 94%. In contrast, omnivores, nectarivores, and granivores were mixed in their responses, ranging from increases (*Lesbia nuna*, *Elliotomyia chionogaster*, *Pheucticus chrysogaster*, *Diglossa sittoides*, and *Sporophila nigricollis*) to declines (*Nothocercus nigrocapillus*, *Odontophorus speciosus*, *Ocreatus under-*

woodii, *Trogon personatus*, and *Chlorornis riefferii*) in agricultural sites.

Species endemic to Peru or of conservation concern

Of 10 Peruvian endemics observed, 5 responded negatively to agricultural disturbance (*Grallaria przewalskii*, *Scytalopus femoralis*, *Pipreola pulchra*, *Leptopogon taczanowskii* [International Union for the Conservation of Nature “IUCN” near threatened “NT”], and *Thripophaga berlepschi* [NT]), 2 responded positively to early

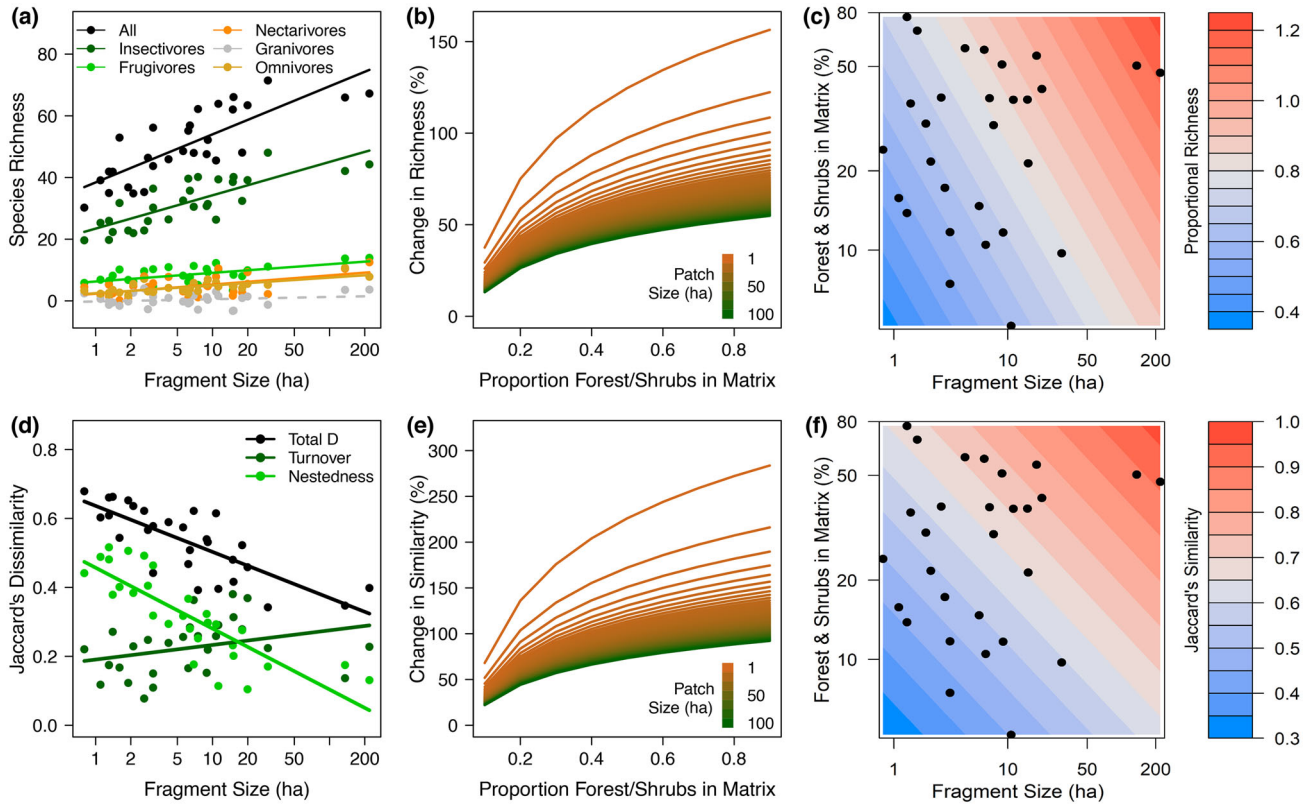


FIGURE 2 Characteristics of cloud forest bird communities in mature forest fragments, Amazonas, Peru (2016–2017): (a) species richness relative to fragment size across trophic groups; (b) relative change in species richness compared with fragment size and amount of forest and shrub cover in the matrix; (c) proportional richness of fragments compared with forests relative to the additive effects of fragment size and matrix habitat; (d) dissimilarity of communities in fragments compared with forests in relation to fragment size; and (e, f) change in fragment similarity relative to fragment size and the proportion of forest and shrub cover in the matrix (solid regression lines, significant [$p \leq 0.05$]).

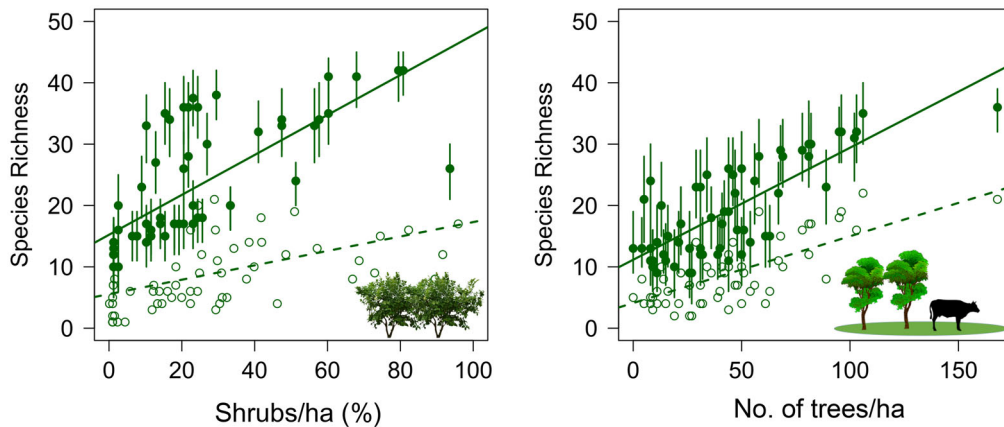


FIGURE 3 Avian species richness relative to amount of residual shrub cover (e.g., fencerows) and number of relict trees in silvopastures in Amazonas, Peru (data collected 2016–2017) (solid points, median and 95% CI species richness from multispecies spatial occupancy models; open circles, observed values).

successional vegetation (*Poecilatricus luluae* [IUCN endangered “EN”] and *Loddigesia mirabilis* [EN]), 1 responded positively to early successional vegetation and silvopasture (*Picumnus steindachneri* [EN]), and 2 were uncertain due to small sample sizes (*Metallura theresiae* and *Grallaricula ochraceifrons* [IUCN vulnera-

ble “VU”]). Two nonendemic species of conservation concern responded negatively to all forms of disturbance: *Sericosypha albo cristata* (VU) and *Andigena hypoglauca* (NT). Complete lists of species responses are in Appendix S8 and densities in Appendix S9.

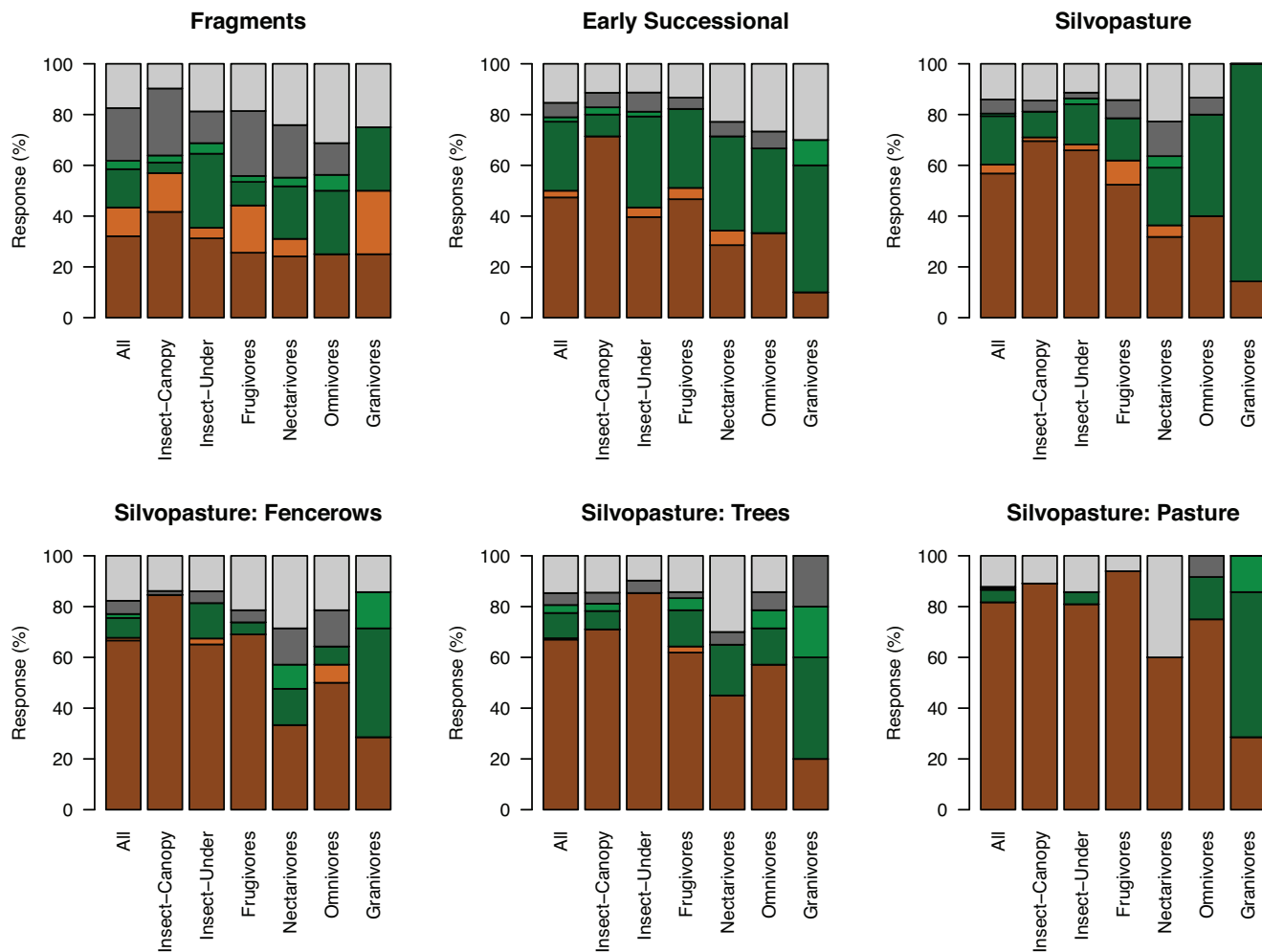


FIGURE 4 Species-specific responses (abundance increase or decrease or no response) to agricultural disturbance in Amazonas, Peru (data collected 2016–2017), by trophic group (brown, decline; orange, decline tendency; dark green, increase; green, increase tendency; dark gray, no response; gray, small sample size).

Andean synthesis

Based on raw occurrences and sensitivities from statistical tests, 25% and 34% of species were negatively associated with all forms of anthropogenic disturbance, respectively (Figure 5; Appendix S1.16). Carnivores (43% and 16%, respectively), canopy invertivores (30% and 38%), understory invertivores (27% and 38%), and frugivores (21% and 38%) were most sensitive. The percentage of species negatively associated with anthropogenic disturbance based on raw occurrences and sensitivities increased as disturbance intensity increased. The highest values were for agricultural landscapes: all species, 53% and 60%, respectively; carnivores, 75% (occurrences); canopy invertivores, 56% and 67%; understory invertivores, 59% and 73%; and frugivores, 67% and 69%. The percentage of endemic species negatively associated with anthropogenic disturbance varied among disturbance types: all forms of disturbance, 22% and 35%, respectively; fragments, 25% and 40%; secondary forest, 32% and 17%; and agriculture, 62% and 50%. Complete lists of species-specific sensitivities are in Appendices S10 and S11.

Negative sensitivity to disturbance based on raw occurrences was best predicted by small range size, relatively greater consumption of arthropods and vertebrates, and specialized foraging strata breadth (Figure 6; Appendix S1.17). Negative sensitivity based on statistical sensitivities was predicted by small range size, small elevational range, relatively greater consumption of arthropods and vertebrates, and specialized foraging strata and dietary breadth. There was an additional negative relationship with residual elevational-range-size variation, meaning that species disappearing from highly disturbed landscapes had narrower elevational ranges than expected given their global range size.

DISCUSSION

Tropical montane birds were sensitive to anthropogenic disturbance across an agricultural land-use gradient in northern Peru and throughout the Andes. Countrysides in Peru with interspersed remnant vegetation retained 20–80% of avian diversity due to opposing mechanisms. Fragments harbored nested

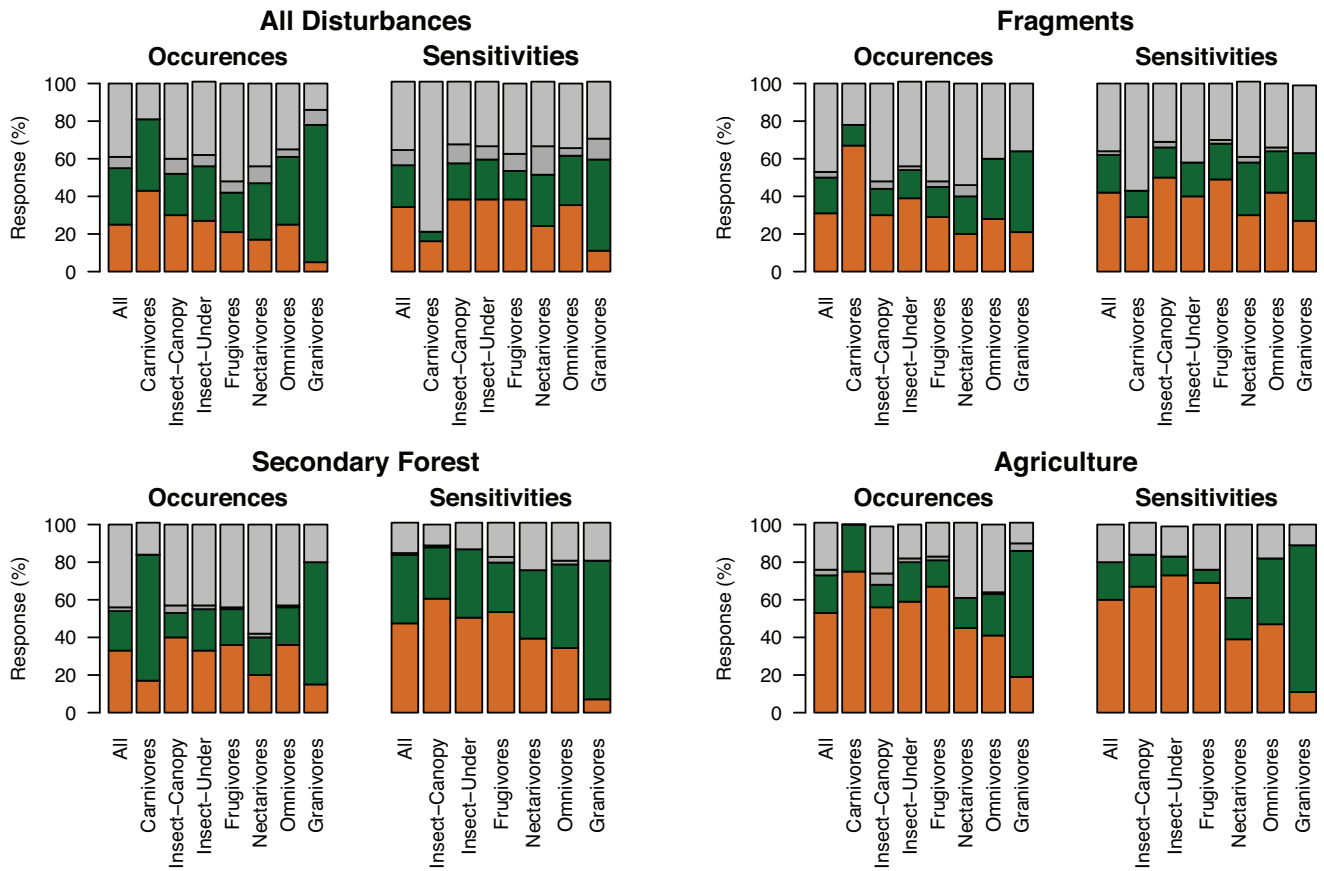


FIGURE 5 Species-specific responses to anthropogenic disturbance across the Andes ($n = 816$ species) based on occurrences and statistical sensitivities by trophic group (orange, negative; green, positive; dark gray, uncertain; gray, no response).

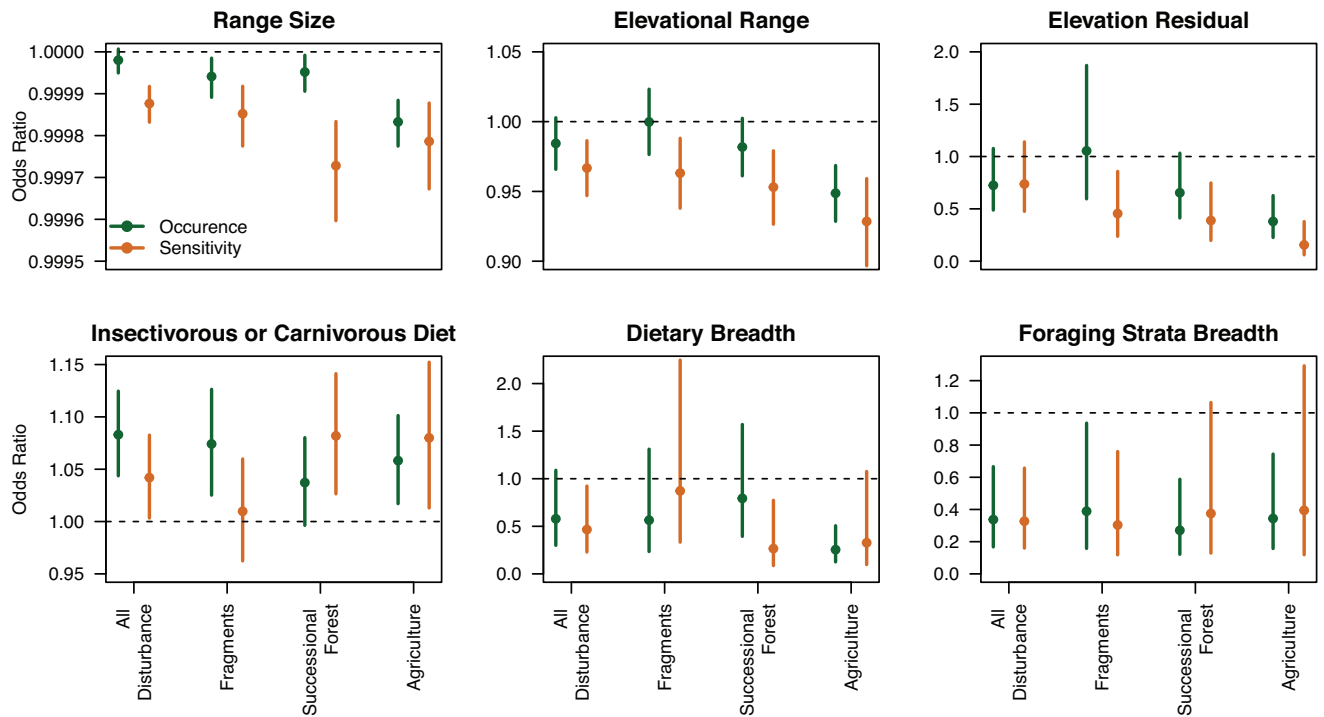


FIGURE 6 Factors predicting negative sensitivity to anthropogenic disturbance for 816 species across the Andes (odds ratio and 95% CI for 797 species with raw occurrence values and 692 species with statistical sensitivities).

subsets of forest communities, whereas communities in early successional and silvopastoral habitats underwent extensive species turnover compared with forests. Canopy and understory insectivores and frugivores were particularly sensitive to disturbance. Across the Andes, >25% of species were negatively affected by all forms of disturbance. This value rose to 60% in high-intensity agricultural landscapes. Species negatively affected by disturbance at the continental scale tended to have small range sizes, narrow elevational ranges, specialized foraging behaviors, and relatively greater consumption of arthropods and vertebrates.

Importance of contiguous forests

Our results from northern Peru align with a general consensus that across biological taxa, contiguous forests contain more biodiversity than countrysides (Phalan, 2018; von Wehrden et al., 2014). Studies from throughout Africa, Asia, and Latin America registered higher species diversity or larger distributions of plants, arthropods, birds, and mammals in large forest tracts than in countrysides (Dotta et al., 2016; Gilroy, Edwards, et al., 2014; Hulme et al., 2013; Kamp et al., 2015; Phalan et al., 2011; von Wehrden et al., 2014; Williams et al., 2017). Although efforts to conserve biodiversity in multiple-use landscapes are undoubtedly important for maintaining human well-being and providing politically feasible alternatives to strict ecological reserves (Fischer et al., 2011), our results support the general consensus that protecting primary forests remains critical for conserving tropical biodiversity, including in montane regions.

Beta diversity

Although we documented high levels of community dissimilarity across our agricultural land-use gradient, the underlying mechanisms varied by habitat type. Communities in fragments, especially in small patches, were nested subsets of forest communities, pointing to the loss of ecological niche space without replacement. Conversely, turnover explained the most dissimilarity between forest communities and those in successional vegetation and silvopasture, suggesting high rates of niche replacement. Separating beta diversity into contrasting ecological processes improves understanding of how changing communities should be managed in disturbed landscapes and emphasizes the importance of quantifying species composition in applied ecological research (Legendre, 2014; Socolar et al., 2016).

Forest fragments

Our results demonstrate the critical role remnant forest fragments play in anchoring forest avian diversity in tropical countrysides, given that fragments most closely resembled the composition, richness, and diversity of contiguous forests. In particular, patch size and matrix composition interacted to

drive proportional richness and compositional similarity, with increased amounts of matrix habitat compensating for reduced patch sizes. Increased availability of habitat in the surrounding landscape likely enhanced patch occupancy by increasing the effective amount of habitat associated with a given patch and ameliorated biological impediments associated with patch isolation, such as dispersal limitation (Fahrig, 2013; Prugh et al., 2008; Watling & Donnelly, 2006). Given that Andean species occupy long, narrow ranges, maintaining permeable landscape matrices that facilitate elevational connectivity across the Andes will help species move in response to a changing climate (Bertuzzo et al., 2016).

In addition to maintaining biodiversity, forest patches provide important ecosystem and cultural services to local communities (Schelhas & Greenberg, 1996). During 2 years of living in rural *campesino* communities as an “embedded researcher” (Jenkins et al., 2012), landholders communicated to us the services they derived from the fragments where we surveyed birds, including protection of water sources, firewood and building materials, clean air, and physiological benefit (Appendix S1.18). Such services have been documented worldwide, where many fragments act as “domestic forests” that provide nontimber forest products, such as palm, mushrooms, herbs, fruits, and remedies from medicinal plants (Ladio & Lozada, 2001; Mathez-Stiefel & Vandebroek, 2012). Forest patches also provide services beneficial to agriculture, including water retention, soil erosion prevention, and habitat for biological pest control and pollinators (Decocq et al., 2016), as well as inspiring participatory learning through the acknowledgment of shared assets and transmission of traditional ecological knowledge (Daniel et al., 2012; Ishizawa & Rengifo, 2009).

Early successional forests

Regenerating shrubs and early successional forests harbored bird communities distinct from those in forests, consistent with previous reports of elevated levels of avian biodiversity in secondary forests in the Andes (Edwards et al., 2017, 2021; O’Dea & Whittaker, 2007). In particular, 2 endemic species to Peru listed by the IUCN as endangered (*Loddigesia mirabilis* and *Poecilatriccus luluae*) increased in abundance in shrubby habitat. Shrubs also buffer the area and edge effects of fragmentation (Gascon et al., 1999) by providing a permeable matrix for dispersal (Van Houtan et al., 2007), spillover habitat for area-sensitive species inhabiting small forest fragments (Powell, Wolfe, et al., 2015), and refugia during demographically sensitive life stages (Vitz & Rodewald, 2006), including for some Andean species (Mamani-Cabana et al., 2023). Early successional forests also provide elevated levels of carbon capture compared with other agricultural regimes (Gilroy, Woodcock, et al., 2014), assuming that reforestation is not monoculture plantations (Putz & Redford, 2009). Active forest restoration provides dual benefits of enhancing overall biodiversity relative to degraded lands (Benayas et al., 2009) and improving human livelihoods through the integration of traditional ecological knowledge and experimental science (Chazdon, 2008).

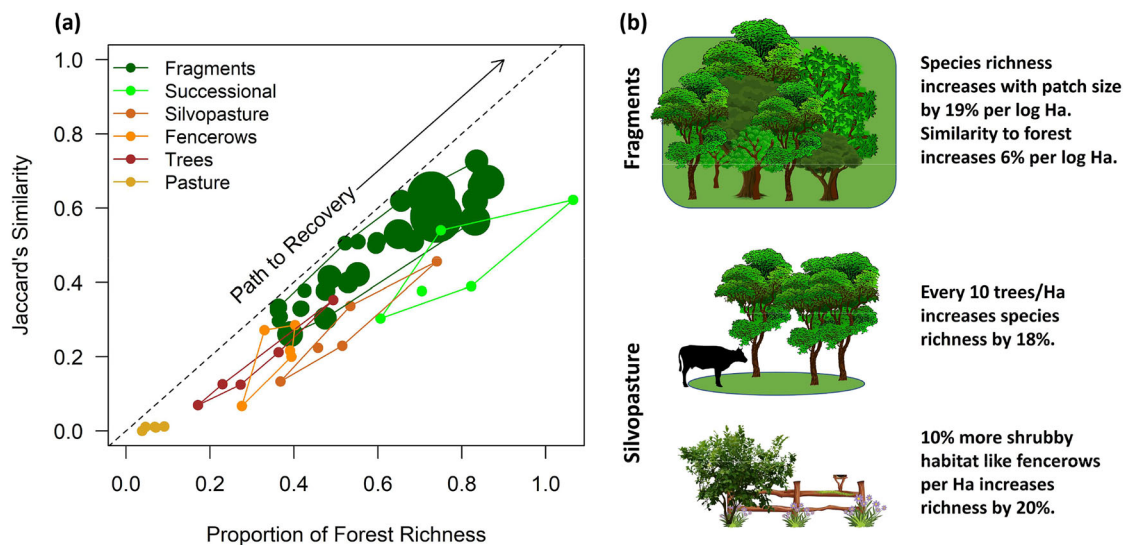


FIGURE 7 Approaches for recovering avian diversity in tropical montane countryside based on (a) the relationship between proportional richness and similarity between countryside habitat types and mature forest (fragment points scaled to patch size) and (b) simple management strategies for maximizing diversity of species in forest fragments and silvopasture.

Silvopasture

Although our results suggest silvopasture is less species rich than forest fragments and early successional vegetation, relictual habitat elements can maintain intermediate levels of avian biodiversity in multiple-use landscapes. Fencerows reduce effective distances among remnant shrub and forest tracts by providing connectivity for dispersal (Gillies & St. Clair, 2008; León & Harvey, 2006). Live fencerows, in particular, provide habitat for pollinators, biocontrol agents, and avian nest sites (Kormann et al., 2016; Otero & Onaindia, 2009; Pulido-Santacruz & Renjifo, 2011) and contain large amounts of plant diversity (Harvey et al., 2005). Silvopastoral systems are widely recognized as an effective pasture management strategy when trees are retained or planted at sufficient densities to promote soil carbon, cattle health, and biodiversity retention without altering grass yields (Montagnini et al., 2013). Arboreal birds, in particular, can maintain flocking and foraging behaviors at a minimum of 25–40% canopy cover (McDermott & Rodewald, 2014; Tarbox et al., 2018). Retention or restoration of fencerows and pasture trees represents easy and effective management strategies for farmers given that they also provide practical human benefits, such as fruit, firewood, timber, fodder for animals, and shade for cattle (Harvey & Haber, 1998; Harvey et al., 2005).

Andean synthesis

Our results for Andean birds support the idea that species adapted to a broader range of environmental conditions (e.g., large global range sizes and broad elevational ranges) are better adapted to anthropogenic disturbance (Ausprey et al., 2022; Karp et al., 2019). In particular, species declining in

high-intensity agricultural landscapes had smaller elevation ranges than expected given their global range size, meaning that adaptations specifically associated with elevation (e.g., rapid changes in temperature) may pose additional constraints to species persistence (Ceresa et al., 2021; Duclos et al., 2019). Our results also point to the sensitivity of species with insectivorous diets, as has been reported at regional scales in the Andes, including in our work in Peru (Jones et al., 2021; Kattan et al., 1994; Renjifo, 1999). Major hypotheses for why insectivores in the Neotropics appear particularly sensitive to anthropogenic disturbance include poor dispersal ability, highly specialized trophic niches, sensitivity to subtle changes in habitat microclimate, and increased prevalence of agricultural pesticides that may reduce prey availability (Jirinec et al., 2022; Powell, Cordeiro, et al., 2015; Sherry, 2021).

We stress the need for reporting species-specific sensitivities in publications focused on the conservation of Neotropical montane birds given that we found only 8 studies in the Andes that reported sensitivities based on statistical tests. We recommend that authors, at a minimum, report presence and absence and, ideally, changes in occupancy, abundance, or both across disturbance gradients. Using approaches that account for abundance is particularly powerful because many species occur at different abundances in disturbed areas, and these patterns are masked in analyses of occupancy. Furthermore, a large percentage of species showed no sensitivity to disturbance, likely due in part to small sample sizes and survey methods that masked intermediate changes in abundance. Refining survey and analytical approaches will improve species status assessment (e.g., IUCN Red List) and future efforts by conservation organizations in the Neotropics to construct species sensitivity scores, as has been done in North America (Partners in Flight, 2022).

Conservation recommendations

By comparing proportional forest richness with community dissimilarity in our Peruvian study system, we assessed how different components of the countryside contribute to the conservation of forest bird communities (Figure 7). Forest fragments represented conservation strongholds, containing bird communities most similar to forests in richness and composition. Hence, we recommend that conservation practitioners interested in maintaining forest biodiversity spare forest fragments, especially large ones, and pursue management practices that increase patch size and connectivity through the maintenance and restoration of early successional vegetation and silvopastoral trees. The latter is particularly important for small fragments, where the restoration of matrix habitat can increase patch-based species richness and similarity to forests the most.

Early successional vegetation and silvopasture sites are far below the one-to-one line in Figure 7, which emphasizes the role of species turnover in producing communities with richness levels comparable to fragments yet different species composition. Although restoring successional habitat to mature forest conditions obviously benefits forest specialists, retaining minimal amounts of successional areas in agricultural landscapes will provide habitat for disturbance-adapted species not found in forests, including endemic species of conservation concern. Maintenance of successional areas should be conducive to human livelihoods and involve low-intensity agricultural practices, such as family vegetable plots (*chakras*). Finally, we recommend maximizing biodiversity potential in high-intensity agricultural plots by maintaining and restoring shrubby fencerows and relict trees. Reforestation with native forest trees and shrubs is particularly critical, given that policies emphasizing plantations of *Alnus* and *Eucalyptus* trees fail to produce bird communities similar to those found in primary forests (Castaño-Villa et al., 2014; Latta et al., 2011). A Spanish translation of the manuscript is provided in the Supporting Information.

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ORCID

Ian J. Ausprey  <https://orcid.org/0000-0002-7127-2746>

Felicity L. Newell  <https://orcid.org/0000-0002-7944-8603>

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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