RESEARCH ARTICLE

Widespread bird species show idiosyncratic responses in residual body mass to selective logging and edge effects in the Colombian Western Andes

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ABSTRACT

Forest fragmentation is a major driver of tropical bird endangerment, yet the mechanisms underlying species losses in fragmented landscapes remain poorly known. Loss of foraging microhabitats and food diversity in fragmented landscapes are potential mechanisms explaining fragmentation sensitivity. We, therefore, measured the body condition (i.e., body mass adjusted for individual size) of 20 tropical understory birds as a proxy for food availability across gradients of fragment patch size and silvicultural histories in the Western Andes of Colombia. Specifically, we asked (1) if body condition correlates with patch size, edge effects, or selective logging disturbance; and (2) if species responses were driven by the same explanatory variables or varied idiosyncratically. We documented significant variation in body condition with covariates in 11 of 20 (55%) understory bird species, and 55% of significant correlations were with fragmentation and selective-logging associated variables. Species responses were idiosyncratic and contrasting, with at least 1 significant response to each fragmentation-related covariate. Most effects, however, were driven by logging-induced changes to vegetation structure including loss of large-diameter trees, reduction in foliage height diversity and canopy cover, and loss of understory vegetation. The body condition of frugivores and nectarivores increased with logging-induced shifts in vegetation structure, with canopy gaps potentially favoring early-successional fruiting and flowering plants. By contrast, some insectivores suffered lower body condition with loss of vegetation structure (reduced foliage height diversity). Overall, our data support the hypothesis that fragmentation and selective logging change food resources available to birds and that some widespread nectarivores, frugivores, and omnivores may benefit from increasing edge density and logging-driven vegetation disturbance. We also documented significant positive effects of breeding condition on body condition, however, highlighting the need to control for this factor. Body condition may therefore be a useful index of habitat suitability when paired with analyses of abundance and demographic changes.

Keywords: Chloropipo flavicapilla, edge effects, forest fragmentation, rainfall effects, selective logging, tropical montane forest, understory insectivores

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LAY SUMMARY

- Body condition, body weight adjusted for body size, is a measure of food availability for birds, but has never been used to evaluate the hypothesis that loss of food leads to the local extirpation of birds in tropical forest fragments.
- We used mist-net captures to measure the effects of forest patch size, amount of forest edge, and selective logging on the body condition of Andean birds across a range of patch sizes in Colombia.
- Half of significant correlations of environmental variables with body condition were with fragmentation- and logging-related covariates, but responses were variable across species (both positive and negative).
- Changes to vegetation structure from selective logging explained two-thirds of significant responses, likely due to differences in the availability of food plants and foraging habitats.
- Contrasting responses to logging disturbance were related to the foraging behavior of each species, suggesting that gain or loss of food resources is a mechanism explaining positive or negative effects, respectively, of logging on tropical bird communities.

Las especies de aves de amplia distribución muestran respuestas idiosincrásicas en la masa corporal residual a la tala selectiva y los efectos de borde en los Andes occidentales de Colombia

RESUMEN

La fragmentación del bosque es uno de los principales responsables de la situación de peligro de las aves tropicales, pero los mecanismos que subyacen a la pérdida de especies en paisajes fragmentados siguen siendo poco conocidos. La pérdida de micro-hábitats de forrajeo y de diversidad de alimentos en paisajes fragmentados son mecanismos potenciales que explican la sensibilidad a la fragmentación. Por tal motivo, medimos la condición corporal (i.e., la masa corporal ajustada por el tamaño individual) de 20 especies de aves del sotobosque tropical como un indicador de la disponibilidad de alimentos a través de gradientes de tamaño de parche y de historias silviculturales en los Andes occidentales de Colombia. Específicamente, preguntamos (1) si la condición corporal se correlaciona con el tamaño del parche, los efectos de borde o el disturbio de la tala selectiva; y (2) si las respuestas de las especies fueron impulsadas por las mismas variables explicativas o variaron idiosincráticamente. Documentamos una variación significativa en la condición corporal con las covariables en 11 de las 20 (55%) especies de aves del sotobosque, y el 55% de las correlaciones significativas fueron con variables asociadas a la fragmentación y la tala selectiva. Las respuestas de las especies fueron idiosincrásicas y contrastantes, con al menos una respuesta significativa a cada covariable relacionada con la fragmentación. Sin embargo, la mayoría de los efectos fueron provocados por los cambios inducidos por la tala en la estructura de la vegetación, incluida la pérdida de árboles de gran diámetro, la reducción de la diversidad de alturas del follaje y de la cobertura del dosel, y la pérdida de la vegetación del sotobosque. La condición corporal de los frugívoros y nectarívoros aumentó con los cambios inducidos por la tala en la estructura de la vegetación, ya que los huecos del dosel potencialmente favorecieron a las plantas con flores y frutos de sucesión temprana. En contraste, algunos insectívoros sufrieron una peor condición corporal con la pérdida de la estructura de la vegetación (reducción de la diversidad de alturas del follaje). En general, nuestros datos respaldan la hipótesis de que la fragmentación y la tala selectiva cambian los recursos alimentarios disponibles para las aves y que algunos nectarívoros, frugívoros y omnívoros de amplia distribución pueden beneficiarse del aumento de la densidad de borde y del disturbio de la vegetación provocado por la tala. También documentamos efectos positivos significativos de la condición reproductiva sobre la condición corporal, destacando la necesidad de controlar este factor. Por lo tanto, la condición corporal puede ser un índice útil de la aptitud del hábitat cuando se combina con análisis de abundancia y cambios demográficos.

Palabras clave: bosque montano tropical, *Chloropipo flavicapilla*, efectos de borde, efectos de lluvia, fragmentación del bosque, insectívoros del sotobosque, tala selectiva

INTRODUCTION

Ongoing habitat loss and fragmentation are major causes of avian extinction in tropical forests (Tracewski et al. 2016), and can also facilitate habitat disturbance (Barlow et al. 2016), particularly changes to vegetation structure resulting from selective logging (Burivalova et al. 2015). But while fragmentation and accompanying logging disturbance have well-known negative effects on biological communities (Wilson et al. 2016, Alroy 2017), including birds (Bregman et al. 2014), mechanisms of avian species loss associated with fragmentation and selective logging remain more elusive (Robinson and Sherry 2012, Visco et al. 2015). One proposed mechanism is the loss of food resources and foraging niches due to a simplification of vegetation structure and changes to floristic composition in fragmented and disturbed forests (Powell et al. 2015, Visco et al. 2015). Many tropical insectivores (Sherry et al. 2020), frugivores (Quitián et al. 2018, Bender et al. 2018), and nectarivores (Weinstein and Graham 2017) are specialized in their foraging ecology, using only specific plants and foraging microhabitats. Therefore, the loss of foraging microhabitats in fragmented and disturbed forest (Visco et al. 2015, Stratford and Stouffer 2015) suggests that food availability for insectivores would decline and that both frugivores and nectarivores would become more dependent on the remaining species of fruiting and

flowering plants (Tinoco et al. 2016, Quitián et al. 2018). Indeed, the isotopic foraging niche width of tropical birds declines in fragmented (Navarro et al. 2021) and selectively logged (Edwards et al. 2013) landscapes, suggesting a reduced breadth of available food resources which may be driving species extirpations. Additional studies, however, are required to show how pervasive this mechanism may be in fragmented tropical landscapes.

Studies testing this reduced food resources hypothesis need measures that are directly tied to food resource use and can be evaluated at the individual level (Johnson 2007). For birds, one such measure is body condition, or the residual of an ordinary least-squares regression of mass against body size (residual mass index; Labocha and Hayes 2012). This index is assumed to be correlated with percentage body fat, and by extension food availability, and these same lipid reserves, in turn, are thought to predict reproductive success and survival (Wilder et al. 2016). While these assumptions do not always hold true (Labocha et al. 2014, Wilder et al. 2016), the residual mass index generally correlates well with percentage body fat for birds (mean $r^2 = 0.42$; Labocha and Hayes 2012). Body condition has been correlated with both food availability in tropical forests (Brown and Sherry 2006, McKinnon et al. 2015) and the reproductive success of at least 1 tropical bird (Milenkaya et al. 2015). Indeed, insectivores and frugivores had a more negative body condition in a tropical forest fragment than

omnivores (Teles et al. 2017), matching trends of fragment extirpations (Bregman et al. 2014). Insectivores also showed decreases in body condition from tropical forest to structurally simplified shade-coffee plantation (Johnson et al. 2006, Sánchez-Clavijo et al. 2020). Body condition could thus serve as an indicator of food availability for resident species in tropical fragmentation studies, as it has for non-breeding migrants (Albert et al. 2020). Despite the promise of body condition as a way of evaluating the reduced food hypothesis, however, a community-wide study of patch-size effects on body condition has never been conducted in the tropics (for single-species studies, see Hermes et al. 2016, Ruiz-Sánchez et al. 2017).

Alternatively, food availability for the individual (and body condition) may not decline in tropical fragments if demographic and density-dependence effects of fragmentation or behavioral plasticity counteract the loss of food resources. Birds might select habitat in accordance with an ideal free distribution (Fretwell and Lucas Jr. 1970), in which lower densities and larger territories in poor-quality habitat result in no change to per capita food availability and therefore body condition (e.g., Castaño et al. 2019). In tropical birds, however, free movement is likely to be constrained by both territorial exclusion (Cruz-Angon et al. 2008) and the ability of a species to navigate across matrix habitat during emigration (Awade et al. 2017). The higher rates of mortality (Korfanta et al. 2012) and nest predation (Newmark and Stanley 2011), and reduced number of breeding species (Rutt et al. 2021), seen in some tropical fragments might also lead to lower densities, counteracting any negative effects of reduced food availability. Some species show higher abundances and lower nest predation rates in fragments (Visco and Sherry 2015), however, suggesting that demographic effects may be system or species specific. Additionally, more behaviorally plastic species can shift to novel foraging microhabitats in forest fragments (Mansor et al. 2018), preventing a loss of food resources. Perhaps for these reasons, decreasing patch size has frequently been shown to be uncorrelated with body condition in north- and south-temperate bird communities (Tellería et al. 2001, Turcotte and Desrochers 2008, Amos et al. 2013). Negative effects of patch size on species richness, however, are more pronounced in tropical birds than in temperate ones (Bregman et al. 2014), and the extent to which food availability is reduced in tropical fragments therefore remains an open question.

In this study, we used body condition as a measure of food availability for a montane understory bird community, testing the reduced food resources hypothesis as a mechanism for fragmentation sensitivity across a fragmented landscape in the Western Andes of Colombia. In a previous study (Jones et al. 2021), we found pronounced differences in species composition and functional diversity along patch-size and selective-logging disturbance gradients in this landscape. We now ask if loss of food resource availability may be a mechanism explaining species extirpation along these gradients. Specifically, our questions were (1) whether food availability, as measured by body condition, correlates with fragmentation (both patch area and changes to biotic conditions at patch edges; Pfeifer et al. 2017) or selective-logging disturbance in a tropical montane bird community; and (2) whether species responses were driven by the same fragmentation or disturbance variable(s) or varied in idiosyncratic ways. A lack of significant declines in body condition with declining patch size would be consistent with the idea that the loss of foraging microhabitats is not a major driver of area sensitivity for our focal species, or that demographic (increased mortality or nest predation) or density-dependent (ideal free distribution) factors counteract this loss. Because body condition indices ostensibly reflect food availability for birds, we predicted that body condition should significantly increase with features of the vegetation structure, density of forest edges, or patch size that are associated with species-specific foraging niches and food plants. We therefore also predicted that logging-induced changes to vegetation structure, which reduce some foraging microhabitats and increase others, would be more important than declining patch size itself in explaining differences in body condition.

METHODS

Study Sites

Study sites were located on the east slope of the Serrania de los Paraguas range in the Colombian Western Andes, specifically in the municipality of El Cairo (4°45′39″N, 76°13′21″W; Figure 1), Valle del Cauca department. This region is a center of avian endemism and threatened species diversity within Colombia (Ocampo-Peñuela and Pimm 2014). The landscape consists of a typical patchwork of forest fragments, cattle pasture, and shade coffee plantations, with ongoing forest clearing for the latter activities. Natural forest cover in this region is subtropical Andean forest, characterized by over 200 tree species, abundant epiphytes, and ~20-m canopies (Aubad et al. 2008). Within this landscape, we identified all isolated forest fragments surrounded by cattle pasture and in the 1,900–2,300 meters above sea level (m.a.s.l.) elevational band using satellite images on Google Earth. We controlled for elevation and matrix type in site selection because Andean bird community composition shifts across elevational gradients (Jankowski et al. 2013), and permeability of matrix type influences the persistence of Andean birds in fragments (Renjifo 2001). We stratified this subset of fragments into large (≥100 ha), medium (30–50 ha), and small (≤20 ha) size categories, before selecting at least 2 of each to survey in detail ($n = 8$ fragments, range: 10–173 ha; Table 1). Selected fragments
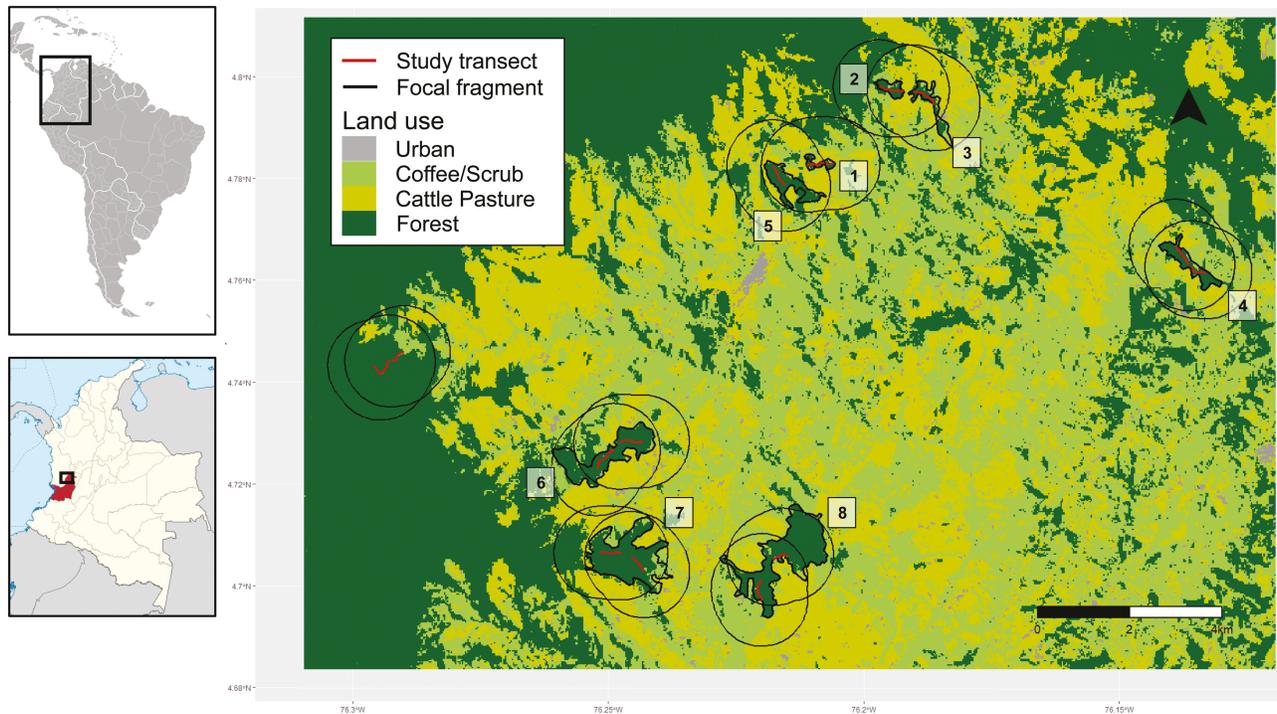
FIGURE 1. Map of study fragments, study transects, and 1-km buffers in El Cairo municipality, Valle del Cauca, Colombia. Black outlines represent fragments selected for the study, whereas red lines represent the transects along which mist-net lines were placed. One-kilometer buffers around each transect (with landcover proportions within the buffer used as a proxy variable for patch size) are shown in black. Numbers correspond to site numbers in Table 1. Land use classifications were generated using supervised image classification of Sentinel-3 imagery from the Google Earth Engine platform. Figure adapted from Jones and Robinson (2020).

were mid- to late-successional forest patches, which we defined as having >10-m canopies, trees of >10 cm diameter at breast height (DBH), a closed canopy, and a diversity of tree age classes. We only sampled 2 small-sized fragments because fragment size tended to increase with elevation in the focal landscape and because we wished to spend approximately equal sample effort at each site (limiting the number of surveys possible within the field season). We additionally sampled a private forest reserve within the same landscape (RNC Cerro El Inglés, ~750 ha) as a reference site. This site is connected to thousands of hectares of continuous forest along the spine of the Western Andes and in the Chocó lowlands to the west. Forest fragments were private lands (sampled with the help of a local NGO: Serraniagua) that varied in their land-use histories, particularly the intensity of selective logging, a common practice in the Colombian Andes (Aubad et al. 2008). Selective logging at our study sites consisted of removal of single marketable trees, creating small canopy gaps of approximately 10–20 m across. To help capture this variability in local disturbance, we established 500-m transects (n = 14 transects; Table 1) through forest interior at each site, placed along existing trails where possible. In large- and medium-sized fragments, we surveyed 2 transects, placed

in locations with more and less selective logging, as determined by visual estimation of tree DBH and canopy openness. We found no evidence that greater selective logging occurred in smaller sampled fragments, as both tree DBH (Pearson's r = 0.25, p = 0.38) and foliage height diversity (Pearson's r = 0.10, p = 0.73) showed little correlation with our measure of patch size (see below). Similarly, there was no significant correlation between elevation and patch size (Pearson's r = 0.34, p = 0.23) or tree DBH (Pearson's r = 0.39, p = 0.17) in the sampled fragments.

Quantification of Patch Size, Edge Effects, and Rainfall
We used a buffer analysis to quantify landscape composition and configuration within a km of each sampling transect. This scale was selected because it affected the occupancy of tropical bird communities in lowland studies (Carrara et al. 2015) and landscape composition at this scale was highly correlated with the composition at other buffer scales at our sites (e.g., 500 m). All landscape analyses were conducted using ArcGIS (ArcMap 10.3.1; Esri, Redlands, CA), specifically the *isectpolyrst* tool in the Geospatial Modelling Environment (version 0.7.4.0; Beyer 2015). Buffers were centered on the full length of the transect, resulting in a non-circular buffer shape (Figure 1).

TABLE 1. Study transects in El Cairo municipality, in the Western Andes of Colombia. Numbered sites refer to study fragments, whereas named transects represent the 500-m transects on which mist-net lanes were placed. Latitude and longitude refer to the center point of each 500-m transect. Sampling periods refer to the June to August 2017 and January to March 2018 sampling periods, respectively. F% = percentage of forest in a 1-km buffer of the 500-m transect. ED = edge density calculated as length of forest edge in meters divided by the total area within a 1-km buffer. DTE = average distance from the transect to forest edge, calculated from the center point of each 100-m segment. RF = average historical yearly rainfall (mm) for the study transect, taken from the WorldClim2 data base. C = total mist-net captures (including recaptures) on a given transect during the sampling season. Spp. = total species richness of birds captured on the transect; for species-specific capture data, see Supplementary Material Table 2. Hr = total number of hours that 12 mist nets were open on the transect during the sampling period of 3 consecutive days. Table modified from Jones and Robinson (2020).

Site	Transect	Latitude	Longitude	Area (ha)	F%	ED	DTE	RF (mm)	June to August			January to March		
									C	Spp.	Hr	C	Spp.	Hr
1	La Cancana	4°46.984'	76°12.511'	10	19.3	18.7	32.2	2,190	64	33	18.0	61	27	27.0
2	La Gitana	4°47.866'	76°11.744'	14	28.9	25.2	47.4	2,546	46	21	23.0	59	29	21.0
3	La Tulia	4°47.793'	76°11.286'	28	13.1	20.2	29.6	2,333	31	20	25.0	57	28	20.0
4	Las Brisas	4°45.904'	76°08.260'	37	32.4	37.9	38.2	2,279	84	27	27.0	84	29	27.5
	El Tigre	4°45.711'	76°08.101'		26.7	30.9	77.6	2,279	47	25	25.0	69	28	28.0
5	Altamira	4°46.857'	76°13.017'	43	23.8	24.1	109.8	2,315	63	26	27.0	77	27	22.0
6	Altomira	4°43.700'	76°14.706'	107	39.1	25.3	150.0	1,994	34	15	26.0	62	24	26.0
	El Eden	4°43.474'	76°15.087'		40	23	111.2	2,388	42	21	24.0	58	21	25.0
7	El Lagito	4°42.277'	76°14.630'	147	41.9	23.5	255.2	2,232	32	17	26.0	65	22	25.0
	La Sonora	4°42.400'	76°14.986'		51.5	29.3	140.0	2,232	68	30	26.0	65	25	24.0
8	La Guardia	4°42.384'	76°12.930'	173	49.4	26.5	102.2	2,291	49	20	26.0	44	21	24.0
	El Rocio	4°41.964'	76°13.254'		43.2	25.2	38.0	2,269	19	8	20.0	34	14	27.0
RN El Ingles	El Brillante	4°44.752'	76°17.448'	750	87.5	12.4	101.6	2,109	82	35	27.0	61	26	26.0
	El Ingles	4°44.526'	76°17.655'		97.1	7.08	601.8	2,193	84	34	27.0	48	33	27.0
									745	102	347.0	844	101	349.5

Following Carrara et al. (2015), we used the proportion of forest cover within the buffer region as a proxy for the patch size of the fragment. We did not use patch size measurements directly because our continuous forest reference site had no patch size. The matrix around our fragments was unshaded cattle pasture, so we, therefore, consider this variable a good proxy for patch size, and the 2 values were highly correlated (Pearson's $r = 0.96$). We quantified fragment configuration (and edge effects) using the "edge density" measure from Carrara et al. (2015), which is defined as the density of forest edge habitat within the 1-km buffer, measured in meters per hectare. We also calculated a straight-line distance to forest edge for each transect, which was the average of 5 measurements taken from the center point of each 100-m transect segment to the nearest forest edge. We measured the proportion of forest cover and edge density using a land-cover use map for our study area from the departmental conservation authority (Corporación Autónoma Regional del Valle del Cauca), which we converted to a 25-m cell-size raster.

Yearly rainfall data for each transect from the WorldClim2 monthly data set (Fick and Hijmans 2017) were collected at ~1-km² resolution. Sampling transects were superimposed on the global raster of rainfall data. We summed the mean monthly historical rainfall data (1970–2000) for each transect to calculate a yearly average; where a transect overlapped multiple raster squares, monthly values for each were averaged.

Quantification of Local Vegetation Structure
For each transect, we measured local vegetation structure and density to quantify the effects of human disturbance, particularly selective logging. Vegetation measurements were taken from June to August 2017, though we observed little annual variation. We followed the sampling methodology of Stratford and Stouffer (2013), which we modified to be used along belt transects. The methodology was broadly comprised of two components: (1) the quantification of canopy height, percentage canopy cover, and foliage height diversity using point sampling situated every 10 m along the transect; and (2) the quantification of tree size category and understory vegetation density, respectively, using 3-m wide belt sampling. Because transects ran along trails, we measured vegetation at least three meters from the trailing edge on a randomly selected side of the trail. For the point sampling, we measured variables at 10-m intervals, for 50 points per transect. As a measure of foliage height diversity, we noted the presence or absence of live vegetation in 5 height bands: <0.5 m, >0.5–3 m, >3–10 m, >10–20 m, and >20 m. We used a laser rangefinder (Raider 550; Redfield, Beaverton, OR) to determine heights above 3 m, sighting through a tube with crosshairs while straddling the point. For each point, we also recorded the highest

canopy height, to the nearest meter. The proportion of canopy cover at each point was calculated to the nearest eighth of the field of view using a vertical densiometer (Densitometer; Geographic Resource Solutions, Arcata, CA). For each transect, we averaged values for both canopy height and canopy cover and calculated the proportion of points at which vegetation was present for each height category. To quantify foliage height diversity, we calculated the Shannon diversity index of the proportion of points with vegetation present in each of the 5 height bands for each transect. Foliage height diversity was highly correlated with canopy height at our sites (Pearson's $r = 0.90$), so we retained foliage height diversity because different tropical bird species and foraging guilds are highly specialized in their use of different vertical foliage strata (Walther 2002, Chmel et al. 2016), and this variable is known to influence fruit tree selection by frugivorous birds (Almazán-Núñez et al. 2021).

For the belt sampling, we surveyed all trees (woody vegetation >2 m in height) on 1.5 m to either side of the observer and measured their DBH. Trees were later categorized into 6 DBH size classes for analysis: 1–7 cm, 8–15 cm, 16–23 cm, 24–30 cm, 31–50 cm, and >50 cm. We also recorded the largest tree DBH recorded on each transect. Because selective logging targets large, old-growth trees we consider this to be a proxy measure for current and historical logging pressure at each site. To capture differences in understory vegetation density, we also recorded the density of shrubs, ferns, lianas (vines), palms, and tree ferns along the same belt survey for each transect. To reduce redundancy and minimize correlation between variables, we used ordinated measures of the tree DBH and understory vegetation data for each transect from respective principal component analyses (PCAs), taken from Jones and Robinson (2020). In each case, we used the first principal component axis; greater values indicate higher densities of large-diameter trees and understory vegetation, respectively. We inverted the sign of the understory vegetation PC axis so that larger values would indicate higher densities for ease of interpretation of results.

Mist Netting and Morphological Measurements
We surveyed understory bird communities along each transect using passive mist netting. Each site was sampled twice, from June to August 2017 and from January to March 2018; both correspond to a local dry season. In each case, we surveyed transects for two and a half consecutive field days, and staggered visits to small, medium, and large fragments to avoid any correlation between fragment size and day of year. We deployed twelve 12 × 3 m mist nets (38-mm mesh; Avinet Research Supplies, Portland, ME) along each transect, placed in locations likely to capture understory birds (i.e., with dense understory vegetation

and outside of direct sunlight). Nets were open from dawn to dusk (approximately 0700–1700 hr) and were operated by 2 or more technicians. We closed nets during periods of heavy rainfall and high winds. All captures were brought to a central banding station where they were identified to species and fitted with an aluminum leg band with a unique number before being released. We did not band hummingbirds (Trochilidae), and instead cut the tip off a unique rectrix for each capture at a site. For each unique capture, we measured the length of the right tarsus and wing chord to the nearest millimeter; tarsus length was not recorded for hummingbirds. We also recorded body mass for each capture. For the first field season, mass was measured in a bag using a spring scale (±0.5 g.; Pesola Precision Scales, Schindellegi, Switzerland). In the second field season, we used a more precise digital scale (±0.01 g.; American Weigh Scales, Cummingham, GA), with the focal individual placed in a measuring cone. We also evaluated the breeding condition of all non-hummingbird captures by scoring the presence and extent of a cloacal protuberance (0–3 scale) and brood patch (0–4 scale) according to the criteria in Pyle (1997). Finally, we identified juvenile individuals, where possible, using a combination of plumage differences, molt limits, and enlarged or colorful rictal flanges. Plumage differences and molt limits are poorly described for our focal species, however.

We then calculated the residual mass index (RMI) for a subset of species with appropriate sample sizes. We selected this index over other common condition indices (e.g., scaled mass index [SMI]; Peig and Green 2009) because it allowed us to use a multivariate measure of body size (see below) and it correlated better with avian relative fat mass in a recent study (Kraft et al. 2019). To ensure that species captures occurred across a wide-enough portion of the gradient to draw strong inference about the effect of fragmentation and disturbance (Labocha and Hayes 2012, Amos et al. 2013), we selected for analysis only species that were captured on at least 8 transects (out of 14), and that had at least 15 unique captures. We chose to calculate RMI for each species separately because each species should have a separate relationship between size and mass (Labocha and Hayes 2012, Amos et al. 2013). For all species except hummingbirds, we calculated a multivariate measure of body size using PCA on the tarsus length and wing chord measurements. We chose a multivariate measure of body size because no one linear measurement of size (wing chord, tarsus length) correlates best with body fat across species (Labocha and Hayes 2012). One or both measures were log transformed for normality where necessary, and obvious outlier points (i.e., those that were measured incorrectly in the field) for tarsus length and wing chord were removed. We then regressed the first PC axis against body mass and retained the residuals as the RMI. For hummingbirds, we regressed wing chord against body mass directly because we did not take tarsus measurements for these species.

Analysis of Fragmentation and Logging Effects on Body Condition

We ran linear mixed models (LMMs; Bolker et al. 2009) to determine the effect of fragmentation and logging disturbance on the body condition of each species with sufficient sample size (*n* = 20 species). In some cases, sample sizes included in analyses were smaller than number of unique captures due to removal of incomplete cases or outlier points. For all species, we fit a global model containing 9 fixed effects representing patch area, edge effects, local vegetation disturbance, rainfall data, and ordinal date (see Supplementary Material Table 1 for variable descriptions); predictor variables were not scaled. We also included 2 random effects of transect (to control for individuals captured on the same transect) and site (to control for transects within the same forest patch). We did not include age as a response variable in the models because we found no significant differences in body condition between adult and juvenile individuals before analysis (Supplementary Material Table 4). We accounted for seasonal effects on body condition by including an ordinal date term in the global model. To control for breeding effects on body condition (Redfern 2010), we additionally included the presence of both brood patch and cloacal protuberance score in the full model for a subset of species. These terms were not included in the models for hummingbirds because we did not collect these data for Trochilids, nor were they included for species where no physiological evidence of breeding was observed during the sampling periods, or boreal migrants (*Catharus ustulatus*). Thus, the global model for each species contained 2 random effects and 9–11 fixed effects depending on whether brood patch and cloacal protrusion were included (global model terms for each species listed in Supplementary Material Table 3).

We used an information theoretic framework to determine the best models explaining body condition, ranking models using AIC values adjusted for small sample size (AIC$_c$; Burnham and Anderson 2002). We considered models equivalent to the best model if their ΔAIC$_c$ value was ≤2 and performed conditional model averaging for all response variables when a single best model did not emerge from the AIC ranking of the full model set. We model averaged across a set of candidate models within 2 ΔAIC$_c$ of the best model rather than the 95% confidence sets because the latter contained hundreds of models (Symonds and Moussalli 2011). We first calculated AIC$_c$ and Akaike weights for all subsets of the global model (see above) using the *dredge* function (*MuMIn* package; Bartoń 2020), and then performed conditional model averaging using the *model.avg* function (same package). We selected conditional model averaging because

unconditional (full) model averaging can bias parameter estimates based on the number of models in the best model set (Powell and Gale 2015). Goodness-of-fit was evaluated using the marginal and conditional r^2 values (Nakagawa and Schielzeth 2013) implemented using the *r.squaredGLMM* function of the *MuMIn* package.

RESULTS

Mist Net Captures and Focal Species
Over two 3-month field seasons, we spent 80 days and ~8,350 passive net hr (12 nets open for 696.5 hr) surveying Andean birds on our fourteen 500-m transects. The number of hours of netting per transect ranged from 44 to 54.5 when pooled across both seasons (mean ± SD = 49.8 ± 3.5; Table 1). We caught 129 bird species belonging to 26 families across 1,589 capture events, of which 1,505 (95%) represented unique (unbanded or unmarked) captures. Of these, we captured 101 species (including 6 boreal migrants) in 844 captures (53%) during the January to March sampling period and 102 species in 745 captures during June to August sampling. The most captured bird families were Trochilidae (24 spp., 36% of total captures), Thraupidae (17 spp.), Tyrannidae (16 spp.), Furnariidae (14 spp.), and Turdidae (6 spp.; see Supplementary Material Table 2 for full species list). Of these, we retained 20 focal species (Supplementary Material Table 2), representing ~64% of unique captures, with adequate sample size for further analyses (range: 8–14 transects, 19–108 unique captures). On average, the sample size for a focal species was 46.1 ± 27.6 unique captures and 11.0 ± 1.7 transects (mean ± SD); full sample sizes are available in Supplementary Material Table 2, while sample sizes included in analyses are presented in Tables 2–4. Focal species spanned a diversity of taxonomic groups, being comprised of 6 non-passerines (hummingbirds), 7 sub-oscine passerines, and 7 oscine passerines.

Linear Mixed Model (LMM) Analysis of Body Condition
We observed significant differences in body condition in response to at least one covariate in 11 of 20 species (55%), and near-significant responses ($p \leq 0.06$) in another 5 species. Four oscine passerines (Table 2), 5 suboscine passerines (Table 3), and 2 non-passerines (Table 4) showed significant responses. Significant differences in body condition were species-specific and the signs of significant effects varied within predictor variables. Twelve of 22 significant responses (55%) were to patch size, edge effect, and vegetation structure variables; whereas 3 responses were to yearly rainfall, 1 to ordinal date, and 5 (23%) were to breeding indicators (presence of cloacal protuberance or brood patch). There was a general trend of increased body condition in breeding individuals, for both the presence of a brood patch and a cloacal protuberance (Tables 2 and 3), and body condition significantly increased with increasing

yearly rainfall on a transect for 2 species. The one exception to this trend was the wren *Henicorhina leucophrys*, which showed a significantly lower body condition with increasing rainfall ($\beta = -0.007$, $p = 0.001$). We also detected a significant effect of ordinal date on the body condition of *Anabacerthia striaticollis* ($\beta = 0.028$, $p = 0.010$). Of the significant fragmentation-related predictors, species responded more frequently to selective logging (8 responses) than to patch size (quantified as percentage forest cover; 1 response) or edge effects (4 responses).

Responses to selective logging (i.e., changes to vegetation structure and tree DBH) were variable in both the vegetation variable affecting body condition and the sign of the effect (Figure 2). The body condition of *Basileuterus tristriatus* ($\beta = 0.21$, $p = 0.07$) and *Adelomyia melanogenys* ($\beta = 0.09$, $p = 0.06$) showed near-significant increases with increasing density of understory vegetation. Conversely, *Arremon brunneinucha* ($\beta = -1.07$, $p = 0.04$), *Myadestes ralloides* ($\beta = -0.56$, $p = 0.006$), and *Ocreatus underwoodii* ($\beta = -0.07$, $p = 0.054$) showed significant or near-significant increases in body condition with declining understory vegetation density. Other significant effects were related to foliage height diversity. The body condition of *Dysithamnus mentalis* was significantly higher ($\beta = 2.13$, $p = 0.006$) on transects with greater foliage height diversity (i.e., a greater number of vertical vegetation height bands). By contrast, we observed a near-significant increase in the body condition of *Uranomitra franciae* with decreasing foliage height diversity ($\beta = -0.16$, $p = 0.051$). Still other effects of selective logging on body condition involved the density of large-diameter trees. *Chloropipo flavicapilla* ($\beta = -1.02$, $p = 0.01$), *Zimmerius chrysops* ($\beta = -0.57$, $p = 0.03$), and *A. melanogenys* ($\beta = -1.18$, $p = 0.002$) showed significant declines in body condition with increasing densities of large-diameter trees, while *Mionectes striaticollis* ($\beta = 0.27$, $p = 0.02$) showed the opposite pattern. Finally, both *M. striaticollis* ($\beta = 0.11$, $p = 0.007$) and *Catharus ustulatus* ($\beta = 0.12$, $p = 0.07$) showed positive responses of body condition to increasing canopy cover.

Responses to patch size and edge effects were less variable across species and generally indicated higher body condition with declining patch size (5 of 8 species where the term was included in the best model set). Only one species showed a significant response to percentage forest cover, and its body condition was higher in smaller patches (*D. mentalis*, $\beta = -0.19$, $p = 0.03$). One hummingbird, however, showed the opposite near-significant trend (*Coeligena coeligena*, $\beta = 0.007$, $p = 0.06$) of higher body condition with increasing percentage forest cover. Edge effects were variable based on the scale at which they were measured. Many species showed a positive correlation between body condition and increasing edge density within 1 km of the sampling transect, including *M. striaticollis* ($\beta = 0.09$, $p = 0.02$), *Anabacerthia striaticollis* ($\beta = 0.73$, $p = 0.002$), and *Heliodoxa rubinoides*

TABLE 2. Model-averaged estimates of environmental covariate effects on the body condition of oscine passerine species. Sample sizes of transects and captures refer to the number of transects and unique capture events included in the analysis, whereas the sample size of models refers to the number of models included in the best model set (i.e., $\Delta AIC_c \leq 2$). Beta estimates are the result of conditional model averaging of the best-model set (where N models > 1). Conditional r^2 values refer to the average r^2 of the fixed effects of the model whereas marginal r^2 values measure model fit while including the random effects of site and transect. Bolded beta estimates are statistically significant, and italicized beta estimates are near-significant ($p \leq 0.06$). FHD = foliage height diversity, the diversity of vertical foliage layers within the forest.

	Myiothlypis coronata			Basileuterus tristriatus			Myioborus miniatus			Arremon brunneinucha		
N transects	11			14			10			11		
N captures	54			35			30			20		
N models	8			7			4			4		
Conditional r^2	0.02			0.14			0.27			0.20		
Marginal r^2	0.02			0.14			0.27			0.75		
	β	SE	p	β	SE	p	β	SE	p	β	SE	p
Forest cover	−0.049	0.052	0.35							−0.066	0.034	0.07
Edge density												
Distance to edge	0.045	0.048	0.34									
Canopy cover												
Understory density				0.207	0.110	0.07				**−1.068**	0.467	0.04
Tree size				−0.218	0.162	0.20						
FHD	0.349	0.403	0.40									
Yearly rainfall	−0.003	0.002	0.18									
BP				*−0.339*	0.163	0.05	0.277	0.158	0.10			
CP	0.458	0.435	0.30				**0.739**	0.280	0.01	*0.013*	0.006	0.05
Ordinal date	0.004	0.003	0.29	0.002	0.002	0.27	0.002	0.001	0.19			

	Myadestes ralloides			Catharus ustulatus			Henicorhina leucophrys		
N transects	14			10			11		
N captures	92			43			24		
N models	8			7			1		
Conditional r^2	0.09			0.08			0.34		
Marginal r^2	0.09			0.10			0.34		
	B	SE	p	B	SE	p	B	SE	p
Forest cover	−0.002	0.003	0.36	0.070	0.039	0.09			
Edge density	0.085	0.058	0.15	−0.198	0.135	0.15			
Distance to edge									
Canopy cover				0.116	0.063	0.07			
Understory density	**−0.556**	0.202	0.006	−0.262	0.260	0.33			
Tree size	−0.239	0.249	0.34						
FHD	−0.306	0.364	0.41						
Yearly rainfall				−0.003	0.003	0.21	**−0.007**	0.002	0.001
BP									
CP									
Ordinal date	0.005	0.004	0.17						

TABLE 3. Model-averaged estimates of environmental covariate effects on the body condition of suboscine passerine species. Sample sizes of transects and captures refer to the number of transects and unique capture events for the species that were included in the analysis, whereas the sample size of models refers to the number of models included in the best model set (i.e., $\Delta AIC_c \leq 2$). Beta estimates are the result of conditional model averaging of the best model set. Conditional r^2 values refer to the average r^2 of the fixed effects of the model whereas marginal r^2 values measure model fit while including the random effects of site and transect. Bolded beta estimates are statistically significant, and italicized beta estimates are near-significant ($p \leq 0.06$). FHD = foliage height diversity, the diversity of vertical foliage layers within the forest.

	Chloropipo flavicapilla			*Zimmerius chrysops*			*Mionectes striaticollis*			*Syndactyla subalaris*		
N transects	8			8			13			11		
N captures	25			28			70			36		
N models	4			8			9			2		
Conditional r^2	0.28			0.18			0.18			0.02		
Marginal r^2	0.28			0.18			0.18			0.02		
	β	SE	*p*	β	SE	*p*	β	SE	*p*	β	SE	*p*
Forest cover				−0.030	0.019	0.14	−0.013	0.008	0.11			
Edge density							**0.086**	0.037	0.02			
Distance to edge				−0.010	0.006	0.09	**0.005**	0.002	0.004			
Canopy cover	−0.099	0.062	0.13				**0.107**	0.039	0.007			
Understory density												
Tree size	**−1.018**	0.387	0.01	**−0.567**	0.244	0.03	**0.273**	0.118	0.02			
FHD				−0.267	0.150	0.11	0.159	0.154	0.31			
Yearly rainfall	**0.005**	0.002	0.03				0.001	0.001	0.34			
BP				**0.423**	0.194	0.04	−0.338	0.184	0.07	0.379	0.358	0.31
CP	**3.490**	1.528	0.03				**2.062**	1.005	0.04			
Ordinal date												

	Anabacerthia striaticollis			*Xiphorhynchus triangularis*			*Dysithamnus mentalis*		
N transects	8			10			11		
N captures	19			26			30		
N models	3			2			6		
Conditional r^2	0.18			0.02			0.34		
Marginal r^2	0.25			0.08			0.46		
	β	SE	*p*	B	SE	*p*	β	SE	*p*
Forest cover							**−0.189**	0.087	0.03
Edge density	**0.728**	0.208	0.002				*0.286*	0.149	0.07
Distance to edge							*0.028*	0.014	0.06
Canopy cover									
Understory density									
Tree size									
FHD							**2.128**	0.733	0.006
Yearly rainfall							**0.010**	0.004	0.03
BP	**1.813**	0.656	0.01						
CP									
Ordinal date	**−0.028**	0.009	0.003	0.010	0.009	0.29	−0.009	0.006	0.16

($\beta = 0.05$, $p = 0.06$), though *Phaethornis guy* responded negatively to this variable ($\beta = -0.02$, $p = 0.03$). By contrast, body condition responded *negatively* to edge effects when they were measured as average distance of the sampling transect to forest edge (*M. striaticollis*, *D. mentalis*; Table 3).

DISCUSSION

Overall, our study provided support for the hypothesis that both fragmentation and selective logging change food availability for tropical birds, both positively and negatively.

While the factors affecting body condition were varied, with at least 1 significant response of body condition to each of area, edge, and logging effects, two thirds of significant responses to these effects were driven by logging-induced changes to vegetation structure. Selective-logging effects on body condition appeared to stem from multiple simultaneous changes to vegetation characteristics: loss of large-diameter trees, reduction in foliage height diversity and canopy cover, and destruction of understory vegetation (Figure 2). Similarly, we found that the body condition of *C. flavicapilla*, a globally threatened, near-endemic

TABLE 4. Model-averaged estimates of environmental covariate effects on the body condition of non-passerine species. Sample sizes of transects and captures refer to the number of transects and unique capture events for the species that were included in the analysis, whereas the sample size of models refers to the number of models included in the best-model set (i.e., $\Delta AIC_c \leq 2$). Beta estimates are the result of conditional model averaging of the best model set. Conditional r^2 values refer to the average r^2 of the fixed effects of the model whereas marginal r^2 values measure model fit while including the random effects of site and transect. Bolded beta estimates are statistically significant, and italicized beta estimates are near-significant ($p \leq 0.06$). FHD = foliage height diversity, the diversity of vertical foliage layers within the forest.

	Uranomitra franciae			*Heliodoxa rubinoides*			*Ocreatus underwoodii*		
N transects	9			9			12		
N captures	42			17			54		
N models	14			2			8		
Conditional r^2	0.13			0.11			0.12		
Marginal r^2	0.13			0.13			0.13		
	β	SE	p	β	SE	p	β	SE	p
Forest cover	*0.016*	0.008	0.07	*0.053*	0.025	0.059			
Edge density	*0.002*	0.001	0.07				*−0.011*	0.006	0.06
Distance to edge	−0.024	0.014	0.09				*0.001*	0.000	0.06
Canopy cover									
Understory density	−0.167	0.093	0.08				−0.072	0.037	0.054
Tree size	−0.164	0.081	0.051				0.068	0.048	0.16
FHD	−0.001	0.001	0.07						
Yearly rainfall	0.002	0.001	0.06	0.001	0.001		0.001	0.001	0.09
Ordinal date									

	Coeligena coeligena			*Adelomyia melanogenys*			*Phaethornis guy*		
N transects	11			10			13		
N captures	55			99			81		
N models	5			5			6		
Conditional r^2	0.06			0.07			0.09		
Marginal r^2	0.06			0.07			0.09		
	β	SE	p	β	SE	p	β	SE	p
Forest cover	*0.007*	0.004	0.06				−0.006	0.004	0.17
Edge density				0.006	0.007	0.42	**−0.020**	0.009	0.03
Distance to edge							0.001	0.001	0.19
Canopy cover	−0.014	0.013	0.32	−0.005	0.008	0.51	0.007	0.011	0.54
Understory density				*0.092*	0.048	0.06			
Tree size				**−0.147**	0.062	0.02			
FHD							−0.074	0.064	0.26
Yearly rainfall				0.000	0.000	0.43			
Ordinal date	−0.002	0.001	0.07						

FIGURE 2. Mechanisms of selective logging effects on understory bird body condition. (**A**) Selectively logged tree in El Cairo municipality, Valle del Cauca department, Colombia. The image showcases damage to understory vegetation and creation of an artificial canopy gap. Photo credit: HHJ. (**B**) Significant and near-significant effects of vegetation structure variables on body condition. Arrows indicate the predicted change in body condition with selective logging. Red and green arrows indicate significant declines and increases in body condition, respectively, while gray arrows indicate near-significant effects ($p \leq 0.06$). Bird species are, from top left to bottom right, *M. striaticollis*, *D. mentalis*, *U. franciae*, *A. melanogenys*, *C. flavicapilla*, *Z. chrysops*, *B. tristriatus*, *M. ralloides*, *A. brunneinucha*, and *O. underwoodii*. Bird illustrations reproduced with permission from Lynx Editions.

manakin, was significantly higher with declining densities of large-diameter trees and increasing yearly rainfall (Figure 3). By contrast, some insectivores (*D. mentalis*, *B. tristriatus*) showed declining body condition with a loss of foliage height diversity. Body condition analyses, therefore, have potential to provide information on habitat suitability when paired with analyses of abundance and demographics. Non-fragmentation effects were primarily driven by significantly higher body conditions associated with the presence of brood patches and/or cloacal protuberances in many passerine species, however, showcasing the need to control for breeding stage and sex in body-condition studies. Additionally, many of the r^2 and beta values from our models were low (e.g., marginal $r^2 < 0.2$), suggesting that many other factors not included in our models affect body condition. Further studies evaluating a greater diversity of correlates of body condition, and validating condition indices developed for temperate species, are urgently needed for tropical birds.

Body Condition: A Tool for Untangling Species-specific Mechanisms?

To our knowledge, this is the first study to examine effects of forest fragmentation on the body condition of a tropical bird community, though others have documented evidence of lower energetic condition in tropical fragments (e.g., greater prevalence of fault bars; Sodhi 2002). Our study found significant differences in the body condition of 11 of 20 (55%) understory bird species in Andean fragments, and 55% of significant species responses were to fragmentation- and disturbance-related variables (e.g., patch size, edge effects, and vegetation structure). This result stands in contrast to community-level studies from north- and south-temperate forests that found no significant effects of fragmentation on body condition (Tellería et al. 2001, Turcotte and Desrochers 2008, Amos et al. 2013). As with previous studies of species occupancy (Banks-Leite et al. 2013, Bhakti et al. 2018), no single scale explained body condition responses in fragments on its own. Instead, we documented species-specific responses, with substantial variation in the sign and magnitude of beta estimates. This idiosyncratic response of body condition mirrors similarly contrasting responses of species occupancy to both patch size (Bregman et al. 2014, Keinath et al. 2017) and selective logging disturbance (Burivalova et al. 2015, Barlow et al. 2016). Tropical bird communities (e.g., Carrara et al. 2015), especially in the Andes (O'Dea and Whittaker 2007, Palacio et al. 2020), undergo species turnover from forest-specialist species to generalist and disturbance-adapted species in fragments and degraded forest. Disturbance-adapted
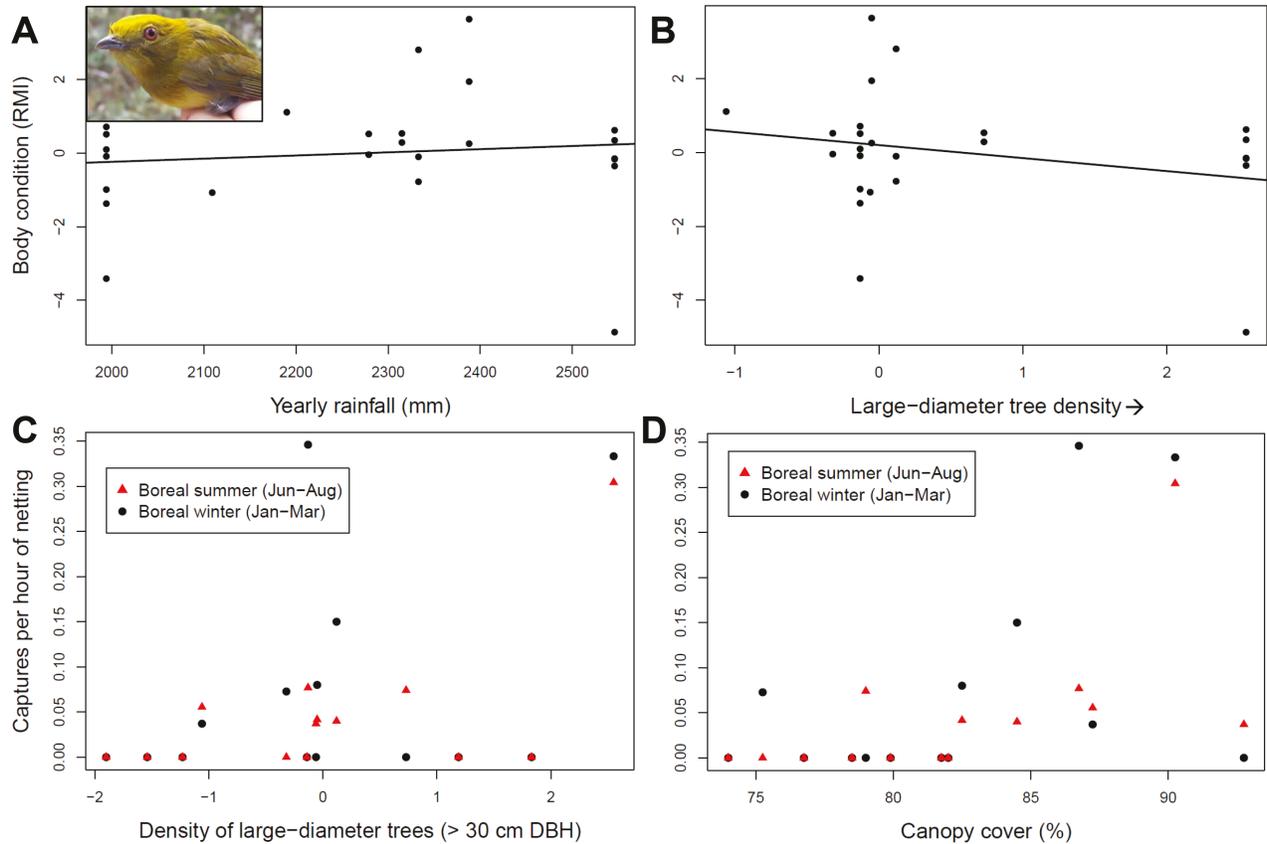
FIGURE 3. Effects of environmental predictors on the body condition and capture rate of *Chloropipo flavicapilla*. There was a significant effect of increasing yearly rainfall (**A**) and decreasing density of large-diameter trees (**B**) on the body condition of this at-risk piprid. The species may prefer intermediate successional stages or treefall gaps, with higher capture rates on transects with intermediate densities of large-diameter trees (**C**) and where small canopy gaps (85–90%) exist (**D**). Photo credit: HHJ.

species may therefore show increases in body condition with fragmentation and disturbance, as we found for species such as *A. brunneinucha*, *D. mentalis*, and *Z. chrysops*, while forest specialists instead have lower body condition in fragments. The loss of forest-specialist species may also explain the lack of significant negative effects of patch size, and the generally positive edge effects, on condition. Edge- and area-sensitive forest specialists (e.g., *Myiophobus flavicans*, *Cyphoryinus thoracicus*, *Sphenopsis frontalis*; Jones et al. 2021) were lost from small and medium fragments in our focal landscape and were consequently not present on enough transects to be included in the analysis. The overall positive response of many species' body condition to increasing edge density and vegetation disturbance, therefore, provides further evidence for the theory that birds that thrive in fragments are generally edge- and disturbance-adapted (Banks-Leite et al. 2010).

Selective Logging Effects: Multiple Mechanisms and Contrasting Responses

Significant and near-significant responses of body condition to vegetation structure variables (*n* = 4; listed in Supplementary Material Table 1) were more common than to edge and patch-size effects, highlighting the importance of changes to vegetation structure as a driver of food availability within fragments (Stratford and Stouffer 2015, Visco et al. 2015, Bhakti et al. 2018). The main driver of these structural changes in our study landscape is illegal selective logging of large-diameter, marketable trees, which shifts plant community composition towards early successional species by favoring colonization of shade-intolerant trees in canopy gaps (Aubad et al. 2008) and occurred both before and concurrently with our study (Figure 2A). However, similar shifts in vegetation structure and composition can occur in fragments even without logging as late-successional tree species are extirpated (Putz et al. 2011). We show for the first time that these logging-based changes to vegetation structure can significantly affect the body condition of understory birds, with species-specific responses. Previous work in a Bornean bird community did not find any significant effects of selective logging on body condition (Messina et al. 2021), though that study used coarser categorical measures of selective logging which, unlike our continuous measures of

vegetation structure, cannot capture the specific structural changes driving changes to bird communities. Neotropical birds are also thought to be more sensitive to logging than Indomalayan species (Burivalova et al. 2014). As in previous occupancy-based studies, we found that reduced foliage height diversity (Sekerçioğlü 2002), lower densities of large-diameter trees (Politi et al. 2012), and reductions to understory vegetation (Thiollay 1997) all had significant effects on body condition. Our finding that body condition responded both positively and negatively to logging also implies that selective logging can cause species turnover, and indeed compositional shifts are commonly observed in selectively logged tropical forests relative to reference sites (e.g., Thiollay 1997, Politi et al. 2012).

We suggest that the observed differences of selective logging on body condition reflect the loss or creation of specialized foraging microhabitats and therefore availability of food resources. While Yap et al. (2007) found few differences in the overall abundance of insect and fruit resources in relation to selective logging, the resulting structural changes can create additional foraging microhabitat for early-successional species (Heltzel and Leberg 2006, LaManna and Martin 2017). The loss of specialized foraging microhabitat is thought to be most disruptive to insectivorous species (Visco et al. 2015, Stratford and Stouffer 2015), and two insectivores were among the few species showing negative responses to selective logging. *D. mentalis*, for example, forages primarily in the forest midstory (Zimmer and Isler 2020) and showed a significant decline in body condition with reduced foliage height diversity, likely because it loses access to foraging microhabitats. Similarly, *M. striaticollis* forages primarily on moss, bark, and outer foliage in the forest midstory (Greeney et al. 2006) and showed significantly lower body condition where logging gaps (reduced canopy cover, low density of large-diameter trees) likely remove this microhabitat. By contrast, the destruction of understory vegetation from selective logging may create foraging microhabitat for species that forage in the leaf litter, such as *A. brunneinucha*. Older harvested stands with high densities of regenerating understory vegetation, however, may also provide habitat for some understory insectivores (Heltzel and Leberg 2006). Nectarivores and granivores, by contrast, are often more abundant in selectively logged forests (Burivalova et al. 2015), which is consistent with our findings (*A. brunneinucha*, *A. melanogenys*, *U. franciae*). Removal of large-diameter trees may simulate canopy gaps and forest edge habitat, which likely create openings for flowering shrubs and small trees preferred by many hummingbirds (e.g., *Bomarea*, *Cavendishia*, *Eugenia*, *Fuchsia*, *Psammisia*; Schuchmann and Boesman 2020). We also found increased body condition of understory and midstory frugivores (*M. ralloides*, *C. flavicapilla*, *Z. chrysops*) with reduced densities of large-diameter trees, which may also be tied to an increased prevalence of early-successional fruiting trees and shrubs (e.g., Melastomataceae; Kessler-Rios and Kattan 2012) or a higher density of mid-story trees growing in older logging gaps. For example, *M. ralloides* primarily forages on berries from Melastomataceid shrubs in the understory and midstory (Collar 2020). One plausible mechanism of logging effects in Andean forests, therefore, appears to be changes to food plant and foraging microhabitat availability that result from shifts in vegetation structure.

Breeding and Sex Effects on Body Condition

We observed significant effects of either brood patch size or cloacal protuberance (but not both) on the body condition of 5 of 13 (38%) passerine species for which we collected these data. In all cases, increasing brood patch or cloacal protuberance scores were correlated with higher body condition. These results agree with previous studies across a range of passerine species showing that female body condition increases with brood patch size during the egg-laying and early incubation stages of nesting (Redfern 2010, Milenkaya et al. 2013). The added mass of developing eggs and gonadal recrudescence, which occur in conjunction with early development of the brood patch, likely explain this increasing female body condition (Redfern 2010, Milenkaya et al. 2013). While it is possible that similar effects on male body condition occur from recrudescence of the testes, we believe that the significant effects observed in our models may instead result from sex-specific differences in body condition. Indeed, male birds are often (Brown and Sherry 2006, Borowske et al. 2018), but not always (Milenkaya et al. 2013), observed to have a higher body condition than females, independently of habitat or seasonal effects. Such patterns could result from the costs of greater female reproductive investment (e.g., Borowske et al. 2018) or exclusion of females from high quality foraging microhabitats by socially dominant males (Cooper et al. 2021). We did not include sex as a covariate for our analyses because most species in our focal community are not sexually dimorphic. Our results, therefore, reinforce the need to account for sex and breeding stage in condition studies of both tropical and temperate birds (Labocha and Hayes 2012, Milenkaya et al. 2013); indeed, these breeding effects may be more important to control for in the tropics given the asynchrony in breeding timing both within and across species.

Conservation Implications: *Chloropipo flavicapilla*

We captured numerous *C. flavicapilla*, a Colombian near-endemic manakin (Pipridae), which is globally listed as Vulnerable (Birdlife International 2022). The habitat requirements of this species are poorly known, as

it has a localized distribution and is uncommon and inconspicuous (Peña and Weber 2000, Kirwan and Green 2012, p. 263). As in Cuervo et al. (2008), we only detected *C. flavicapilla* using mist nets, which we, therefore, recommend as the preferred survey method for this species. The species was thought to be area-sensitive (Kirwan and Green 2012), though we encountered it even in small (10–20 ha) fragments and it has persisted in other fragmented landscapes (López-Lanús et al. 2000). Our data agree with the idea that this manakin prefers tall secondary forest (López-Lanús et al. 2000) and it may benefit from older selectively logged forest, where plant composition is closer to a secondary forest (Aubad et al. 2008). The body condition of this species significantly, but weakly, increased with declining densities of large-diameter trees, and on transects with more yearly rainfall (Figure 3A and B). These trends may be tied to the abundance of preferred understory fruiting plants (e.g., *Palicourea*, Rubiaceae: Peña and Weber 2000), which are perhaps disturbance associated. The species may also prefer humid ravines (López-Lanús et al. 2000), and its capture rate increased with yearly rainfall on the transect. We argue that its rarity may be due to its association with tall second growth, requiring several decades of regeneration, and/or canopy gaps. In support of this idea, capture rates for the species appeared to be highest at intermediate densities of large-diameter trees and high, but not complete (~85%), canopy cover (Figure 3C and D). Studies identifying the preferred fruits consumed by *C. flavicapilla*, and their associations with disturbance, successional stage, and rainfall patterns should therefore be a priority.

Conclusions

Our results suggest that fragmentation and selective logging can influence the availability of food resources for tropical birds, though we did not directly measure food availability at our study sites. Previous work found that avian trophic niche width declined in selectively logged (Edwards et al. 2013) and fragmented (Navarro et al. 2021) forest, suggesting a loss of overall food availability or variety. Furthermore, our body-condition-based results are consistent with our focal species' ecology. For example, the body condition of the traplining hummingbird *P. guy* declined with greater edge density, matching a radiotelemetry study showing this species has difficulty crossing matrix habitat (Hadley and Betts 2009). Because both mass and body size measures are commonly recorded while mist netting, we suggest that body condition measures be adopted more widely to complement occupancy-based estimates of habitat suitability. To be most successful, body condition measures should aim to sample the widest range of environmental conditions possible and may fail to detect significant effects where sampling locations are homogenous (Amos et al. 2013). Given the importance of

breeding state on body condition (see above), we also believe that it is essential to control for this factor in analyses of body condition. Simultaneous collection of fat and pectoral muscle scores may also allow for a more nuanced picture of changes to energy reserves (e.g., Cooper et al. 2015). We caution, however, that RMI is a crude measure of body condition, and that more precise measures of blood chemistry or lipid mass contents will provide a more informative (though costly) picture of an individual's physiological state (Wilder et al. 2016). Demographic effects of fragmentation, such as lower densities (Ruiz-Sánchez et al. 2017), or increased mortality (Korfanta et al. 2012), can obscure or counteract the negative effects of reduced food resources, and studies of body condition should therefore ideally be paired with demographic measures. Nevertheless, we believe that body condition has the potential to help us better understand species-specific responses to fragmentation through cheaply available data collected for other purposes (e.g., species inventories, color-banding studies).

SUPPLEMENTARY MATERIAL

Supplementary material is available at *Ornithological Applications* online.

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Data deposits: Analyses reported in this article can be reproduced using the data provided by Jones et al. (2022).

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