

Hummingbird diversity in a fragmented tropical landscape in the Chocó biogeographic zone

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Abstract

Forest loss and fragmentation drive widespread declines in biodiversity. However, hummingbirds seem to exhibit relative resilience to disturbance, characterized by increasing abundance alongside declining species richness and evenness. Yet, how widespread this pattern may be, and the mechanisms by which it may occur, remain unclear. To fill in this knowledge gap, we investigated habitat- and site-level patterns of diversity, and community composition of hummingbirds between continuous forest (transects $n = 16$ in ~3500 ha) and more disturbed surrounding fragments ($n = 39$, 2.5–48.0 ha) in the Chocó rain forest of northwestern Ecuador. Next, we assessed within-patch and patch-matrix characteristics associated with hummingbird diversity and composition. We found higher hummingbird species richness in forest fragments relative to the continuous forest, driven by increased captures of rare species in fragments. Community composition also differed between continuous forest and fragments, with depressed evenness in fragments. Increased canopy openness and density of medium-sized trees correlated with hummingbird diversity in forest fragments, although this relationship became nonsignificant after applying false discovery rate ($p < .01$). Higher species richness in fragments and higher evenness in the continuous forest highlight the complex trade-offs involved in the conservation of this ecologically important group of birds in changing Neotropical landscapes.

Abstract in Spanish is available with online material.

KEYWORDS

composition, countryside biogeography, Ecuador, evenness, fragmentation, Hill numbers, Reserva Ecológica Mache-Chindul

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1 | INTRODUCTION

Habitat loss and fragmentation are one of the main factors affecting biodiversity in Neotropical forests around the world. The conservation of continuous primary forest has been largely endorsed, as biodiversity often declines following habitat loss (Gardner et al., 2007; Gibson et al., 2011). In addition, fragmented secondary forests as a result of habitat loss seem to take many decades to recover species composition in plants and animals despite relatively fast recovery in richness (Chazdon, 2003; Dunn, 2004). Yet, the response to habitat loss and fragmentation can vary by study area and the level of fragmentation (Caro, 2010; Fahrig, 2017), foraging guild (Barlow et al., 2007; Hendershot et al., 2020), and by taxon (Medellín et al., 2000; Renjifo, 2001). Better understanding the ways in which habitat loss and fragmentation impact biotic communities, and the proximate factors that drive observed patterns, continues to be a research priority for ecologists and conservationists.

Hummingbirds display mixed responses to habitat loss and fragmentation (Barlow et al., 2007; Blake & Loiselle, 2001; Bustamante-Castillo et al., 2018; Renjifo, 1999; Vetter et al., 2011). On the one hand, hummingbird abundances and species richness may be higher or similar in isolated fragments and agricultural plots compared with primary forests (Barlow et al., 2007; Stouffer & Bierregaard, 1995; Tinoco et al., 2018). On the other hand, species richness does appear to decrease in smaller fragments (Hadley et al., 2017; but also see Graham & Blake, 2001), and community evenness may also decrease over the long term (~10–20 years) as generalist species become more dominant (Bustamante-Castillo et al., 2018; Stouffer & Bierregaard, 1995; Tinoco et al., 2018). This latter pattern suggests that hummingbirds may follow the general response of community composition to disturbance where only a few species become more common and rare species decline (Barlow et al., 2007; Graham & Blake, 2001; Hendershot et al., 2020; Medellín et al., 2000; Pardini et al., 2009; Wenzel et al., 2020). However, more studies from a greater range of disturbed landscapes and study systems are required to better resolve how human activities may impact the diversity of hummingbirds.

Better understanding determinants of hummingbird diversity is important because they are one of the most abundant and diverse bird families throughout Neotropical forests (Billerman et al., 2020). Hummingbirds, along with other animal pollinators, contribute to the maintenance and function of tropical ecosystems, where wind pollination is relatively rare (Ollerton et al., 2006, 2011). For example, they are the main pollinators for iconic tropical plant families such as Heliconiaceae and Bromeliaceae (Bawa, 1990; Bawa et al., 1985; Stratton, 1989; Feinsinger, 1983; Stiles, 1975, 1978). Identifying the community dynamics of how hummingbirds are distributed in a fragmented landscape and relating these patterns to fine-grained habitat characteristics may help guide a local-level conservation strategy that benefits the tropical ecosystem at large.

The Chocó bioregion, which extends from southern Panama through western Colombia and into northwestern Ecuador, is a biodiversity “hotspot” known for high levels of bird diversity and

endemism. Previous work within the Mache-Chindul Ecological Reserve (REMACH) in northwest Ecuador has documented an abundant and species-rich hummingbird community, with 21 species recorded to date within the reserve (Carrasco et al., 2013). Although the region has been identified as a priority for conservation in mainland Ecuador, ongoing deforestation has reduced the amount of continuous forest and resulted in extensive forest loss and fragmentation (Kleemann et al., 2022; van Der Hoek, 2017).

We investigated habitat- and site-level patterns of diversity and community composition of hummingbirds between continuous forest (in this case, a continuous area of ~3500 ha of forest with relatively little human intervention) and nearby forest fragments (size range: 2.5–48.0 ha) surrounded by the agricultural matrix in the Chocó rain forest of northwestern Ecuador. Sites in both continuous forests and fragmented forests were established in a mix of primary and secondary habitat. To better understand the environmental factors that may drive observed patterns of diversity and community composition, we also assessed within-patch and patch-matrix characteristics associated with hummingbird diversity and composition. In this study, within-patch characteristics include canopy openness, fragment size, and the density of mid- to large-sized trees, while patch-matrix characteristics consist of elevation and surrounding forest cover. Canopy openness may have a strong positive relationship with diversity as the greater light availability in the understory increases vegetative productivity (Chazdon & Fetcher, 1984; Dáttilo & Dyer, 2014). Affinity to light-dependent resources (i.e., nectar) has been pointed out as one of the contributing factors to hummingbirds' resilience to disturbance (Blake & Loiselle, 2001). Fragment size has also been known to have a positive association with hummingbird species richness and overall avian richness (Boecklen, 1986; Daily et al., 2001; Hadley et al., 2017; Martensen et al., 2012). In addition, density of mid- and large-sized trees, an index of forest maturity, may affect structural heterogeneity suitable for nesting and foraging (Bonino & Araujo, 2005; Paillet et al., 2017). As a patch-matrix characteristic, elevation often affects hummingbird communities on the gradient of temperature and precipitation with the mid-elevation peak in species richness (González-Caro et al., 2012). Lastly, high surrounding forest cover may provide additional food resources and facilitate hummingbird movement (Hadley & Betts, 2009; Volpe et al., 2014).

We hypothesized that continuous forest and fragments will host different proportions of common and rare hummingbird species. More specifically, we anticipated a higher number of rare species in the continuous forest and similar number of common species between the continuous forest and fragments as habitat loss, in general, appears to affect species richness more severely than abundance (Gibson et al., 2011). We also predicted community composition would be dissimilar between the continuous forest and fragments, with a more uneven community in fragments, as a few common species may become more common and rare species decline as a result of long-term disturbance (Hendershot et al., 2020; Medellín et al., 2000; Stouffer & Bierregaard, 1995). Lastly, we predicted that canopy openness would be most strongly and positively associated

with hummingbird diversity and composition in both continuous and fragmented forests, as high canopy openness appears to increase plant productivity that may provide key resources (i.e., flowers) for hummingbirds. Assessing different relative abundances in diversity and composition and identifying environmental characteristics that correlate with the population may help understand patch-level dynamics shaping hummingbird communities in this tropical biodiversity hotspot.

2 | METHODS

2.1 | Study area

We conducted this study in a ~24,000 ha area within the Chocó bioregion that covers Bilsa Biological Station of the Jatun Sacha Foundation (BBS; 79°45'W, 0°22'N, 121–662 m a.s.l.) and the surrounding fragments in northwestern Ecuador (Figure S1). Bilsa Biological Station is a continuous forest (transects $n = 16$, ~3500 ha) that protects one of the last large blocks of intact Chocó wet forest in Ecuador, including old-growth forest and forests that were selectively logged or clear-cut about 30–40 years ago (Durães et al., 2013). The surrounding forest fragments ($n = 39$, 2.5–48.0 ha, mean = 16.6 ha) lie within an agricultural matrix of pasture interspersed with cacao, corn, passion fruit, and other crops. The oldest fragments in the study area are estimated to have been isolated from the continuous forest for approximately 60 years (J. Karubian, unpublished data). Therefore, some fragments may be as mature as some BBS transects, although with more of a history of disturbance.

The area receives annual precipitation of 2500–4000 mm, and the average temperature ranges from 23 to 25.5°C (Clark et al., 2006). The wet season spans from January to June and the dry season from July to December (Carrasco et al., 2013; Ortega-Andrade et al., 2010). The sampling occurred throughout the year in both the rainy and the dry seasons. Durães et al. (2013) and hummingbird captures from Jama-Coaque Bird Observatory in the same region (M. Ellis, unpublished data) found no differences in community structure between seasons.

2.2 | Bird sampling

We captured birds with mist nets (12 m, 36 × 36 mm mesh) in fragments ($n = 39$ sites) and at BBS ($n = 16$ plots) during 3 consecutive days of surveying per site. Each BBS survey consisted of eight mist nets placed 25 m apart in a 200-m linear area. In each fragment, four nets were placed near the forest edge, and four placed inside the forest, approximately 300 m from the edge. The first 2 days, we set mist nets from 06:30 h to 13:30 h; the third day from 06:30 h to 12:00 h to allow moving to the next fragment to set up the mist nets. From 2013 to 2017, we completed 196 days of sampling, distributed across all months of the year. Mist netting may cause a

potential bias in sample collection as understory-subcanopy species are more likely to be captured than canopy species (Barlow et al., 2007). However, this potential bias may not be strong for hummingbirds in lowland tropical forests because most hummingbirds visit substantially more species in the understory-subcanopy, such as flowering shrubs, than in the canopy (Bawa, 1990; Bawa et al., 1985; Crespo et al., 2022). Also, comparisons of mist netting and point count methods have resulted in similar estimates of hummingbird diversity (Blake & Loiselle, 2001; Whitman et al., 1997). Moreover, canopy height was not significantly different between the two habitat types ($p > .05$). Still, we acknowledge the possibility that our findings may be more relevant to the forest understory community rather than the entire hummingbird community. We identified bird species following the nomenclature in Ridgely and Greenfield (2006) and reflected current nomenclature referring to Remsen et al. (2021). We banded the birds with standard aluminum metal rings and certified the bird sampling under Tulane University Animal Care Committee (IACUC-395). This work was conducted under Contrato de Acceso a Recursos Genéticos MAEDNB-CM-2015-0017 granted to Universidad Tecnológica Indoamérica.

For comparisons of overall diversity between BBS and fragments, we used coverage-based rarefaction, which allowed us to compare samples by their completeness rather than size. This adjustment was necessary because size-based rarefaction tends to heavily depend on the sample size, when sample size may not be enough to represent the true community due to the wealth of rare species in the tropical hummingbird community (Chao & Jost, 2012; Dornelas et al., 2013). For site-level comparisons, we adjusted both diversity and number of captures by first dividing their values by the associated number of net hours for the given site and sampling event, then multiplying by 100 to yield the standardized number of captures or species per 100 net hours to assess the completeness of surveys and compare among sites with different sampling effort (Wolfe et al., 2015). The last of these approaches is less than ideal for diversity comparisons since species accumulation curves do not increase linearly. Still, it may be the most satisfactory option available in instances where only a handful of individuals are captured and species accumulation curves do not reach their inflection point, as we observed at the level of individual sampling sites (Figure S2).

2.3 | Within-patch characteristics

All the patch characteristics of BBS and fragment study sites were collected at three locations along each banding transect of 250 m—at the beginning (0 m), in the middle (100 m), at the end (200 m)—and then averaged. The distance from the BBS to each fragment (0.011–16.9 km, mean = 5.8 km) strongly correlated with elevation and was therefore omitted from the analysis. We also found canopy height was strongly correlated with the number of trees (diameter at breast height > 50 cm). Since the elevation and the number of trees were better predictors of hummingbird diversity, we excluded

canopy height and surrounding forest cover within 2 km from all models.

We measured patch characteristics per each BBS and fragment transect by canopy openness, and the number of mid-sized trees (defined as 10–50 cm diameter at breast height; DBH, dbh10) and large trees (defined as ≥ 50 cm DBH, dbh50). We measured canopy openness using a concave spherical densiometer (Forestry Suppliers no. 43888). Independent measures were taken in each of the four cardinal directions and then averaged for a single score for each transect. The number of cells (96 total) containing open canopy were scored and multiplied by 1.04 to arrive at a score potentially ranging from 0 (i.e., completely closed) to 100 (i.e., completely open canopy). The number of mid-sized trees was counted within a 10-m-radius circular plot, and the number of large trees was counted within a 20-m-radius circular plot. The number of large trees (DBH > 50 cm) was measured within a 20-m circular plot because 10-m-radius plots were not large enough to derive meaningful biological differences that might have existed between habitat types.

2.4 | Patch-matrix characteristics

We measured patch-matrix characteristics such as size, elevation, and the proportion of surrounding forest cover per each transect in BBS and fragment. We estimated the fragment size by manually walking the boundaries of each fragment and BBS with a handheld GPS and calculating their area in QGIS (QGIS.org, 2012). We measured elevation with a handheld GPS at each mist net sampling point and averaged the elevation measurements to a single value per site. Lastly, we measured forest cover using a contemporary map at 30-m resolution scale from the Global Forest Watch dataset (Hansen et al., 2013) to quantify the proportion of surrounding forest cover within 0.5 and 2 km radii per fragment for each sampling event between 2013 and 2017 (Browne & Karubian, 2016). The given resolution was sufficient to estimate forest cover 0.5 and 2 km radii per fragment. To obtain the forest cover map, we classified forest cover in a given pixel of size 30×30 -m grid cells across our study area as either forest or nonforest, based on whether there was >95% canopy openness in the year 2013. Next, we converted grid cells to nonforest if the cell had forest loss between 2013 and the year of sampling (Browne & Karubian, 2016; Hansen et al., 2013). We calculated the proportion of grid cells classified as forests within circular plots of 2 km and 500 m from the center of each BBS transect and fragment and selected the 500 m in all subsequent analyses because it was a better predictor of bird diversity (Cook et al., 2020).

Although the Global Forest Watch dataset may overestimate forest cover by classifying certain types of plantations as high tree cover (Tropek et al., 2014), the contemporary map of forest cover in our study region matched with the areas cleared for agriculture 3–5 years ago and areas surrounding forest boundaries (Browne

& Karubian, 2016). The surrounding forest cover within 2 km was strongly correlated with forest cover within 500 m of sampling sites. Since forest cover within 500 m was a better predictor of hummingbird diversity, we excluded surrounding forest cover within 2 km from all models.

2.5 | Bird diversity analysis

Multilevel indices are suited for comparisons between habitats with particularly diverse hummingbird communities in varying degrees of abundance. To detail the pattern of hummingbird diversity in a fragmented landscape, we used multilevel indices called Hill diversity numbers. Hill diversity numbers weigh different categories of relative abundance—rare ($q = 0$), common ($q = 2$), and neither rare nor common (i.e., typical, $q = 1$)—expressed with the unit “effective number of species,” or diversity equivalent to the number of equally abundant species in a perfectly even community. Hill diversity numbers increase linearly, doubling when two distinct communities with the same values are combined, just as species richness does (Chao et al., 2014; Chiu et al., 2014; Hill, 1973). Hill numbers are mathematical transformations of standard diversity indices, where q references a constant in the transformation formula: species richness ($q = 0$), Shannon–Wiener diversity ($q = 1$), and Simpson's diversity ($q = 2$) (Jost, 2006). Transforming these indices into the Hill number framework allows them to be presented side by side with the same units and on the same scale. In a theoretical community with perfect evenness, one where all species are equally abundant, all Hill number orders of q are equal. Using these Hill numbers together better illustrates differences in community evenness, an important component of diversity (Chao et al., 2014).

We used 95% confidence intervals generated from 2000 bootstrap replications to identify statistically significant differences in hummingbird diversity between BBS and forest fragments overall, standardized by captures in 100 net hours. We also used t-tests to look for differences in diversity per 100 net hours among the individual sites to determine whether there were site-level differences. We generated sample coverage estimates and rarefaction curves to statistically account for sampling completeness. Then, we produced Hill number diversity estimates with confidence intervals at the forest level using the iNEXT package in R (Chao et al., 2014; R Core Team, 2020). Our estimated sample coverage and stopping point used for rarefaction between forest types was 99%. For estimates of diversity at the site level, we used package hillR (Li, 2018).

2.6 | Community composition analysis

We used nonmetric multidimensional scaling (NMDS) using the Bray–Curtis dissimilarity index (two communities are more dissimilar when the index is closer to 1), along with two nonparametric

TABLE 1 Names, numbers of captures, and captures in fragments and BBS (Bilsa Biological Station) in the Mache Chindul Reserve in northwest Ecuador, from 2013 to 2017.

Scientific name	Common name	Code	Ecuador status	Total fragment captures	Fragment captures/100nh	Total BBS captures	BBS captures/100nh
<i>Phaethornis yaruqui</i>	White-whiskered Hermit	WWHE	LC	256	4.35	91	3.39
<i>Threnetes ruckeri</i>	Band-tailed Barbthroat	BTBA	LC	139	2.36	24	0.89
<i>Eutoxeres aquila</i>	White-tipped Sicklebill	WTSI	LC	53	0.9	24	0.89
<i>Thalurania colombica</i>	Crowned Woodnymph	CRWO	LC	28	0.48	58	2.16
<i>Heliodoxa jacula</i>	Green-crowned Brilliant	GCBR	LC	18	0.31	31	1.15
<i>Phaethornis strigularis</i>	Stripe-throated Hermit	PHST	LC	14	0.24	3	0.11
<i>Chlorestes julie</i>	Violet-bellied Hummingbird	VBHU	LC	10	0.17	3	0.11
<i>Polyerata amabilis</i>	Blue-chested Hummingbird	RTHU	LC	9	0.15	–	–
<i>Amazilia tzacatl</i>	Rufous-tailed Hummingbird	BCHU	LC	7	0.12	–	–
<i>Phaethornis longirostris</i>	Long-billed Hermit	LBIH	LC	6	0.1	–	–
<i>Florisuga mellivora</i>	White-necked Jacobin	WNJA	LC	3	0.05	–	–
<i>Glaucis aeneus</i>	Bronzy Hermit	BRHE	NT	2	0.03	–	–
<i>Uranomitra franciae</i>	Andean Emerald	ANEM	LC	2	0.03	2	0.07
<i>Heliathryx barroti</i>	Purple-crowned fairy	PCFA	LC	1	0.02	–	–
<i>Androdon aequatorialis</i>	Tooth-billed hummingbird	TBHU	LC	–	–	1	0.04

dissimilarity indices from the C_{qN} family (Sørensen, $q = 0$; Morisita-Horn, $q = 2$) to examine dissimilarity in hummingbird community composition between BBS and fragments. We omitted three species that had less than three captures in the entire dataset to reduce noise in NMDS: Purple-crowned Fairy (*Heliathryx barroti*), Tooth-billed Hummingbird (*Androdon aequatorialis*), and Bronzy Hermit (*Glaucis aeneus*) (Table 1). We evaluated compositional dissimilarity in hummingbird communities using the “anosim” function (permutation = 1000) in the “vegan” R package (Oksanen et al., 2019) and identified the parameters that affect dissimilarity in hummingbird communities between continuous forest and fragments post hoc in NMDS ordination species with the “envfit” function (permutations = 999). Unfortunately, Horn ($q = 1$) index has not been implemented by the vegan package yet, and we therefore excluded it from the analysis of dissimilarity and nonmetric multidimensional scaling analysis.

2.7 | Model analysis

We used linear modeling to fit Hill numbers—effective numbers of species converted from species richness, Shannon-Wiener index, and Simpson's evenness—to environmental covariates with conditional model averaging (including all models $<10 \Delta AIC$ of the top model) to identify significant environmental predictors

of hummingbird diversity and differences in effects between BBS and forest fragments (Burnham & Anderson, 2002; Symonds & Moussalli, 2011). Prior to scaling and centering all environmental covariates, we took the square root of the number of trees and fragment area. We checked for collinearity of covariates with exploratory plots, Pearson coefficients, and variance inflation factors. Before fitting our full model, we checked model assumptions—linearity, homoscedasticity, independence, and normality—with the “gvlma” and “olsrr” packages in R (Pena & Slate, 2006). Lastly, we used the false discovery rate (FDR) to reduce the possibility of Type I error (Benjamini & Hochberg, 1995; Pike, 2011).

2.8 | Standardizing elevation

Elevation is known to be an important driver of avian distributions in the Neotropics (Blake & Loiselle, 2001; Bleiweiss, 1998; González-Caro et al., 2012; McCain, 2009). We used elevation both as an explanatory variable and a threshold to standardize sample size ($n = 16$) between two habitats. The elevation range of our forest fragments was substantially wider than that of our BBS sampling sites (Table 2), so we conducted all analyses both with our full dataset and again while controlling for elevation. To control for elevation, we chose fragments that were at a similar elevation as the BBS transects above 370 m.a.s.l. This filter resulted in a more balanced

	BBS (n = 16)	Fragments (n = 39)	<i>p</i> ^c	Fragments (>370m, n = 16)	<i>p</i> ^d
Elevation (m)	526 ± 57.9	353 ± 128	<.0001	479 ± 85.2	.080
No. of medium trees ^a	13.0 ± 2.03	11.5 ± 4.02	.0930	12.1 ± 3.69	.445
No. of large trees ^b	1.68 ± 1.40	1.29 ± 0.71	.318	1.36 ± 0.59	.435
Openness (%)	12.0 ± 2.05	10.2 ± 4.12	.0476	8.65 ± 2.79	.00076
Surrounding forest cover in 500m (%)	89.8 ± 6.6	63.4 ± 15.6	<.0001	62.2 ± 14.7	<.0001
Size (ha)	~3500	16.6 ± 12.5	-	21.4 ± 14.4	-

Note: Values represent means ± 1 SD. Significant *t*-test *p*-values are bolded.

^aNumber of trees with DBH = 10–50 cm with a 10-m radius circular plot.

^bNumber of trees with DBH ≥ 50 cm within a 20-m radius circular plot.

^cSignificance in difference between BBS (n = 16) and Fragments (n = 39).

^dSignificance in difference between BBS (n = 16) and Fragments > 370 m (n = 16).

dataset, including all 16 of our BBS sites and 16 of our 39 forest fragment sites for comparisons of diversity, but it sacrificed a substantial amount of data used to inform our models.

3 | RESULTS

3.1 | Hummingbird diversity

From 2013 to 2017, we captured 785 individual hummingbirds of 15 species in 8573 net hours. We recorded nine species in the BBS continuous forest (n = 16) and 15 species in the surrounding forest fragments (n = 39). Six of the 15 species in the fragments were unique to forest fragments, whereas just one of the nine species in the continuous forest was unique to the continuous forest (Table 1). Overall capture rates were similar between fragments and continuous forest, but fragments had approximately twice as many raw net hours and double the number of sites surveyed across a greater elevational range than continuous forest (Table S1). Nonetheless, the capture rate and the diversity patterns for fragments changed little when we limited our analyses to the same elevation range (>370 m a.s.l.) encompassing continuous sites and similar sampling effort (Table S1).

When comparing cumulative captures from fragments vs. continuous forest (α-diversity), fragments had higher raw (Table 1) and estimated (Figure 1, q = 0) richness of rare species than continuous forest, even when controlling for elevation. The effective number of “typical” species (i.e., neither common nor rare; q = 1) did not significantly differ between fragments and continuous forest. The abundant (q = 2) species estimate was higher in the continuous forest than in fragments, although not significantly, based on overlapping 95% confidence intervals (Figure 1); this difference remained nonsignificant when controlling for elevation (Table S2). We observed greater spread between orders of q in forest fragments relative to continuous forest (Figure 1), indicating a less even

TABLE 2 Habitat structure of 16 BBS (Bilsa Biological Station) sites, 39 fragments, and 16 of 39 fragments of which elevation range coincided with that of continuous forest.

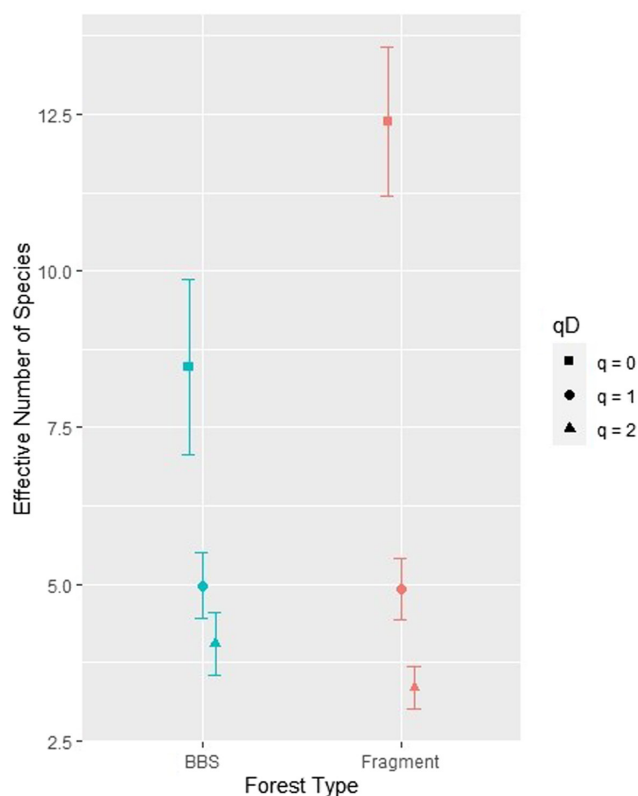


FIGURE 1 Diversity comparison of effective number of species between Bilsa Biological Station sites (n = 16) and all fragments (n = 39). We used coverage-based rarefaction to control for sampling effort, and Hill numbers to compare effective number of species with weights favoring rare species (q = 0), neither rare nor common species (q = 1), and common species (q = 2). The dots indicate means, and the bars represent the 95% confidence intervals of sample coverage.

community by abundance. When comparing site-level patterns of diversity (β-diversity) in fragments vs. continuous sites, we found no significant differences for any order of q (p > .1, Table S2).

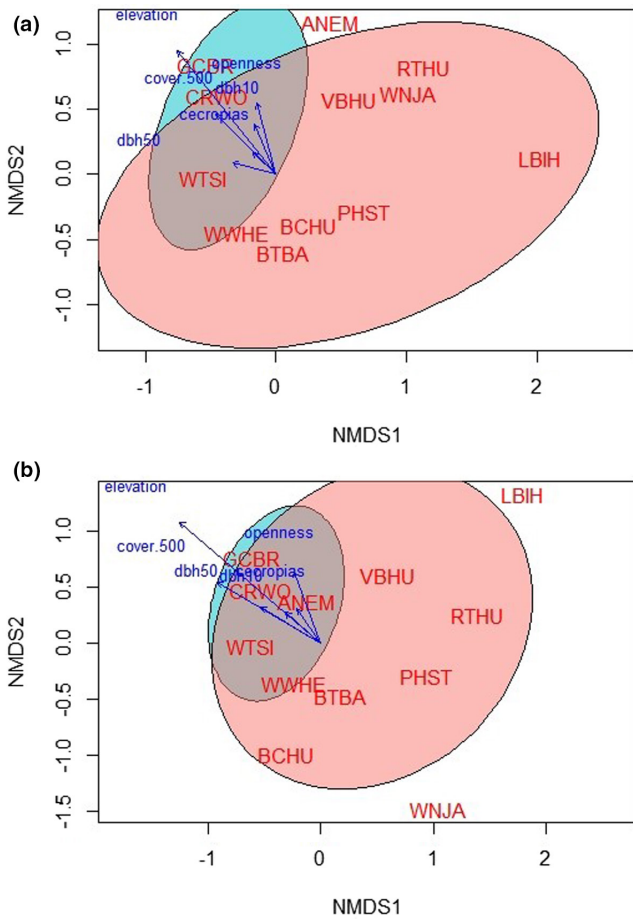


FIGURE 2 Visualization of nonmetric multidimensional scaling (NMDS) ordination on hummingbird species composition with environmental variables in Bilsa Biological Station (BBS) and fragments. Bilsa Biological Station is marked by the upper-left ellipse and fragments the ellipse slightly below. (a) NMDS at $q = 0$ (rare species). Stress = 0.18. $r = .055$, $p = .20$; (b) NMDS at $q = 2$ (common species). Stress = 0.198. $r = .22$, $p = .005$. The closer species are linked to more similar environmental variables than those farther apart. The orientation of axes is arbitrary. Full species name for each species code is provided in Table 1.

3.2 | Community composition

Analysis of Similarity (ANOSIM) showed that the communities are dissimilar between BBS and fragments for common species (Figure 2b: $q = 2$, $r = .22$, $p = .005$), but not rare species (Figure 2a: $q = 0$, $r = .055$, $p = .19$). Patch-matrix characteristics, mainly elevation and surrounding forest cover, affected community dissimilarity between the continuous forest and fragments. For rare species ($q = 0$), sites more similar in elevation ($R^2 = .55$, $p = .001$), surrounding forest cover in 500 m ($R^2 = .16$, $p = .009$), and canopy openness ($R^2 = .12$, $p = .030$) had more similar communities (Figure 2a). For common species ($q = 2$), elevation ($R^2 = .50$, $p = .001$) and surrounding forest cover in 500m ($R^2 = .21$, $p = .006$) had a similar effect (Figure 2b).

The NMDS ellipse of fragments was typically larger than that of BBS, encompassing a greater number of species than BBS. The NMDS

TABLE 3 Linear model effects of environmental variables on hummingbird species diversity in fragments and continuous forest.

	Elevation			No. of medium trees ^a			No. of large trees ^b			Openness			Cover 500 m ^c			
	Est.	SE	p	Est.	SE	p	Est.	SE	p	Est.	SE	p	Est.	SE	p	
Fragments (n = 39)																
q = 0	0.19	0.15	.22	0.34	0.13	.012	0.14	0.18	.42	0.33	0.13	.015	-0.13	0.19	.50	
q = 1	0.21	0.11	.07	0.18	0.09	.06	0.11	0.13	.42	0.24	0.10	.017	-0.16	0.14	.25	
q = 2	0.20	0.10	.044	0.12	0.08	.14	0.08	0.11	.49	0.18	0.08	.039	-0.14	0.12	.25	
BBS (n = 16)																
q = 0	-0.27	0.52	.61	-0.51	0.44	.27	-0.27	0.16	.12	0.13	0.48	.80	-0.38	0.71	.60	
q = 1	-0.49	0.46	.32	-0.55	0.39	.19	-0.19	0.14	.21	0.27	0.43	.54	-0.22	0.64	.74	
q = 2	-0.57	0.44	.23	-0.56	0.38	.17	-0.15	0.14	.28	0.36	0.41	.40	-0.14	0.62	.83	

Note: None of the models are statistically significant with false discovery rate ($p < .05/5 = .01$), but nearly significant variables ($p < .02$) are underlined. Data on the mean and SD of predictor variables are available in Table 2. Size is included in the fragments model but not shown in this table because it was not included in BBS model and was insignificant ($p > .4$).

^aNumber of trees with DBH = 10–50 cm with a 10-m-radius circular plot.

^bNumber of trees with DBH ≥ 50 cm with a 20-m-radius circular plot.

^cPercent surrounding forest cover in 500 m radius.

ellipse of BBS tightly centered around environmental correlate axes, extended by Green-Crowned Brilliant. Overall, Green-Crowned Brilliant and Crowned Woodnymph were strongly associated with all the environmental variables—especially elevation and surrounding forest cover (Figure 2). By contrast, White-Whiskered Hermit and Band-tailed Barbthroat showed few associations with the environmental variables, as would be expected for generalists (Figure 2).

3.3 | Within-patch and patch-matrix characteristics

Continuous forest sites ($n = 16$) were higher in elevation, canopy openness, and surrounding forest cover than fragments ($n = 39$) (Table 2). The differences in canopy openness and surrounding forest cover persisted when we restricted comparisons to fragments in the same elevation range. The numbers of mid-sized (dbh10) and large trees (dbh50) trees with various sizes were similar between fragments and BBS (Table 2).

None of the environmental variables were significant in both forest types after applying FDR ($p < .01$, Table 3). However, canopy openness and the number of mid-sized trees were nearly significant ($p < .02$) based on Hill numbers in fragments. Effective number of rare species ($q = 0$) in fragments had a positive relationship with increasing canopy openness and the number of mid-sized trees with DBH 10–50 cm (Table 3), which were among the strongest predictors of all correlates (Table S4). Effective number of typical species ($q = 1$, neither rare nor common) in fragments also showed a positive relationship with canopy openness (Table S4, $q = 1$). There were no relationships for abundant species ($q = 2$) in fragments, and none of the Hill numbers ($q = 0, 1, 2$) showed significant relationships with environmental covariates in BBS ($p > .1$, Table 3; Table S4). The variables that were not suitable for habitat-to-habitat comparison because of their significant interaction effects—elevation and DBH > 50 cm—were not marked predictors of the effective number of species in either fragments or BBS (Table S3; Table 3).

4 | DISCUSSION

Understanding the environmental factors that affect hummingbird diversity and community composition in modified landscapes has important implications for guiding conservation practices. Our mist netting study from the Ecuadorian Chocó highlights a degree of subtlety in how hummingbird communities may respond to habitat loss and fragmentation. As hypothesized, continuous forest and fragments accommodated hummingbird communities with different diversity patterns. More specifically, fragments had a more uneven community despite the higher species richness than the continuous forest by accommodating relatively few common species and many rare species. Canopy openness showed a positive relationship for both rare and typical species ($q = 0$ and $q = 1$) in fragments. The number of mid-sized trees (dbh10), another within-patch characteristic, also showed a similar relationship with rare species in fragments. Lastly, elevation and

surrounding forest cover, the two patch-matrix characteristics in the study, affected community dissimilarity between the continuous forest and fragments. Overall, these results emphasize the value of both continuous forest and surrounding fragments for hummingbird conservation in community evenness and species richness, respectively, while identifying key environmental factors driving those effects.

4.1 | Diversity and community composition

Species richness, or the effective number of rare species ($q = 0$), was higher in fragments than in our continuous forest site (BBS), and the community was dissimilar between the continuous forest and fragments weighted on common species ($q = 2$). This result matches our hypothesis that hummingbird species with different relative abundances (common vs. rare) will have different distributions between the continuous forest and fragments; however, it negates our prediction that the continuous forest will accommodate more rare species than fragments.

Canopy openness and the number of mid-sized trees were the strongest predictors of hummingbird diversity in fragments. At the same time, none of the measured environmental parameters had significant relationships with diversity in the continuous forest. In summary, fragments hosted higher species richness positively correlated with canopy openness and mid-sized trees, while the continuous forest showed a different community structure compared with fragments with no environmental variables correlated with diversity.

A few ecological factors may explain higher species richness in fragments. Secondary, regenerating forests may accommodate more diverse vegetation structures and experience species turnover throughout the study period (Blake & Loiselle, 2001). The fragments assessed in this study represented a range of forest types, from younger than 20 years old up to relatively pristine forests. As the avian species richness (but not composition, see Hendershot et al., 2020) has been documented to recover after 20 years of clearing (Dunn, 2004), some of the older fragments may have reached a comparable habitat quality as the relatively pristine continuous forest for hummingbirds. At the same time, the younger fragments may have attracted more rare species of hummingbirds with regenerating trees and more flowers.

We also note that the finding of higher species richness should be interpreted with caution, given the potential for incomplete sampling in this study. For example, eight of 15 species have less than 10 captures, and one species, the White-Whiskered Hermit, accounts for 44% of the total raw captures. Moreover, higher sampling effort in fragments may have influenced species richness, although we accounted for the twofold difference in sampling effort by employing rarefaction on raw net hours and controlling for elevation. For instance, the raw species richness was higher for the fragments (9 vs. 16), but this trend was reversed when standardized by elevation and 100 net hours (Table S1). Given these conditions, effective numbers of species for typical (neither rare nor common, $q = 1$) and common species ($q = 2$) may be more reliable than species richness ($q = 0$).

The significant difference in species composition between the two habitats and the higher effective number of abundant ($q = 2$) species in the continuous forest (Figure 1) suggest a difference in community composition pattern between the habitats. The continuous forest accommodated a smaller number of rare species and a larger number of common species than fragments. This pattern suggests a greater evenness in the continuous forest than in fragments. Since the White-whiskered Hermit dominated both habitats, community evenness largely depended on other species that occupied each habitat in similar abundances, such as Crowned Woodnymph and Green-Crowned Brilliant. The discrepancy between the White-whiskered Hermit and the next abundant species was smaller in the continuous forest than in fragments. The higher estimate of the effective number of common species ($q = 2$) in BBS reflects this smaller abundance gap between the White-whiskered Hermit and subdominant species in the continuous forest. Overall, fragments tended to host one dominant species and many rare species, while the continuous forest accommodated more significant subdominant species and less rare species.

Crowned Woodnymph and Green-crowned Brilliant were strongly associated with elevation and surrounding forest cover. Crowned Woodnymph particularly was identified as “forest-dependent” species that prefers tree cover to agricultural landscape according to Estrada-Carmona et al. (2019). Green-crowned Brilliant's affinity for continuous forest persisted even when we controlled for elevation. Continuous forest may have provided a more favorable habitat for Crowned Woodnymph and Green-crowned Brilliant with higher elevation and surrounding forest cover, contributing to more even communities than in fragments despite the prevalence of White-whiskered Hermit.

4.2 | Within-patch characteristics

Canopy openness and the number of mid-sized trees were strong predictors of hummingbird diversity in fragments, albeit not significant after applying FDR ($p < .01$). Hummingbird species richness had a positive relationship with canopy openness only in fragments. This result suggests that canopy openness promotes hummingbird diversity only to a certain extent (Chazdon & Fetcher, 1984; Svenning, 2002), where heterogeneous light conditions support plant growth, diversity, and pollination visit (Chazdon & Fetcher, 1984; Dáttilo & Dyer, 2014). The number of medium trees (DBH = 10–50 cm) positively correlated with species richness in fragments. Subcanopy trees and shrubs with DBH > 10 cm but < 50 cm, or the members of the Melastomataceae and Rubiaceae families, are important sources of flower and nectar resources for hummingbirds in our project area (J. Karubian, unpublished data). Also, hummingbirds use fern, moss, lichen, and spider or caterpillar silk species to build their nests (Graves & Forno, 2018; Osorio-Zuñiga et al., 2014; Riba & Herrera, 1973), and principally forage on epiphytes that grow on tree surfaces (Dziedzich et al., 2003). Younger, smaller trees may provide equivalent nesting materials as large trees (Paillet et al., 2017)

with higher light filtration; for example, several smaller trees can host a similar amount of biomass of lichens as a single large host tree (Schei et al., 2013).

4.3 | Patch-matrix characteristics

Elevation and surrounding forest cover were not significantly associated with hummingbird diversity. Our elevation range (223–586 m) may have been too narrow or far lower than the mid-elevation peak (1800–2700 m) in hummingbird species richness documented by González-Caro et al. (2012). The surrounding forest was a strong predictor of diversity in terrestrial mammals and birds (Cook et al., 2020), large frugivorous birds (Walter et al., 2017), and seed dispersal in palm trees (Browne & Karubian, 2016) in our study area. However, since hummingbirds are highly mobile species, the percentage of forest cover surrounding the forest may not significantly affect their distribution, as long as there is a corridor to pass through the matrix in the range of 48–97% of forest surrounding the fragments in our study (Volpe et al., 2014; Table 2).

Fragment size was not significantly related to species richness in our study but was the strongest predictor of species richness in Hadley et al.'s (2017) study. The range of fragment sizes in our study was smaller but the sample size was larger than that of Hadley et al. (2017) (4.7–27.7 ha, 39 fragments vs. 1.7–1359 ha, 14 fragments). This difference may mean that the effect of fragment size on species richness is noticeable only when the range of fragment size is large enough. Another possibility is that fragments may have been well-connected among themselves in our study. Traplining hermit species are known to forage long distances to revisit renewing nectar sources (Stiles, 1975; Volpe et al., 2014). Nonhermit species can also defend a large area for food source or mating chances (Armstrong, 1987; Bertin & Wilzbach, 1979; Feinsinger & Chaplin, 1975). In sum, the mobility of hummingbirds and connectedness between the sites within the fragments may have contributed to few significant correlations.

4.4 | Conservation implications

The findings from this study point to the conservation value of both fragments and adjacent continuous forest. Continuous forest accommodated even communities, while forest fragments supported more distinct hummingbird communities than continuous forest. Regenerating and maintaining fragmented forests may improve the quality of both continuous forest and surrounding fragments for conserving diversity and composition of hummingbirds, as well as other bird guilds (Latta et al., 2017). Selective logging in secondary forests may have relatively modest impacts for hummingbird communities, which our data suggest are associated with canopy openness and number of mid-sized trees. This may explain the relative resilience of hummingbirds to fragmentation compared with other more vulnerable species, such as insectivores and granivores (Barlow et al., 2007; Stouffer & Bierregaard, 1995).

Yet, hummingbirds can also be negatively impacted by habitat modification; for example, despite high mobility and positive association with gaps (Pollock et al., 2020; Volpe et al., 2014), hummingbird composition has decreased in recent decades in Costa Rican forests (Hendershot et al., 2020). Therefore, despite this study documents the resilience of hummingbird population in a fragmented landscape, significant difference in composition of common species between the continuous forest and fragmented secondary forests may have long-term influence in the larger tropical forest network that may take longer to reverse (Chazdon, 2003; Dunn, 2004).

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CONFLICT OF INTEREST STATEMENT

The corresponding author confirms on behalf of all authors that there have been no involvements that might raise the question of bias in the work reported or in the conclusions, implications, or opinions stated.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in the Dryad Digital Repository: <https://doi.org/10.5061/dryad.dv41ns22s> (Huh et al., 2022).

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