



Dietary and habitat specialization, eye size, clutch size, and aerial lifestyle predict avian fragmentation sensitivity in an Andean biodiversity hotspot

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Abstract

The fragmentation of tropical forests remains a major driver of avian biodiversity loss, particularly for insectivores, yet the mechanisms underlying area sensitivity remain poorly understood. Studies in lowland systems suggest that loss of food resources, changes to light microenvironments, increased nest predation, and dispersal limitation are possible mechanisms, but these are untested for montane tropical bird communities. In this study, we related avian functional traits to area sensitivity (quantified using beta estimates from a multi-species occupancy model) to test the above four hypotheses for a cloud forest bird community (both resident species and just resident insectivores) in the Colombian Western Andes. We found that species with more specialized diets and those that use the canopy and subcanopy (loss of food hypothesis), larger relative eye sizes (light microhabitat hypothesis), and larger clutch sizes (nest predation hypothesis) were significantly more area sensitive. By contrast, there was no support for the dispersal limitation hypothesis; instead, we found that insectivores with more pointed wing shapes, and more aerial lifestyles, were significantly more fragmentation sensitive. These results suggest that reduced vegetation structure, loss of late-successional plant species, and loss of epiphytic plants may reduce food availability in fragments. Similarly, the ability to tolerate higher light intensity near fragment edges, or when traversing matrix habitat, may be important for persistence in fragments and suggests that habitat configuration may be of special importance in fragmented Andean landscapes. Overall, a lack of information on foraging, movement, and breeding ecology complicates avian conservation in the Andes.

Keywords Functional traits · Forest fragmentation · Nest predation · Dispersal ability · Foraging specialization · Light environment

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Extended author information available on the last page of the article

Introduction

Among the most important drivers of biodiversity loss is the conversion of forest to other land uses, a trend that has continued unabated over the past decade (Heino et al. 2015; Watson et al. 2016), particularly at the tropical latitudes that house most of the world's biodiversity (Lewis et al. 2015; Barlow et al. 2018). High rates of forest loss, especially in intact forested landscapes, are a leading cause of vertebrate endangerment (Tracewski et al. 2016; Betts et al. 2017), an effect amplified by forest fragmentation, or division of forest remnants into isolated patches of varying configuration and size that are separated by non-forest 'matrix' (Haddad et al. 2015). Forest fragmentation has particularly negative effects on tropical biodiversity, which declines with decreasing fragment area and increasing isolation (Fletcher et al. 2018; Betts et al. 2019). One ongoing conservation challenge in tropical fragmented landscapes, however, is understanding the mechanisms underlying sensitivity to patch area, even for well-studied taxa such as birds (Stratford and Robinson 2005; Sodhi et al. 2008; Robinson and Sherry 2012; Powell et al. 2015; Visco et al. 2015; Sherry 2021). Bird species respond differently to fragmentation, with some functional groups showing greater sensitivity than others (Bregman et al. 2014; Keinath et al. 2017). Insectivores, a group that makes up ~60% of both all tropical forest (Şekercioğlu 2012) and all Neotropical (Sherry et al. 2020) bird species, are particularly sensitive to fragmentation (Şekercioğlu et al. 2002; Bregman et al. 2014; Pavlacky et al. 2015; Powell et al. 2015; Sherry 2021). Therefore, mechanisms explaining area sensitivity are particularly needed for this diet guild.

One potential mechanism is the loss of specialized foraging microhabitats or resources in fragments. Many tropical forest insectivores show extreme foraging specialization (Sherry et al. 2020) and are often restricted to specific vertical forest strata (Marra and Remsen 1997; Walther 2002a) and foraging substrates, such as hanging dead vegetation (Mansor et al. 2019) or lianas (Schnitzer et al. 2020). Similarly, many montane frugivores (Dehling et al. 2014; Bender et al. 2018; Quitian et al. 2018), and nectarivores (Tinoco et al. 2017; Weinstein and Graham 2017; Sonne et al. 2019) are specialized on specific plant species that may be lost from forest fragments. Globally, bird species with more stereotyped foraging behavior are more at-risk than species with more plastic behavior (Ducatez et al. 2020), and dietary specialization has been linked to avian fragmentation sensitivity in some tropical forest habitats (Hadley et al. 2018; dos Anjos et al. 2019). Therefore, the simplification of vegetation structure in fragments and consequent loss of species-specific foraging microhabitats (Michel et al. 2015; Stratford and Stouffer 2015) and late-successional fruiting and flowering plants (Putz et al. 2011) in fragments may be important drivers of extirpations. In particular, dietary and microhabitat specialists should be most area sensitive if loss of food or foraging microhabitats is a dominant mechanism of area sensitivity.

Alternative hypotheses, however, abound. Fragment edges, for example, may alter the normally stable abiotic conditions of the forest understory, including light intensity, temperature, and humidity (Stratford and Robinson 2005; Robinson and Sherry 2012; Powell et al. 2015). Of these, light intensity may be most important because tropical forest birds are restricted to specific light microenvironments linked to their foraging stratum (Ausprey et al. 2021; Walther 2002b), and light intensity is more affected by edge effects than temperature or humidity (Patten and Smith-Patten 2012). Forest-interior birds have large eyes relative to their bodies (Ausprey 2021) and avoid high-light-intensity microhabitats (Pollock et al. 2015); this trait has been associated with increased edge avoidance

(Martinez-Ortega et al. 2014) and disturbance sensitivity (Ausprey et al. 2021; but see Rutt et al. 2019). A third hypothesis is that many tropical bird species are dispersal limited (Visco et al. 2015), due in part to morphological adaptations to their specialized foraging ecology (Salisbury et al. 2012; Sherry et al. 2020). Many such species have a poor flight capacity (Moore et al. 2008), an aversion to gap crossing (Lees and Peres 2009; Ibarra-Macias et al. 2011), a short perceptual range (Awade et al. 2017), and therefore a limited ability to disperse among fragments (e.g., Woltmann et al. 2012). Wing shape, quantified as the hand wing index (HWI) has been shown to strongly correlate with dispersal distance (Arango et al. 2022), and is a strong predictor of fragmentation sensitivity globally (Weeks et al. 2023). The recent publication of a global HWI dataset (Sheard et al. 2020) allows us to test the dispersal limitation hypothesis indirectly through this trait.

The fourth hypothesized mechanism underlying area-sensitivity is an increase in nest predation due to a greater abundance of mesopredators in fragments ('mesopredator release': Crooks and Soulé 1999). The evidence for higher nest predation rates in tropical fragments, however, remains mixed (Robinson and Sherry 2012; Visco et al. 2015). While increased nest predation rates in fragments occur in some systems (Young et al. 2008; Newmark and Stanley 2011), nest predation rates can also decline in tropical fragments (Spanhove et al. 2014; Visco and Sherry 2015). This discrepancy may result from differences in nest predator identity and fragmentation sensitivity (Vetter et al. 2013; Visco et al. 2015); therefore, system- and landscape-specific tests of the nest predation hypothesis are required. If nest predation is an important factor, it should not affect all species equally. For one, nest type affects the nest predation rates of tropical birds, with open-cup nests being depredated at higher rates than covered and cavity nests (Brawn et al. 2011; Newmark and Stanley 2011). Cavity-nesting birds, in particular, appear to be less affected by forest disturbance as long as suitable nesting cavities are present (Cockle et al. 2015). Second, larger clutch sizes should buffer against the negative effects of predation and increase the demographic impact of a successful nesting attempt; greater fragmentation sensitivity has been significantly linked to smaller clutch sizes (Pavlacky et al. 2015). Finally, species with slow life histories should be more vulnerable to higher predation because of their smaller breeding populations and the greater demographic cost of a nest predation event (Owens and Bennett 2000). Alternatively, if primary nest predators themselves are fragmentation sensitive (e.g., Visco and Sherry 2015), then we might predict the opposite.

In this study, we tested these four hypothesized mechanisms of fragmentation sensitivity in a montane avifauna of the Colombian Western Andes. In a previous study (Jones et al. 2021), we used a multi-species occupancy model to derive beta estimates of the effects of patch size on species occupancy across a gradient of fragment sizes and a continuous forest reference site in the same landscape. In this study we relate these beta estimates to functional traits predicted to be associated with each of the four hypotheses (see Table 1 for hypotheses and predictions). Specifically, we asked: (1) if loss of foraging microhabitats, sensitivity to changing light intensity, dispersal limitation, or increased nest predation explain fragmentation sensitivity, and (2) if the mechanisms of sensitivity differ across the full bird community and the insectivore guild. We hypothesized that if loss of foraging microhabitats is a major mechanism, then species with more specialized diets and using specific foraging microhabitats, strata, and substrates should show a greater fragmentation sensitivity. Alternatively, greater sensitivity should be associated with a smaller HWI if dispersal limitation is a major mechanism, and with larger relative eye size if light sensitivity is a driver. Finally, we predicted that species with larger clutch sizes, 'fast' life histories, and cavity nests would be less fragmentation sensitive if altered nest predation is the dominant mechanism.

Table 1 Hypotheses, species traits, and predictions for factors influencing area, edge, and logging sensitivity of Andean birds

Hypothesis	Species Trait	Description	Prediction
Loss of food resources and foraging micro-habitats	Diet specialization	Gini specialization index of a species' use of insect, fruit, seed, nectar, and vertebrate food resources	Dietary specialists should be more vulnerable to fragmentation because of loss of specialized food resources
	Foraging stratum	Multivariate measure of presence/absence of use of six different height bands	Understory and midstory (lower) foragers should be more vulnerable to fragmentation because structural changes to vegetation are more important than to the canopy
	Foraging maneuver*	Multivariate measure of foraging maneuver use (presence/absence of each maneuver)	Anecdotal evidence suggests that aerial foragers are more fragmentation sensitive
	Foraging substrate- distance from trunk*	Multivariate measure of foraging substrate, near trunk vs. far from trunk	Far from trunk substrates should be more affected by structural change in fragments
	Foraging substrate- degree exposed*	Multivariate measure of foraging substrate, exposed vs. occluded substrates	More occluded substrates such as dead leaves and vines should be more commonly lost with fragmentation
Dispersal limitation	Use of bamboo habitat	Presence/absence of use of <i>Clusquea</i> bamboo	Bamboo specialists should be more sensitive to fragmentation due to loss of bamboo in fragments
	Use of ravine habitat	Presence/absence of use of Andean ravines and streams	Topographic specialists should be more vulnerable to fragmentation because fragments may not contain their specialized habitat
	Use of treefall gap	Presence/absence of use of treefall gaps	Treefall gap specialists should be less vulnerable to fragmentation since they are preadapted to disturbance
Light sensitivity	Hand wing index (HWI)	A measure of wing shape (rounded vs. pointed) associated with dispersal behavior	Species with a smaller hand wing index (more rounded wing shape) should be more sensitive to fragmentation because of reduced dispersal ability
	Relative eye size	Residual of eye size regressed against body size	Species with larger relative eye sizes should be more sensitive to fragmentation because they will be more vulnerable to glare effects in brighter fragments

Table 1 (continued)

Hypothesis	Species Trait	Description	Prediction
Increased predation risk	Nest type	Categorical description of nest type (cavity, dome, cup, platform)	Cavity nesters should be least sensitive to fragmentation due to the greater protection of nest from predators
	Maximum clutch size	Largest clutch size recorded for the species in the literature	Species with larger clutches should be less sensitive to fragmentation because successful breeding attempts add more individuals to the local population
	Generation length	An estimate of the average age of the breeding population, a proxy for life history strategy	Species with a lower generation length (faster life history) should be less vulnerable to fragmentation since more breeding individuals are present in the population and the loss of a nest is less costly to the overall population

Predictions describe the predicted direction of effect if the hypothesis in question is a driver of sensitivity. Species traits are predictor variables included in linear mixed models of sensitivity. Species traits with an asterisk were only included in the models for insectivores

Methods

Study system

Field work was conducted in subtropical Andean forest and forest fragments in the municipality of El Cairo (4° 45' 39" N, 76° 13' 21" W; Valle del Cauca department) in the **Western Andes of Colombia**. Little is known about fragmentation sensitivity in tropical montane avifaunas, which represent hotspots of avian diversity (Sherry 2021). Andean cloud forests, in particular, contain a high richness of endemic and endangered birds (Orme et al. 2005; Kier et al. 2009) and are suffering extensive levels of deforestation for conversion to agriculture and cattle ranching (Tejedor-Garavito et al. 2012; Tracewski et al. 2016; Karger et al. 2021). Our study sites consisted of mid- to late-successional forest fragments embedded in an agricultural landscape of shade coffee and cattle pasture. We stratified forest fragments within the same elevational band (~1900–2300 m.a.s.l.) and same matrix type (cattle pasture) into large (≥ 100 ha), medium (~30–50 ha), and small (≤ 20 ha) size categories, and surveyed at least two replicates of each category ($N = 8$ fragments, range = 10–173 ha). We also surveyed a continuous-forest reference site in the same landscape connected to thousands of hectares of forest, the Reserva Natural Comunitaria Cerro El Inglés. A full description of the study system and study sites is available in Jones and Robinson (2020). Because local vegetation structure and land-use histories varied across and within fragments, largely due to selective logging, we established 500-m transects within forest interior as the sample unit ($N = 14$ transects). To maximize ecological variability within sites, we placed one transect in disturbed (logged) forest and another in relatively undisturbed forest in large fragments, where possible.

Collection of fragmentation sensitivity data

We obtained quantitative estimates of area sensitivity for all bird species encountered in our focal landscape from a multispecies occupancy model, which allowed us to estimate species occupancy while accounting for imperfect detection (Devarajan et al. 2020). The full model is specified in Jones et al. (2021); in brief, we fit a hierarchical model (Kéry and Royle 2016, Ch. 2), implemented in a Bayesian framework without data augmentation, that combined a state process model (i.e., the transect-level occupancy of each species) described by a Bernoulli distribution with an observation model of repeated detections from different survey techniques (i.e., the technique-specific detection probability) described by a binomial distribution. Input data consisted of presences and absences of each species along a transect on a sampling day from one of three complimentary survey techniques: audio-visual transect walks, understory mist netting, and playback surveys for owls. We sampled each of the 14 transects with each technique for 2.5 sequential survey days [surveys were not conducted concurrently; see Jones et al. (2021) for details of survey methods]. We then used an intercept term for survey type in the detectability sub-model to integrate the presence-absence data across techniques. Therefore, each modeled species had a unique detectability for each survey method, and we let species occupancy and detection parameters covary within the model. We fitted five fixed-effect covariates on occupancy: percentage forest cover and edge density (m/ha) within 1 km of the transect, an index of vertical vegetation structure along the transect, and two PCA axes describing the densities of understory vegetation and large-diameter trees, respectively. We also included

a random effect of site ($N=9$) to account for the non-independence of survey transects in the same forest fragment. Methods of predictor variable collection are described in Jones et al. (2021).

We used the median of the joint posterior distributions of beta estimates of percentage forest within 1 km of the transect on transect-level occupancy to quantify the area sensitivity of each species. We selected beta estimates for percentage forest within 1 km of the transect because this covariate was explicitly accounted for in the design (see above) and had the greatest number of significant effects on species occupancy (Jones et al. 2021). Positive values of this variable indicate higher species occupancy with greater percentage cover. Following Carrara et al. (2015), we used percentage forest as a proxy for patch size because our continuous forest reference site had no value for patch size. The matrix around our study sites was largely composed of treeless cattle pasture, and the percentage forest variable was highly correlated with patch size (Pearson's correlation=0.96).

Collection of avian functional traits

We collected 13 avian functional traits, representing four mechanisms of fragmentation sensitivity, for our analyses (Table 1). Data on foraging microhabitat, foraging behavior, and diet were obtained from *Birds of the World* species accounts (Billerman et al. 2021), supplemented by the authors' field observations. Avian taxonomy therefore follows the eBird/Clements checklist. For all species ($N=178$), we recorded use of five diet categories (insects, fruits, seeds, nectar, and vertebrates), use of six forest strata (ground, understory, midstory, subcanopy, canopy, aerial), and use of three microhabitats: ravines and small streams, bamboo patches (*Chusquea* spp.), and treefall gaps. For an additional subset of insectivores ($N=80$) we also recorded the use of 11 foraging maneuvers (glean, sally, sally-glean, probe, peck, hang, hover-glean, hammer, flake, flush-pursue, gape) and eight foraging microhabitats (air, trunk, branch/twig, live leaf, dead leaf, vine, epiphyte, ground). We defined foraging maneuvers according to Remsen and Robinson (1990). For each diet category, we assigned a diet use score ranging from 0 (no use) to 3 (majority of the diet). We scored all other categorical variables as used (1) or not used (0). All categories were non-exclusive, and all species were scored by HHJ. We then created continuous measures of height stratum, foraging maneuver, and foraging microhabitat by ordinating these variables using principal coordinates analysis (PCoA; Gower 2015) with the Gower dissimilarity index. Following the methods of Morelli et al. (2019), we measured diet specialization using the Gini coefficient, a measure of statistical dispersion, on the diet use scores. Greater values of the Gini coefficient indicate greater dietary specialism.

We used lateral eye size as a proxy for light sensitivity, as this trait is correlated with a species' light microhabitat (Ausprey et al. 2021). Eye sizes were obtained from two sources. For one subset of species ($N=72$; 40%), we used mean eye size values from mist net captures in Peru, measured using calipers to the nearest 0.1 mm (data from Ausprey et al. 2021). For the other subset of species ($N=106$; 60%), we measured lateral eye size from photos following the methods of Ausprey et al. (2021). We selected six images of each species in which the individual was at eye level and the bill and eye within the same focal plane. To ensure replicability, we used images from Cornell's Macaulay Library with a unique identifier; all photos were measured by HHJ. We then scaled the photos in *ImageJ* using measurements of bill height at the nares from a database of Colombian bird morphology (Montoya et al. 2018) complemented with measurements from mist net captures (G. Londoño, unpublished data). To obtain a final eye size we multiplied the mean photo

measurement by 1.03, as Ausprey et al. (2021) found that photo measurements were 3% smaller than field measurements. We then calculated relative eye size as the residual of the regression between log-transformed body mass (the mean mass of the male from *Birds of the World*) and log-transformed eye size (Figure S1). The hand wing index (HWI), a measure of wing shape (rounded versus pointed), correlates well with dispersal distance (Dawideit et al. 2009), and we used this trait as a proxy for dispersal ability. Larger values indicate a more pointed wing shape, which is associated with a higher flight performance, while lower values indicate a more rounded wing. Measurements of HWI were taken from the Sheard et al. (2020) global data set, sourced from museum collections and field data.

Finally, we collected data on reproductive traits from two sources. Nest type and maximum reported clutch size were taken from *Birds of the World* accounts, and we included information on nest type and clutch size from recent published literature where these were not described in the species account. When we could not find published accounts of nest type or clutch size, we used the values of the nearest congener. We divided nest type into four exclusive categories (cavity, dome, cup, platform) and reported the most common type for the species. To measure life history strategy, we obtained estimates of generation length, the average age of a species' breeding population, from Bird et al. (2020).

Data analysis

We used phylogenetic least square (PLS) models to test for significant correlations between functional traits and sensitivity to fragment area (quantified as percentage forest within 1 km, see above). We tested for effects on both (1) the full resident bird community (N = 166 species; Fig. 1) and (2) only resident insectivores (N = 73 species). We excluded Nearctic-Neotropical migrant species (N = 14) from the analysis because these species do not breed in Andean forests, so functional traits based on nesting ecology are not appropriate for them. We also excluded the swift *Chaetura cinereiventris* from the insectivore analysis because this species had a large outlier value for HWI that was biasing analyses. The full community is here defined as all species detected at least once during field sampling with three different methods [mist netting, audio-visual transects, owl playbacks; see Jones et al. (2021)] for which we could estimate area sensitivity. We created phylogenies for both resident species and insectivores by subsetting the global Jetz et al. (2012) phylogeny; this phylogeny does not contain data for the recently described *Scytalopus alvarezlopezi*, so we substituted its sister species *S. stilesi* in the phylogeny. In each case, we downloaded 1000 trees from the Bird Tree website (www.birdtree.org) using the Hackett et al. (2008) backbone phylogeny, and then calculated a 50% majority-rule consensus tree using mean edge lengths with the *consensus.edge* function of the *phytools* package (Revell 2022). We ran phylogenetic least square models using the *phylolm* function of the same package (Tung Ho et al. 2020) and using the Brownian motion evolutionary model. We assumed that the area sensitivity of tropical resident birds should be the result of their natural history, itself shaped by numerous selective pressures. Because a species' natural history should change gradually over time, and area sensitivity is not a trait that should evolve towards an optimum value, we believe that Ornstein–Uhlenbeck models are not appropriate for our data (Symonds and Blomberg 2014). Similarly, we selected the Brownian motion model over Pagel's λ because that model estimated λ to be near zero, but phylogenetic effects on fragmentation sensitivity are frequently described for Andean bird families (e.g., greater sensitivity of Cotingidae, Icteridae, Trogonidae; Renjifo 1999; Santillan et al. 2019).

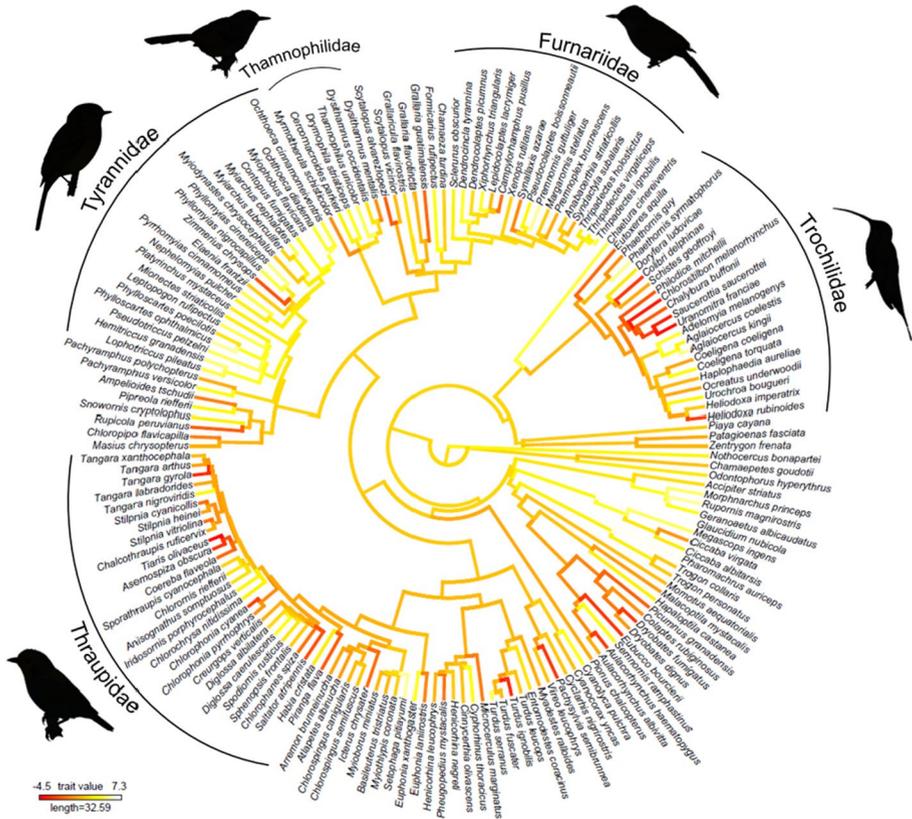


Fig. 1 Fragment area sensitivity plotted onto a phylogeny of Andean birds. Plotted species ($N=166$) represent all resident species detected during field surveys; Neotropical-Nearctic migrant species were excluded from analyses. Light yellow colors indicate greater fragmentation sensitivity, while red colors indicate species more commonly encountered in fragments

We fit models with ten and thirteen predictor variables for resident species and insectivores, respectively; all continuous predictor variables were z-scale transformed prior to analysis to allow for direct comparison of effect sizes. The continuous predictor variables all showed a Pearson correlation of less than 0.5, indicating a lack of multicollinearity. The foraging maneuver and foraging substrate variables were the only covariates with a correlation >0.4 and removing these variables did not affect covariate significance in the averaged model. We then used an information theoretic framework to address model selection uncertainty, comparing models using the Akaike Information Criterion adjusted for small sample sizes (AIC_c ; Burnham and Anderson 2002). For both subsets of species, we ranked all subsets of the global model, considering models equivalent to the best model if their ΔAIC_c value was ≤ 2 . We then performed full model averaging of the candidate model set (i.e., all models within 2 ΔAIC_c of the best model), as there was no single best model. We used full model averaging because this method is recommended when evaluating the relative importance of predictor variables (Nakagawa and Freckleton 2011). AIC_c values and Akaike weights for all model subsets were calculated using the *dredge* function of the *MuMIn* package (Bartoń 2022), whereas model averaging was conducted using the

model.avg function. Because p-values from model averaging do not account for the false discovery rate, we instead considered covariates to be significant when the 95% confidence interval did not overlap zero. We evaluated model goodness-of-fit using the adjusted r^2 values calculated by the *phylolm* function, averaged across the candidate model set.

Results

Principal coordinates ordination of foraging height, behavior, and substrate

Based on the examination of a scree plot, we retained the first coordinate axis for the ordination of vertical foraging stratum use; this axis had an Eigenvalue of 13.50 and explained 52.40% of the variance (Table S1). Use of the ground (-0.26) and understory (-0.21) strata had negative loadings, while use of the subcanopy (0.21) and canopy (0.27) had positive loadings (Table S2, Figure S2). As such, we interpreted this axis as a measure of vertical stratum use. We similarly retained only the first axis from our ordination of foraging maneuver use (Eigenvalue=2.03, percentage variance explained=37.68%; Table S3). On this axis, aerial foraging maneuvers had high positive loadings (sally=0.12, hover glean=0.16, flush-pursue=0.17; Table S4, Figure S3) whereas near-perch maneuvers had negative loadings (probe= -0.17 , hang= -0.16 , flake= -0.17). As such, we interpreted this axis as a measure of the extent to which a species uses aerial versus near-perch maneuvers. Finally, we retained the first two axes from our PCoA of foraging substrate. The Eigenvalues were 3.10 and 2.67 for the first and second axes, respectively, and these axes explained 29.52% and 25.41% of the variance (Table S5). The first axis had high positive loadings for use of the trunk (0.30) and epiphyte (0.31) substrates, and high negative loadings for use of live leaves (-0.11) and air (-0.11) as a substrate (Table S6, Figure S4). We interpreted this axis as a measure of near-trunk versus far-from-trunk foraging substrate use. The second axis had high positive loadings for use of the ground (0.16), dead leaves (0.20), and vine tangles (0.11) as substrates, and high negative loadings for use of air (-0.14), branches and twigs (-0.13), and trunk (-0.21 ; Table S6). We therefore interpreted this axis as a measure of exposed (negative values) versus occluded (positive values) foraging microhabitats.

PLS analysis of area sensitivity

We found support for three of the four hypotheses for resident species: loss of foraging microhabitats and food, changing light intensity, and increased nest predation (Table 2, Fig. 2). Standardized (z-scale transformed) effect sizes were similar (≈ 1) across predictors associated with the three hypotheses, suggesting the multiple mechanisms were all similarly important. For resident birds, dietary specialists were more area sensitive ($\beta=1.09$, 95% CI 0.46, 1.73), as were species that more frequently use the subcanopy and canopy ($\beta=0.69$, 95% CI 0.01, 1.37; Fig. 3b); these results were both in the direction expected based on the loss of food resources hypothesis. Also as predicted, species with larger clutch sizes ($\beta=-1.15$, 95% CI -1.93 , -0.37) were less area sensitive, whereas species with larger relative eye size were more area sensitive ($\beta=0.89$, 95% CI 0.09, 1.68; Fig. 3c). For the insectivore subset, we also found that species which forage at higher strata ($\beta=0.90$, 95% CI 0.02, 1.77) were significantly more area sensitive, while those with larger maximum clutch sizes were less area sensitive ($\beta=-1.51$, 95% CI -2.30 , -0.72). Counterintuitively, species with a larger hand-wing

Table 2 Phylogenetic least squares analysis of functional trait predictors of fragment area sensitivity for Andean birds

Resident species					
N = 4 candidate models					
Mean Adj. $r^2 = 0.16$					
Variable	β	Std. Error	Z value	UCI	LCI
Intercept	5.02	4.27	1.18	13.38	-3.34
Use of bamboo stands	0.44	0.27	1.65	0.96	-0.08
Use of treefall clearings	-0.17	0.30	0.59	0.41	-0.75
Diet specialization (Gini index)	1.09	0.32	3.37	1.73	0.46
Vertical stratum use (PCoA)	0.69	0.34	2.00	1.37	0.01
Maximum clutch size	-1.15	0.40	2.90	-0.37	-1.93
Generation length	-0.41	0.59	0.69	0.75	-1.57
Relative eye size	0.89	0.41	2.19	1.68	0.09
Insectivores					
N = 9 candidate models					
Mean Adj. $r^2 = 0.19$					
Intercept	2.69	2.81	0.96	8.19	-2.82
Use of bamboo stands	0.58	0.30	1.94	1.17	-0.005
Use of treefall clearings	-0.23	0.38	0.61	0.51	-0.98
Use of ravines or streams	-0.29	0.44	0.65	0.58	-1.15
Vertical stratum use (PCoA)	0.90	0.45	2.01	1.77	0.02
Distance from trunk of foraging substrate	0.37	0.56	0.65	1.47	-0.74
Maximum clutch size	-1.51	0.40	3.74	-0.72	-2.30
Generation length	0.46	0.51	0.89	1.46	-0.55
Relative eye size	0.86	0.57	1.50	1.97	-0.26
Hand wing index (HWI)	1.67	0.80	2.10	3.24	0.11

Models were run for the full resident bird community (N = 166 species) and just resident insectivores (N = 73 species). Model results presented are conditional model averaged best model subsets (all models within $2 \Delta AIC_c$ of the best model), and PLS models used the Brownian motion covariance model. Significant predictor variables (i.e., where the 95% confidence interval does not overlap zero) are bolded

index (more pointed wing shape) were also significantly more area sensitive for this subset of species ($\beta = 1.67$, 95% CI 0.11, 3.24). Finally, we found a near-significant effect of use of *Chusquea* bamboo stands on insectivore area sensitivity ($\beta = 0.58$, 95% CI -0.005, 1.17). Model goodness-of-fit was relatively low, with a mean adjusted r^2 of 0.16 and 0.19 for the full community and insectivore subset, respectively.

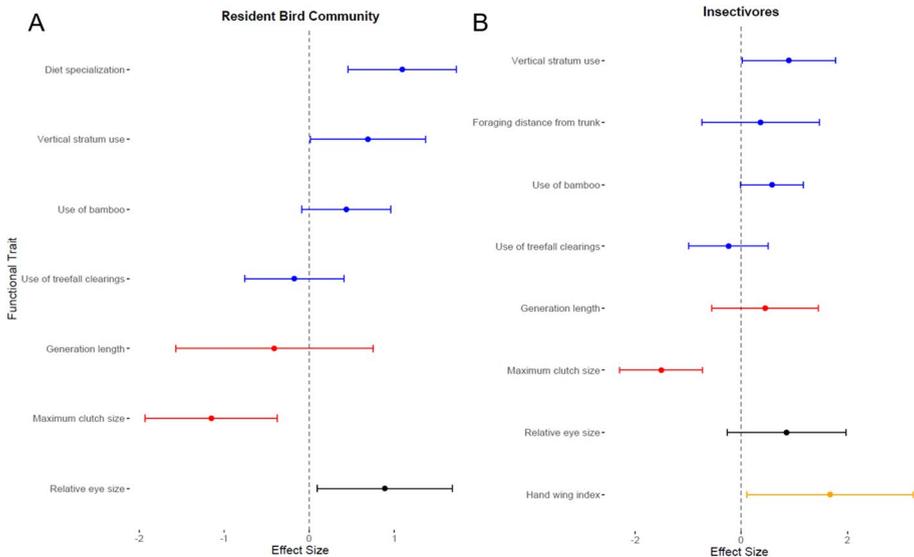
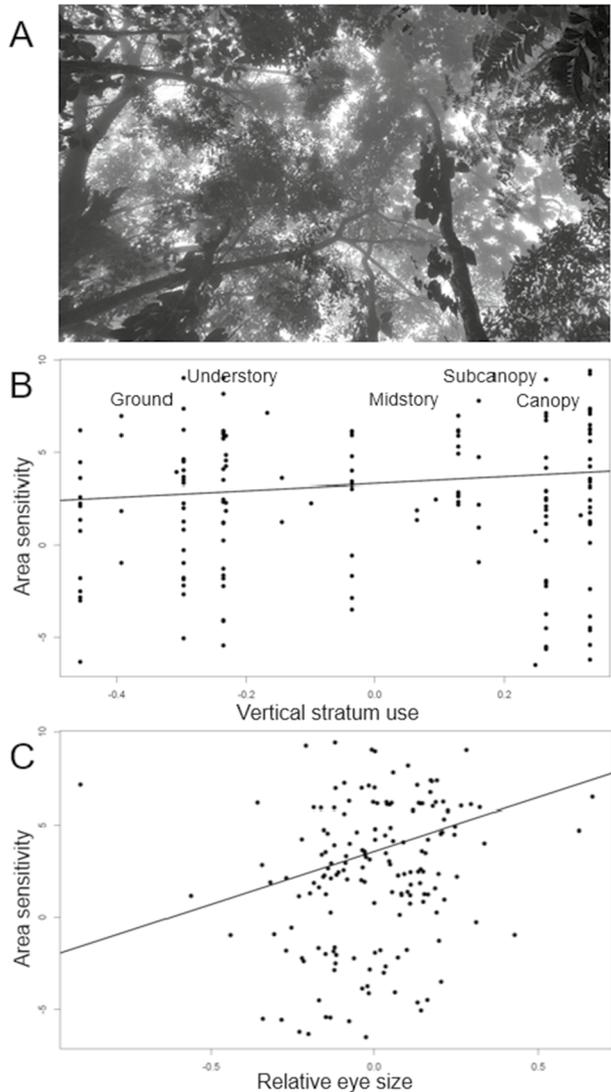


Fig. 2 Effect sizes and 95% confidence intervals of functional traits on fragment area sensitivity. Effect sizes are from phylogenetic linear models using a Brownian motion model of evolution, run for the full community of resident species (A) and a subset of just insectivores (B). Colors correspond to the mechanism of fragmentation sensitivity: loss of food resources (blue), changes to predation patterns (red), changes to light intensity (black), and dispersal limitation (orange)

Discussion

In this study, we used functional traits to test hypothesized mechanisms of fragmentation sensitivity for a cloud-forest bird community, finding indirect support for the changes to food and foraging microhabitat availability, increased predation pressure, and changes to light intensity hypotheses as drivers of bird extirpation in Andean fragments (Robinson and Sherry 2012; Powell et al. 2015; Visco et al. 2015; Ausprey et al. 2021). Conversely, there was no support for the dispersal-limitation hypothesis, and we instead found that insectivores with a larger HWI were more fragmentation sensitive. Overall, multiple simultaneous mechanisms with relatively even effect sizes appeared to explain bird extirpations in Andean fragments, and dietary specialists, subcanopy and canopy-dwellers, species with small clutch sizes, species with large relative eyes, and long-winged insectivores were particularly area sensitive. Many field studies have documented changes to the richness and composition of Andean bird communities after fragmentation (Kattan et al. 1994; Renjifo 1999; Castaño-Villa and Patino-Zabala 2008; Palacio et al. 2020; Jones et al. 2021), but here we test specific mechanisms of fragmentation sensitivity while controlling for phylogeny. Similarly, many studies have examined how avian functional diversity is affected by forest fragmentation (Santillán et al. 2019; Gómez et al. 2021; Ausprey et al. 2022), or which functional traits best predict sensitivity to fragmentation (Lees and Peres 2008; Vetter et al. 2011; Bregman et al. 2014; Keinath et al. 2017), but these functional traits are seldom, if ever, related to mechanisms of fragmentation sensitivity. We believe our methods have promise for testing and disentangling competing hypotheses of fragmentation sensitivity with field data from landscape-level studies.

Fig. 3 Andean forest vegetation structure and climate contribute to novel patterns of fragmentation sensitivity. **A** View of late-successional subtropical Andean forest subcanopy and canopy under heavy fog and cloud cover. Note the low-light conditions, prominent subcanopy stratum, and abundant epiphytic plants. **B** Area sensitivity was higher for species that use the canopy and subcanopy than the understory, perhaps because epiphytes and subcanopy tree species are lost from fragments. Labels correspond to the weighted averages of use of each stratum category from a PCoA. **C** Species with larger relative eye size were more fragmentation sensitive, perhaps because of adaptation to low-light conditions



However, our models did not have a high goodness-of-fit, suggesting that our hypotheses cannot explain all fragmentation sensitivity. This may be partly attributable to stochastic, rather than deterministic, species extirpations, yet lowland tropical bird communities consistently show non-random patterns of species loss (Hill et al. 2011; Luther et al. 2020). Instead, other mechanisms of extirpation may be taking place that we cannot easily quantify using functional traits. First, the connectivity of forest fragments to both upslope and downslope forest, and the persistence of habitat at these elevations, may be important for elevational migrants (e.g., Hilty 1997), though such behavior remains poorly described for Andean birds (Barçante et al. 2017; Jahn et al. 2020). The distance (and isolation) of a fragment from the center of a species' elevational distribution may also be important (Terborgh 1985; Kattan et al. 1994; Mills et al. 2023), since populations at the periphery

of their elevational range may face less suitable habitat and climate and occur at lower densities. Second, Andean landscapes are topographically variable, and relief type influences microclimate and plant communities. Most forest fragments in our study landscape are located on hilltops, yet Ribon et al. (2021) found that many Atlantic Forest species were specialized by relief type, and many preferred ravine microhabitats. Genera associated with ravines and streams in the Andes (e.g., *Doryfera*, *Habia*, *Ochthoeca*) may also be more fragmentation sensitive (Palacio et al. 2020; this study), and topographical complexity could be an important factor for cloud forest species conservation (Martinez-Morales 2005). Third, the elevational ranges of tropical montane birds are increasingly recognized to be constrained by competition with closely related species, often congeners (Jankowski et al. 2010; Freeman et al. 2019, 2022). Because fragments in the Andes are frequently invaded by downslope (Renjifo 1999) and edge-adapted (Jones et al. 2021) species, they may territorially exclude congeners from fragment habitat. We encourage future work to empirically evaluate these hypotheses for Andean avifauna.

Foraging and ecological specialization predict fragmentation sensitivity

Increasing dietary specialization, as quantified by the Gini index, was significantly associated with increased fragmentation sensitivity, suggesting a loss of overall food sources, host plants, or foraging microhabitats for specialists in fragments. This agrees with the findings that ecologically specialized forest species are more fragmentation sensitive (Khimoun et al. 2016; Keinath et al. 2017). Dietary specialists are likely to occur at lower densities on the landscape, a trait associated with fragmentation sensitivity by Renjifo (1999). We found that 53 (84%) of the 63 most specialized species by diet (i.e., where the Gini index = 1) in our community were insectivores, a guild considered particularly sensitive to fragmentation (Bregman et al. 2014; Sherry 2021). Because insectivores are specialized by foraging substrate and stratum (Sherry et al. 2020), the overall simplification of forest structure due to fragmentation (Rocha-Santos et al. 2016) is thought to lead to the loss of species-specific foraging microhabitats (Michel et al. 2015; Stratford and Stouffer 2015). This hypothesis is further corroborated by the fact that avian body condition was significantly correlated (both positively and negatively) with changes to vegetation structure in the same landscape (Jones et al. 2022). Nectarivores and frugivores that are specialized on late-successional plant species might also be affected by the retrogressive succession process in fragments, where the plant species composition more closely approximates early successional communities (Aubad et al. 2008; Putz et al. 2011; Rocha-Santos et al. 2016). For example, more morphologically specialized Andean hummingbirds (likely indicating greater specialization on plant species) were found to be more fragmentation sensitive (Hadley et al. 2018) and both frugivores and nectarivores showed high turnover across the El Cairo fragmentation gradient (turnover represented > 90% of beta dissimilarity in assemblage composition of these guilds; Jones et al. 2021).

Birds that use the subcanopy and canopy were also more sensitive to patch area than those using lower strata. This result agrees with Palacio et al. (2020), who found that Andean canopy species were more vulnerable, and Renjifo (1999), who reported the relative resilience of understory birds in Andean fragments. The finding, however, contrasts with the conventional wisdom that it is understory species, particularly insectivores, that are more fragmentation sensitive (Şekercioğlu et al. 2002; Powell et al. 2015). While many understory species were area sensitive (e.g., *Grallaricula flavirostris*, *Sclerurus obscurior*, *Formicarius rufipectus*, *Cyphorhinus thoracicus*, *Ochthoeca* chat-tyrants), we found

a trend, also noted by Renjifo (1999), of many understory genera sharing fragmentation-averse and fragment-loving species pairs (e.g., *Scytalopus vicinior* and *S. alvarezlopezi*, *Grallaria flavotincta* and *G. guatemalensis*). The frequent landslide disturbance in Andean forests (Crausbay and Martin 2016), leading to dynamic and heterogeneous landscapes with forest patches of different ages (Freund et al. 2021), may create niches for more early-successional understory species, leading to a less-sensitive assemblage. Andean canopy and subcanopy birds may also be more uniquely fragmentation sensitive, however. Many subcanopy and midstory trees are late successional species which are lost during retrogressive succession (see above), and such species tend to have larger fruits (Opler et al. 1980). Large fruits are the primary food source for many large-bodied frugivores (e.g., genera *Trogon*, *Pharomachrus*, *Snowornis*, *Semnormis*, *Pipreola*), a guild that is extremely fragmentation sensitive in the Andes (Palacio et al. 2020; Gómez et al. 2021). The subcanopy also contains the highest abundances of epiphytic plants (Hernandez-Perez et al. 2018; Alzate et al. 2019), which represent important foraging habitat for many specialized insectivores (e.g., *Margarornis stellatus*, *Pseudocolaptes boissonneautii*, *Xiphorhynchus triangularis*) and provide nectar and fruit for canopy specialists. However, epiphytic plant diversity decreases in cloud forest fragments, particularly near edges (Koster et al. 2009; Hundera et al. 2013; Bianchi and Kersten 2014;), likely resulting in the loss of key food resources for canopy species in fragments.

Changes to light microhabitat: edges, canopy gaps, and dispersal limitation?

A large relative eye size was significantly correlated with fragmentation sensitivity, suggesting that increases to light intensity in forest fragments may be an important mechanism of extirpation. This result extends the findings of Ausprey et al. (2021) from a gradient of human land use intensity to a gradient of forest fragment sizes. While changes to temperature and humidity in fragments have often been discussed as a mechanism of fragmentation sensitivity (Stratford and Robinson 2005; Robinson and Sherry 2012), light intensity may change more in fragments than these other factors (Patten and Smith-Patten 2012). Large relative eye size has been correlated with use of darker forest interior microhabitats (Ausprey 2021; Ausprey et al. 2021), yet tropical forest fragments show higher understory light intensities due to edges and canopy gaps (Reis et al. 2021) associated with reduced canopy cover from retrogressive succession and selective logging disturbance (Aubad et al. 2008; Rocha-Santos et al. 2016). Lowland forest-interior birds have been shown to select for darker microhabitats (Pollock et al. 2015; Jirinec et al. 2022), and this pattern correlates with relative eye size (Martinez-Ortega et al. 2014). Forest-specialist species in tropical montane forests also show reduced richness (Martinez-Morales 2005) and occupancy (Jankowski et al. 2021; Jones et al. 2021) with increasing edge density, and changes to light intensity may explain this pattern. Mist net captures show that the composition of Andean understory bird communities was affected up to 200 m away from fragment edges (Restrepo and Gómez 1998), and sensitivity to high-light environments may be even more pronounced in montane forests because of the lower light availability associated with higher fog and cloud cover (e.g., a reduction in incident light by ~80%; Bittencourt et al. 2019). In addition, large relative eye size may influence the ability of a species to disperse across fragmented landscapes. Such species are likely more susceptible to glare in bright, non-forest matrix (Fernandez-Juricic et al. 2012), and it may be the ability to tolerate higher light intensity, rather than wing shape, that explains dispersal success in the El Cairo landscape. The high potential for edge and dispersal effects based on light intensity

strongly suggests that habitat configuration (i.e., fragmentation per se; Fletcher et al. 2018), in addition to habitat loss, is an important determinant of fragment extirpations in Andean cloud forests.

Clutch size effect: changes to predation in Andean fragments?

Species with larger maximum clutch sizes, both amongst insectivores and the full community, were significantly less likely to be fragmentation sensitive, yet the nest predation hypothesis was not fully supported as there was no significant effect of generation length or nest type on sensitivity. We found a relatively small range of maximum reported clutch sizes (1–5), but the species with single-egg clutches were high-montane species with restricted elevational ranges (e.g., *Chlorochrysa nitidissima*, *Dendrocincla tyrannina*, *Snowornis cryptolophus*), a pattern that may be common in tropical mountains (Boyce et al. 2015). The evidence for higher nest predation rates in Andean fragments is equivocal (Arango-Velez and Kattan 1997; Trujillo and Ahumada 2005) and is based on artificial nest studies, which may not accurately describe patterns of predation (Robinson and Sherry 2012). System-specific factors, likely including nest predator identity, influence whether fragmentation has negative or positive effects on tropical nest survival (Vetter et al. 2013) and, while the Andes have lower nest predation rates than the lowlands (Londoño et al. 2023), they also harbor a distinct nest predator community. This community contains fewer snakes and primates and is dominated by large-bodied birds (e.g., *Turdus* thrushes, *Aulacorhynchus* toucanets) and medium- and small-bodied mammals (Arango-Velez and Kattan 1997; Londoño et al. 2023). A camera-trap study in the El Cairo landscape found that large-bodied mammals were extirpated from fragments, while the occupancy of many medium-sized mammals that may predate nests increased (e.g., *Eira barbara*, *Procyon cancrivorous*, *Dasyprocta punctata*; Bedoya-Durán et al. 2023). Thus, the ‘mesopredator’ release hypothesis (Crooks and Soulé 1999) may hold true in subtropical Andean forests, where larger clutch sizes could help buffer against a higher predation rate. The invasion of Andean fragments by lowland bird species (see above) might also increase the density of nest-predating birds in small fragments, such as *Turdus ignobilis* or *Cyanocorax yncas*. Alternatively, changes to vegetation structure associated with fragmentation, such as lower canopy cover, could affect nest predation rates even in the absence of changes to predator densities by making nests more conspicuous (Nana et al. 2015). A better understanding of how nest predator communities are affected by fragmentation (e.g., Tallei et al. 2022), and empirical data on nest survival and conspicuousness in fragments are sorely needed for the Tropical Andes.

Positive HWI effect: the importance of aerial lifestyles?

There was no statistical support for the dispersal limitation hypothesis, as measured by the HWI, and we instead found that, among insectivores, there was a positive association between fragmentation sensitivity and HWI. This is a surprising result, given that tropical insectivores are thought to be dispersal limited (Powell et al. 2015), and that dispersal limitation (measured using HWI) was a strong predictor of fragmentation sensitivity globally (Weeks et al. 2023). Yet this finding agrees with Ausprey et al. (2022), who also found that wing pointedness increased with fragment size in the Andes. HWI has also been positively correlated with the ‘aerial lifestyle’ of a species, however, encompassing both aerial foraging maneuvers and the extent to which species make flights in the course of their

daily movement patterns (Weeks et al. 2022). Insectivores with a higher HWI included both aerially foraging insectivores (e.g., *Hapaloptila castanea*, *Pachyrampus versicolor*), particularly tyrant flycatchers (genera *Phyllomyias*, *Phylloscartes*, *Octoeca*), as well as woodpeckers (Picidae) and woodcreepers (subfamily Dendrocolaptinae), which make long flights from one foraging tree to another. Woodcreepers have previously been described as fragmentation sensitive at middle elevations in the Andes (Castaño-Villa and Patino-Zabala 2008; Santillán et al. 2019). Species with aerial lifestyles may be more sensitive for a few reasons. For one, aerial foragers have larger relative eye sizes (Ausprey 2021) and may be more sensitive to changes to light intensity (see above). Many Andean flycatchers also use upward-sally maneuvers to live foliage, and as such are particularly sensitive to simplified vegetation structure in fragments. Species that make long flights between foraging patches may use specialized resources, especially large-diameter trees, which require larger home ranges and more frequent movement. Not only are large-diameter, late-successional trees lost from fragments (Aubad et al. 2008), but habitat fragmentation may limit movement to other foraging patches. Indeed, large-bodied frugivores that track fruiting events on the landscape (Chatterjee and Basu 2018; Bonfim et al. 2021) and granivores that track bamboo seeding events (e.g., *Spodiornis rusticus*, Sanchez 2005) may be similarly vulnerable. Thus, a better understanding is needed of home range sizes and daily and seasonal movement patterns of Andean birds.

Conclusions and conservation implications

The unique structural features and disturbance regimes of Andean forests produce patterns of fragmentation sensitivity that are both similar to, and strikingly different from, the Neotropical lowlands. As in other systems, foraging and vertical stratum specialization was a good predictor of fragmentation sensitivity, suggesting that loss of food and foraging strata is a major mechanism. However, subcanopy and canopy species, rather than understory birds, were more area sensitive, perhaps because some understory species are adapted to post-landslide successional habitat. We suggest that illegal logging disturbances that simplify vegetation structure and the negative effects of edges on epiphytes and late-successional plants may be particularly important in reducing food sources in fragments. There was no evidence of dispersal limitation in our focal community; instead, insectivores that make more frequent flights in their foraging or daily movements were more vulnerable. The ability of a species to tolerate increased light intensity during cross-fragment dispersal, or within edge and canopy gap habitat in fragments, may thus be a more important driver of sensitivity in forests characterized by frequent fog and cloud cover. Minimizing edge effects and maintaining patches of large-diameter, late-successional trees on the landscape are therefore critical for successful management of area-sensitive species in Tropical Andean cloud forest. Our results highlight the paucity of natural history knowledge (foraging ecology, home range sizes, seasonal and altitudinal movement patterns, identity of nest predators) necessary to effectively implement avian conservation strategies in Andean landscapes.

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Data availability The datasets generated during the current study will be archived at The Institutional Repository at the University of Florida upon acceptance of the manuscript.

Declarations

Competing interest The authors have no relevant financial or non-financial interests to disclose.

Ethical approval Animal capture and manipulation protocols were approved by the Institutional Animal Care and Use Committee of the University of Florida (permit #201709853). Research in Colombia was conducted under the research permit of the Universidad del Valle (permit #1070). Permission to work in forest fragments was obtained from private landowners prior to visiting each site.

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