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“Effects of landscape composition, configuration, and vegetation structure on bird communities of the pine-oak forests of El Salvador”

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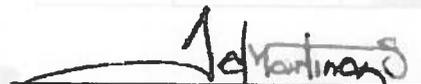
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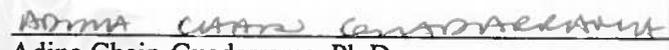
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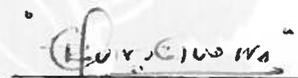
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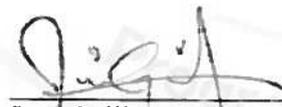
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Effects of landscape composition, configuration, and vegetation structure on bird communities of the pine-oak forests of El Salvador

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Abstract: Despite the disastrous consequences of habitat loss and fragmentation on biodiversity, studies about this topic are scarce in Central America, even less in El Salvador. We assessed the effects on habitat loss and fragmentation at the landscape level in the pine-oak forests of El Salvador, which is an important global biodiversity hotspot and currently endangered. We defined four regions in pine-oak forests across northern El Salvador (Montecristo, Miramundo, El Manzano, and Morazán regions). We established 20 point-counts (five point-counts per region), where we surveyed birds and made vegetation plots for three months in 2021. We created four buffers around each point-count (100, 300, 500, and 1000 m of radii) and calculated nine landscape metrics for each buffer; we made a regression analysis to evaluate the predicting power of vegetation structure and the landscape variables over the bird community. We found that bird communities responded strongly to landscape variables; we did not find any relationship with vegetation structure. We found that Montecristo and Miramundo regions share similar bird communities. El Manzano and Morazán regions also share similar bird communities, being the former regions different from the latter regions. Our results suggest that bird communities at the pine-oak forest are affected by forest fragmentation, especially highland birds, frugivorous and forest-dependent birds. We highlight the importance of continuing with systematic studies in northern areas of El Salvador since these areas are key areas for biodiversity but long understudied.

Keywords: biodiversity, habitat loss, forest fragmentation, neotropical birds, scale of effect.

Introduction

Land-use change continues to be one of the main threats to Mesoamerican biodiversity. Mesoamerica is considered a global biodiversity hotspot due to its species richness, endemism, and irreplaceability of ecosystems (Meyers *et al.*, 2000; Olson & Dinerstein, 2002). Examples of these unique ecosystems are the highland forests of northern Central America: cloud and pine-oak forests, which provide vital ecosystem services such as freshwater (Aldrich *et al.*, 2000), soil erosion control, and climate regulation (Kappelle & Juárez, 2006). However, despite its importance, the Central American Pine-Oak Forest Ecoregion (CAPOE hereafter) faces similar threats to other forested ecosystems, including land-use change, degradation, and fragmentation mainly resulting from advances of the agricultural frontier (Hernández-Baños *et al.*, 1995; Lineal & Laituri, 2013; Kappelle, 2006) and is currently considered an endangered ecosystem (Olson & Dinerstein, 2002). Likewise, and despite being the most densely populated and deforested country in continental America (Dull, 2008; Crespín & Simonetti, 2015), the highland forests of northern El Salvador are still a refuge for several endemic and threatened birds such as the globally endangered golden-cheeked warbler (*Setophaga chrysoparia*) (Rappole *et al.*, 1999; Vallely & Dyer, 2018). Several species new to science have been found in this region, such as *Hampea reynae*, *Casearia sanchezii*, *Petrejoides salvadorae*, and *Lempira metapanensis* (Fryxell, 1980; Schuster, 1989; Linares & Angulo, 2009; Rowell, 2012), and large and medium-sized mammals such as pumas (*Puma concolor*) and collared peccaries (*Pecari tajacu*) are almost restricted to the northern forests of El Salvador (Castillo-Mendoza, 2017; Argueta-Rivera *et al.*, 2020; Morales-Rivas *et al.*, 2020), highlighting the importance of this region for biodiversity conservation.

In combination with abiotic factors (e.g., climate, topography, and soils), agriculture and other human activities are essential drivers in shaping landscape patterns (Foley *et al.*, 2005; Turner & Gardner, 2015). The interaction of these factors creates heterogeneous landscapes consisting of different land covers and land uses which are usually intertwined across gradients of

agricultural intensification (Foley *et al.*, 2005; Fischer & Lindenmayer, 2007). The multiple possible combinations of land covers and land uses have direct impacts on biological communities persisting in these landscapes, as well as in ecological processes (Gustafson, 1998; Fischer & Lindenmayer, 2007; Katayama *et al.*, 2014). Among these biological communities, birds, key organisms in seed dispersal and pollination processes (Whelan *et al.*, 2008), are sensitive to forest loss and fragmentation (Sekercioglu *et al.*, 2004), making them an ideal subject for studying impacts of fragmentation and landscape patterns on biodiversity.

Birds respond differently to local and landscape scale factors. Bird abundance is correlated to vegetation structure at the local scale, including tree density, tree height, and tree diameter (Calamari *et al.*, 2018; Bhakti *et al.*, 2018). However, landscape pattern variables may be more critical at predicting changes in bird species richness and diversity (Fahrig, 2003; Morante-Filho *et al.*, 2021). For instance, several studies have found that the amount of forest cover (i.e., landscape composition) is the most crucial variable predicting bird diversity (Fahrig, 2003; Zurita & Bellocq, 2011; Carrara *et al.*, 2015; Gonçalves-Bonfim *et al.*, 2021; Morante-Filho *et al.*, 2021), but that the spatial arrangement of different landscape elements (i.e., landscape configuration) can also play an important role shaping the bird community (Westphal *et al.*, 2003; Haddad *et al.*, 2015; Calamari *et al.*, 2018). Traditional approaches to studying bird communities persisting in human-modified landscapes have focused on the patch-level characteristics (i.e., vegetation structure and composition). However, fragmentation is a landscape-level process (Fahrig, 2003; Radford & Bennet, 2007) with possible direct impacts on these communities; therefore, it is essential to design studies that take into consideration landscape patterns which can help better understand bird responses to land-use change (Radford & Bennet, 2007).

Assessing the relationships between biological communities and landscape elements is critical to inform biodiversity conservation strategies. Biodiversity dynamics cannot be fully understood without considering the influence of the surrounding landscape (Mazerolle & Villard, 1999; Dauber *et al.*, 2003; Walz & Syrbe, 2013). At such, studies that have considered the landscape for biological conservation have recommended the maximization of forest area, prioritization of large patches of forest, increase of the narrowest sections of large patches to avoid edge effects, and increase the benefits of a permeable matrix (Stouffer & Bierregaard, 1995; Ewers & Didham, 2008; Uezu & Metzger, 2011; Gonçalves-Bonfim *et al.*, 2021). However, studies at the landscape level are scarce in the Central American region (but see Cerezo *et al.*, 2010; 2016), particularly in El Salvador.

In this study, we assess the effect of different landscape composition and configuration metrics and local-scale vegetation variables on bird communities of the pine-oak forests in four regions of northern El Salvador. Despite the ecological importance of the highland forest ecosystems, few studies of bird communities have been carried out in the pine-oak forests in El Salvador. To our knowledge, none of them has evaluated landscape effects. Our research questions aim to answer: Are studied regions different in bird richness, abundance, and diversity? At which scale, bird richness, abundance, and diversity respond (i.e., local vegetation or surrounding landscape). Do different bird feeding guilds respond differently to landscape patterns and local vegetation? Testing whether local and landscape variables are good predictors of bird richness, abundance and diversity can provide elements that will help inform conservation strategies aiming to conserve the pine-oak ecosystem and the associated bird communities.

Methods

Study area

The CAPOE ranges from Chiapas (southern Mexico) to the northwestern region of Nicaragua, covering an area of 103,842.71 km², out of which an estimated 26,728.35 (26%) remains forested (ACBPEM, 2008). Vegetation on this ecoregion is characterized by the dominant presence of pines (*Pinus* spp.) and oaks (*Quercus* spp.) (ACBPEM, 2008; WWF, 2021). In El Salvador, the pine-oak forests were formerly widespread at elevations ranging from 800 to 2000 m a.s.l., but have been reduced to the extent that nowadays can only be found in some northern parts of the country, usually in association with other tree species such as *Cedrella* spp. and *Liquidambar styraciflua* (Lauer, 1953; Harcourt & Sayer, 1996). According to Holdridge's Life Zone Classification, three main life zones can be found across the CAPOE, the very humid subtropical forests with an annual temperature oscillating between 12 to 24 °C, the humid tropical forests with an annual mean temperature of 24 °C, and the very humid montane forests with an annual temperature oscillating between 18 to 24 °C, all three life zones have annual precipitation between 2000 to 4000 mm (Holdridge, 1978).

In El Salvador, pine-oak forests are primarily found in Morazán, Chalatenango, and Santa Ana. The main economic activity in these departments is agriculture (e.g., corn planting and cattle raising) (DIGESTYC, 2019). However, human migration (exacerbated by the 1980 civil war), rugged topography, poor soils, and relatively low population density made agriculture activities impractical in some areas, allowing the preservation of forests patches (Masing, 1962; Pagiola & Dixon, 1998; Binford, 2013). Many of these areas where forests persist are considered critical for biodiversity conservation (Henríquez, 2009), providing habitat to several bird species not known to occur anywhere else in the country, including the pheasant cuckoo (*Dromococcyx phasianellus*) and fulvous owl (*Strix fulvescens*), both populations of these species are considered to be of least concern according to the IUCN Red List of Threatened Species but present decreasing population trends. The highland guan (*Penelopina nigra*) is another species associated with the CAPOE forests and is considered to have vulnerable populations with decreasing trends (Thurber *et al.*, 1987; Komar, 2002; IUCN, 2021).

Site selection

The main criteria considered for the selection of our study regions were: (i) areas with the presence of pine-oak forests, (ii) accessibility, and (iii) security (i.e., the selected region was considered safe to conduct fieldwork). Based on these criteria we selected four regions: Montecristo, Miramundo, El Manzano and Morazán (Figure 1). Montecristo is the most well-known and studied of the four regions selected, including the Montecristo National Park (MCNP). In this region, dry forests, pine-oak forests, cypress plantations, and cloud forests are the dominant ecosystems (Cardoza-Ruiz, 2011). Miramundo is dominated by pine-oak and cloud forests, although these forests have been significantly reduced mainly due to agricultural expansion (Daugherty, 1973). Morazán has pine-oak and deciduous forests (Herrera-Serrano & Domínguez-Miranda, 2020), while El Manzano has been poorly studied, and little information is available about this region; however, in terms of forests, it is dominated by pine-oaks (Bolaños, 2009). In general, except for the MCNP and recent work conducted in Morazán, very few studies have been carried out in the northern parts of El Salvador.

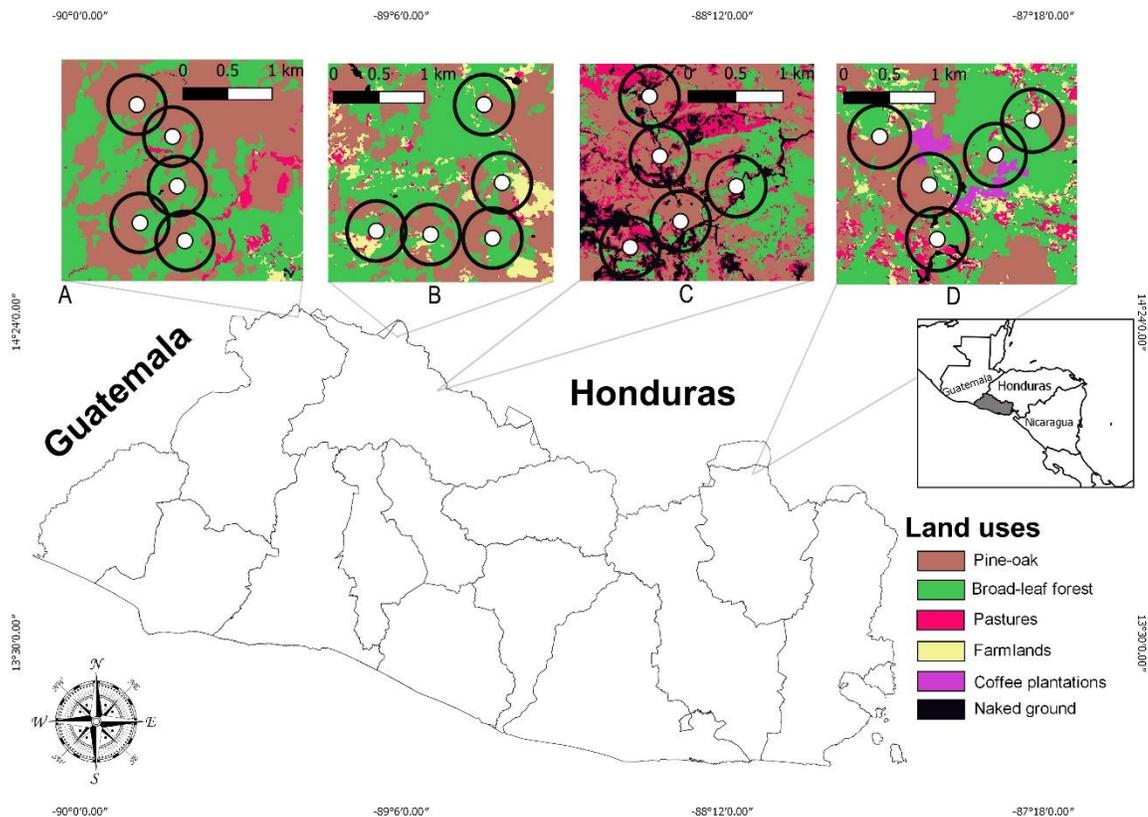


Figure 1

Diagram depicting (i) location of El Salvador related to other Central American countries, (ii) study regions, and (iii) point-counts within study regions. A= Montecristo, B= El Manzano, C= Miramundo and D= Morazán. In each study region, the white filled circles indicate locations where bird point-counts and local vegetation data was collected; and the black open circles illustrate buffers around these locations where landscape metrics were calculated at four different scales

Bird surveys

In each of the four study regions, we established five study sites where we established point-counts to assess bird communities (Figure 1). Bird point-counts were separated by a minimum linear distance of 500 m to secure the independence of observations. They were established 30 m from the patch edge to avoid the edge effect. Each point-count was visited five times from January to April 2021. We used a latin square sampling design to ensure we evaluated each point-count at a different time of the day in each of the five visits. We used 30 m fixed-radius point-counts and evaluated them for 10 min following Ralph *et al.* (1996); however, all birds detected (i.e., whether seen or heard) within or beyond the 30 m fixed-radius were recorded. Additionally, based on Stotz *et al.* (1996) and Komar & Domínguez (2001), we classified detected birds into highland forest specialists (i.e., birds that inhabit only in a specific highland forest), highland forest generalists (i.e., birds that inhabit in any highland forest), forest generalists (i.e., birds that inhabit any forest) and generalists (i.e., birds that can be found in any habitat). We also classified birds according to their feeding guild in (i.e., frugivores, insectivores, omnivores, and nectarivores), based on information available from Billerman *et al.* (2021). Lastly, we reviewed the local conservation status according to the Ministry of

Environment of El Salvador (MARN) (MARN, 2015) and the International Union for Conservation of Nature’s Red List of Threatened Species (IUCN, 2021).

Local vegetation sampling

To assess local vegetation structure, we randomly established two 4 × 20 m plots in the areas surrounding bird point-counts. We measured all arboreal individuals whose diameter at breast height (DBH) was > 20 cm. All measured individuals were identified at the species level, and their height was estimated using a Rangefinder (Bushnell V5). Species identification was conducted with the help of botanists from the La Laguna Botanical Garden, El Salvador.

Land use map

We used Rapid Eye satellite images from 2016 with a spatial resolution of 10 m and generated land use maps for selected study regions. The images were first pre-processed to solve issues caused by clouds and shades. Then, we created the following thematic legends: pine-oak forest, broadleaf forest, pastures, croplands, coffee plantations, and bare ground. We used the Random Forest algorithm (*randomForest*) for the classification, one of the most commonly used supervised classification methods due to its robustness and ease of interpretation (Cánovas-García, 2016). We used the R Statistics software for the classification process. Our final pine-oak classification corresponds to an association between *Pinus* spp., *Quercus* spp., and other plant species (Siles *et al.*, 2017).

Landscape metrics

We calculated nine different metrics at each study site to evaluate landscape characteristics at landscape and class level (Table 1). Selected metrics have been previously used to assess the effect of landscape characteristics on avian communities (Trzcinski *et al.*, 1999; Magness *et al.*, 2006; Rehm & Baldassarre, 2007; Zurita & Bellocq, 2010; Morelli *et al.*, 2013; Peak & Thompson, 2013; Carrara *et al.*, 2015).

We used FRAGSTATS (McGarigal *et al.*, 2012) to calculate all metrics based on the 8-cell neighborhood rule. Class-level metrics were calculated for both pine-oak and broadleaf forest classes. Metrics were calculated at four scales by creating buffer zones (i.e., 100, 300, 500, and 1000 m radius) around each study site (i.e., bird point-counts and local vegetation data were collected). Buffers at 500 and 1000 m had a considerable overlap between each other; however, Zuckerberg *et al.* (2012) found no evidence that overlapping buffers are a problem for statistical analysis. Several metrics are theoretically related; therefore, to avoid redundancy, we selected independent metrics and provided additional instead of redundant information (Cushman *et al.*, 2008).

Table 1
Selected landscape metrics and their definition based on McGarigal et al. (2012)

Level	Metric	Definition	Range (units)
Landscape	Landscape shape index (LSI)	LSI is a measure of landscape disaggregation. The greater the value of LSI, the more dispersed are the patch types	LSI ≥ 1, without limit (none) LSI = 1 when the landscape consists of a single square patch of the corresponding type; LSI

		(classes) LSI measures the perimeter-to area ratio for the landscape as a whole, and it can also be interpreted as a measure of the overall geometric complexity of the landscape. LSI provides a standardized measure of total edge or edge density that adjusts for the size of the landscape.	increases without limit as landscape shape becomes more irregular or as the length of edge within the landscape of the corresponding patch type increases.
Landscape	Contagion index (CONTAG)	CONTAG summarizes both class dispersion (i.e., the spatial distribution of a patch type) and interspersions (i.e., the intermixing of units of different patch types). It is based on cell adjacencies and the probability of finding a cell type <i>i</i> next to cell type <i>j</i> .	$0 < \text{CONTAG} \leq 100$ (percent) Holding dispersion constant, a landscape in which the patch types are well interspersed will have lower contagion than a landscape in which patch types are poorly interspersed. Also, holding interspersions constant, a landscape in which the patch types are aggregated into larger, contiguous patches will have a more significant contagion than a landscape in which the patch types are fragmented into many small patches.
Landscape	Patch richness (PR)	PR measures the number of different patch types in the landscape. Patch richness is partially affected by scale, and larger areas are richer because there is generally more significant heterogeneity than in smaller areas.	$\text{PR} \geq 1$, without limit (none)
Landscape	Shannon diversity index (SHDI)	SHDI refers to the diversity of patches in the landscape. It is a measurement of diversity used in ecology, applied here to landscapes.	$\text{SHDI} \geq 1$ (none) $\text{SHDI} = 0$ when the landscape contains only 1 patch (i.e., no diversity) and increases as the number of different patch types increases or the proportional distribution of area among patch types becomes more equitable
Class	Percentage of landscape (PLAND)	PLAND equals the percentage of the landscape	$0 < \text{PLAND} \leq 100$ (percent) PLAND approaches 0 when the corresponding patch type (class) becomes increasingly rare in the landscape. $\text{PLAND} = 100$ when

		comprised of the corresponding patch type (class)	the entire landscape consists of a single patch type; that is when the entire image is comprised of a single patch.
Class	Number of patches (NP)	NP refers to the number of patches of a given patch type (class). It is the most straightforward measure of subdivision.	NP \geq 1, without limit (none). NP = 1 when the landscape contains only 1 patch of the corresponding patch type, i.e. when the class consists of a single patch.
Class	Edge density (ED)	ED equals the sum of the lengths (m) of all edge segments involving the corresponding patch type (class, divided by the total landscape area).	ED \geq 0, without limit (meter per hectare). ED = 0 when there is no class edge in the landscape; the entire landscape consists of the corresponding patch type.
Class	Mean Euclidean nearest neighbor distance (ENN_MN)	ENN_MN is the straight-line distance to the nearest neighboring patch of the same patch type, based on the distance between cell centers of the two closest cells form the respective patches. Constitutes the most straightforward measure of patch isolation.	ENN > 0, without limit (meters). ENN approaches 0 as the distance to the nearest neighbor decreases.
Class	Aggregation index (AI)	AI is the ratio of the observed number of like adjacencies to the maximum possible number of like adjacencies, expressed as a percentage.	0 < AI \leq 100 (%) (percent). AI equals 0 when the patch types are maximally disaggregated (i.e., when there are no like adjacencies); AI increases as the landscape is increasingly aggregated and equals 100 when the landscape consists of a single patch.

Statistical analysis

First, to explore similarities in species composition among studied regions, we ran a Principal Component Analysis (PCA) with species whose individuals accounted for 75% of the total accumulated frequency. Then, to evaluate relationships between the bird communities of the pine-oak forests and local vegetation structure and landscape metrics, we performed a stepwise regression method, which involves the selection of predictor variables to evaluate their predictability capacity. We checked for multicollinearity based on the Variance Inflation Factor (VIF), variables with a VIF more significant than 10 were excluded from the analyses. We used bird species richness (SR), Shannon-Wiener index (SWI), Simpson index (SI), and abundance

as response variables and vegetation structure and landscape metrics as predictors variables. Vegetation structure variables included the Shannon-Wiener index (SWI_v) and Simpson index (SI_v) and average DBH and height. Landscape metric variables included the nine metrics (Table 1) calculated at four different scales (i.e., 100, 300, 500, and 1000 m radius). The graphical study of residuals assessed normality and homoscedasticity assumptions. We also summarized all vegetation structure variables in a single value using a PCA, taking the values along the first PCA axis to measure vegetation complexity.

We explored the relationship between bird abundance (classified according to habitat preference and feeding guild), vegetation structure, and landscape metrics. Overdispersion was detected by assessing the relationship between the deviance and degrees of freedom; whenever this relationship was > 2.5 , we used a Negative Binomial distribution instead of a Poisson distribution. All statistical analyzes were conducted using the InfoStat software (Di Rienzo *et al.*, 2021) and its R interface (R Core Team, 2021). We considered that there was a significant relationship between variables when p -value < 0.05 .

Results

Bird community

We registered 600 bird individuals belonging to 93 species and 30 families. El Manzano presented the highest species richness (46), followed by Miramundo (41), Montecristo (39), and Morazán (32). Only three species were shared between regions, Yellow-backed Oriole (*Icterus chrysater*), Dusky-capped Flycatcher (*Myiarchus tuberculifer*), and Black-throated Green Warbler (*Setophaga virens*). In terms of species diversity, we found the highest SWI for Montecristo (2.60), followed by El Manzano (2.58), while Miramundo and Morazán mean SWI corresponded to 2.50 and 2.33, respectively. The mean SI was relatively similar between Montecristo, Miramundo, and El Manzano (0.66, 0.60, and 0.64 respectively), but for Morazán was smaller (0.09).

Out of the 93 bird species detected, 81% were residents, 18% were migratory, and 1% were classified as transient. Based on their preferred diet, 57% were classified as insectivores, 13% as omnivores, 12% as frugivores, 6% respectively as granivores and nectarivores, and 3% as carnivores. Regarding habitat preference, 37% of the species were classified as generalists, 28% as highland forest specialists, 18% as forest specialists, and 17% as highland forest generalists. The most common species detected was the bushy-crested jay (*Cyanocorax melanocyaneus*), followed by the brown-backed solitaire (*Myadestes occidentalis*) and the slate-throated warbler (*Myioborus miniatus*). Thirty-four out of the 93 species detected represented 75% of all individuals registered across all study sites (Table 2). Also, we found 10 species that are locally threatened according to local authorities (MARN, 2015), of which only one had a global conservation status, the Highland Guan (*Penelopina nigra*), considered globally Vulnerable (IUCN, 2021).

Comparison between regions

The analysis of species composition revealed along Axis 1 (PC1 22.8%) that Montecristo and Miramundo bird community composition differed from those in Manzano and Morazán, and that communities from Montecristo and Miramundo were more similar between them in comparison with those from El Manzano and Morazán (Figure 2).

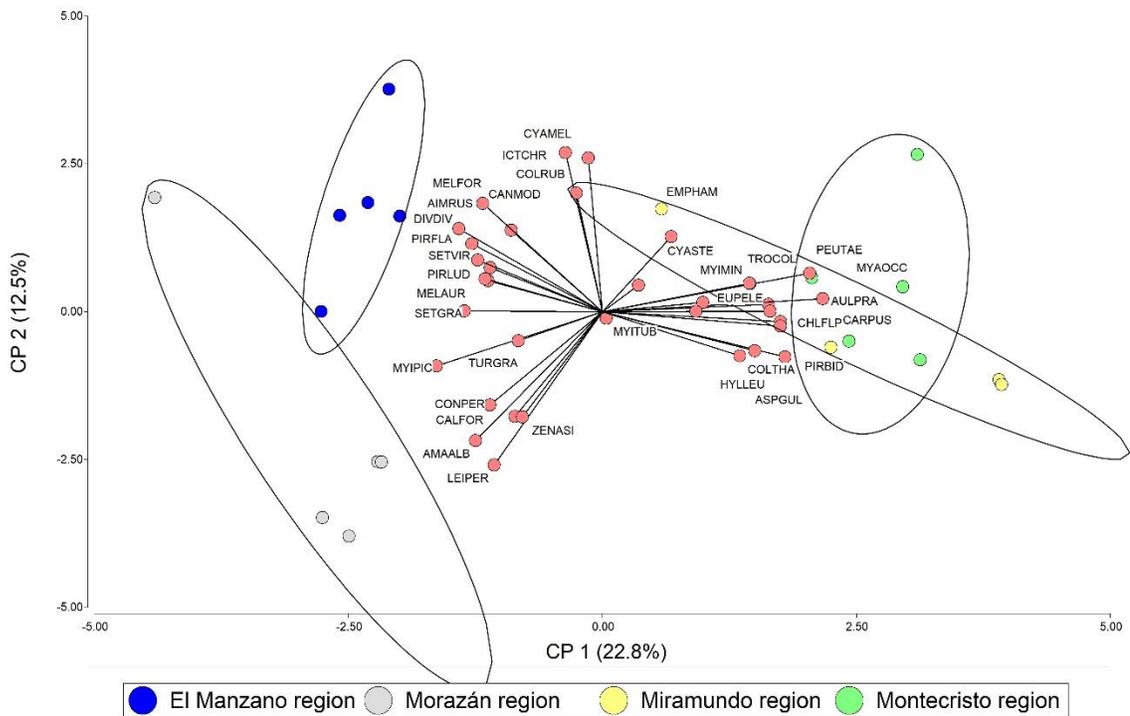


Figure 2

Principal component analysis with species whose individuals accounted for 75% of the total accumulated frequency detected across regions. Only six-letter code-names shown on the figure, for a complete name of species, see Table 2

Vegetation

We measured 309 trees from which we identified 29 species belonging to 19 families. Out of these 29 species, six could only be identified to the genus level. Most individuals were *Pinus* sp. (23%). Other dominant species found were *Quercus elliptica* (15%) and *Pinus oocarpa* (12%). *Perymenium grande* (3%) and *Myrsine juergensenii* (3%) were also frequent. Species richness was higher in Montecristo, with 21 species, followed by Miramundo (12 species), El Manzano (9 species), and Morazán (6 species). We found five species locally threatened according to local authorities (MARN, 2015), two of which had a global conservation status, Red Pine (*Pinus tecunumanii*) and *Casearia sanchezii*, respectively listed as Vulnerable and Endangered (IUCN, 2021).

Table 2

Bird species representing 75% of all individuals registered across study sites. Status refers to whether the species are R= residents or M= neotropical migrants. IUCN status, LC= least concern. IUCN trends refer to whether the population trend is S= stable, D= decreasing, I= increasing or U= unknown. AA= accumulated abundance, RA= relative abundance and ARA= accumulated relative abundance. Taxonomy according to the American Ornithological Society (AOS), including updates of Chesser et al. (2020); IUCN status, and trends (IUCN, 2021)

Family	Scientific name	Alpha code	English name	Status	IUCN status	IUCN trends	AA	RA	ARA
Corvidae	<i>Cyanocorax melanocyaneus</i>	CYAMEL	Bushy-crested Jay	R	LC	S	36	0.06	0.06
Turdidae	<i>Myadestes occidentalis</i>	MYAOCC	Brown-backed Solitaire	R	LC	D	25	0.04	0.10
Parulidae	<i>Myioborus miniatus</i>	MYIMIN	Slate-throated Redstart	R	LC	D	24	0.04	0.14
Parulidae	<i>Leiothlypis peregrina</i>	LEIPER	Tennessee Warbler	M	LC	S	22	0.04	0.18
Icteridae	<i>Icterus chrysater</i>	ICTCHR	Yellow-backed Oriole	R	LC	D	20	0.03	0.21
Troglodytidae	<i>Cantorchilus modestus</i>	CANMOD	Cabanis's Wren	R	LC	U	19	0.03	0.24
Parulidae	<i>Cardellina pusilla</i>	CARPUS	Wilson's Warbler	M	LC	D	18	0.03	0.27
Parulidae	<i>Myioborus pictus</i>	MYIPIC	Painted Redstart	R	LC	D	18	0.03	0.30
Paserellidae	<i>Chlorospingus flavopectus</i>	CHLFLP	Common Chlorospingus	R	LC	D	17	0.03	0.33
Parulidae	<i>Setophaga graciae</i>	SETGRA	Grace's Warbler	R	LC	D	16	0.03	0.36
Tyrannidae	<i>Myiarchus tuberculifer</i>	MYITUB	Dusky-capped Flycatcher	R	LC	D	16	0.03	0.39
Parulidae	<i>Setophaga virens</i>	SETVIR	Black-throated Green Warbler	M	LC	D	15	0.03	0.41
Corvidae	<i>Calocitta formosa</i>	CALFOR	White-throated Magpie-Jay	R	LC	S	15	0.03	0.43
Peucedramidae	<i>Peucedramus taeniatus</i>	PEUTAE	Olive Warbler	R	LC	D	14	0.02	0.46

Emberizidae	<i>Aimophila rufescens</i>	AIMRUS	Rusty Sparrow	R	LC	S	13	0.02	0.48
Icteridae	<i>Dives dives</i>	DIVDIV	Melodious Blackbird	R	LC	I	12	0.02	0.50
Ramphastidae	<i>Aulacorhynchus prasinus</i>	AULPRA	Northern Emerald-Toucanet	R	LC	D	12	0.02	0.52
Columbidae	<i>Zenaida asiatica</i>	ZENASI	White-winged Dove	R	LC	I	11	0.02	0.54
Picidae	<i>Melanerpes formicivorus</i>	MELFOR	Acorn Woodpecker	R	LC	S	10	0.02	0.56
Picidae	<i>Colaptes rubiginosus</i>	COLRUB	Golden-olive Woodpecker	R	LC	D	10	0.02	0.57
Cardinalidae	<i>Piranga flava</i>	PIRFLA	Hepatic Tanager	R	LC	I	9	0.02	0.59
Turdidae	<i>Turdus grayi</i>	TURGRA	Clay-colored Thrush	R	LC	I	9	0.02	0.60
Picidae	<i>Melanerpes aurifrons</i>	MELAUR	Golden-fronted Woodpecker	R	LC	I	8	0.01	0.61
Trochilidae	<i>Hylocharis leucotis</i>	HYLLEU	White-eared Hummingbird	R	LC	U	8	0.01	0.63
Cardinalidae	<i>Piranga bidentata</i>	PIRBID	Flame-colored Tanager	R	LC	D	8	0.01	0.64
Trogonidae	<i>Trogon collaris</i>	TROCOL	Collared Trogon	R	LC	D	8	0.01	0.66
Psittacidae	<i>Amazona albifrons</i>	AMAALB	White-fronted Parrot	R	LC	I	8	0.01	0.67
Trochilidae	<i>Colibri thalassinus</i>	COLTHA	Mexican Violetear	R	LC	U	8	0.01	0.68
Corvidae	<i>Cyanocitta stelleri</i>	CYASTE	Steller's Jay	R	LC	I	7	0.01	0.69
Momotidae	<i>Aspatha gularis</i>	ASPGUL	Blue-throated Motmot	R	LC	D	7	0.01	0.70
Tyrannidae	<i>Empidonax hammondii</i>	EMPHAM	Hammond's Flycatcher	M	LC	I	7	0.01	0.72
Cardinalidae	<i>Piranga ludoviciana</i>	PIRLUD	Western Tanager	M	LC	I	7	0.01	0.73
Tyrannidae	<i>Contopus pertinax</i>	CONPER	Greater Flycatcher	R	LC	D	6	0.01	0.74
Fringillidae	<i>Euphonia elegantissima</i>	EUPELE	Elegant Euphonia	R	LC	D	6	0.01	0.75

Relationships between local vegetation, landscape metrics, and bird diversity

Bird species richness positively responded to pine-oak patch isolation, pine-oak forest percentage of cover and edge density of broadleaf forest at 500 m scale, and negatively to edge density of broadleaf forest at 1000 m scale (Figure 3). Bird SWI positively responded to pine-oak aggregation index (Figure 4), while SI positively responded to broad leaf forest edge density, both at the 500 m scale (Figure 5). The scale at which landscape metrics better predicted bird richness and diversity changes was in those landscapes with a 500 m radius (Table 3). Across all models, all but one explicatory variable was positively correlated with the response bird diversity variables. We did not find any significant correlation between birds' richness and diversity and vegetation variables.

Table 3

Significant relationships between bird community response variables and landscape metrics. SR= Species richness, SWI= Shannon-Wiener index, SI= Simpson index (SR $R^2=0.79$, SWI $R^2=0.51$, SI $R^2= 0.43$). ENN_MN= Euclidean mean distance, AI= Aggregation index, ED= Edge density, PLAND: percentage of cover.

Level	Metrics (scale in m)	Metric type	Bird community		
			SR	SWI	SI
Class	Pine-oak ENN_MN (500)	Configuration	0.00010		
Class	Pine-oak AI (500)	Configuration		0.00300	
Class	Pine-oak ED (500)	Configuration			0.00360
Class	Pine-oak forest PLAND (500)	Composition	0.00100		
Class	Broad-leaf ED (500)	Configuration	0.00120		
Class	Broad leaf forest ED (1000)	Configuration	0.00400		

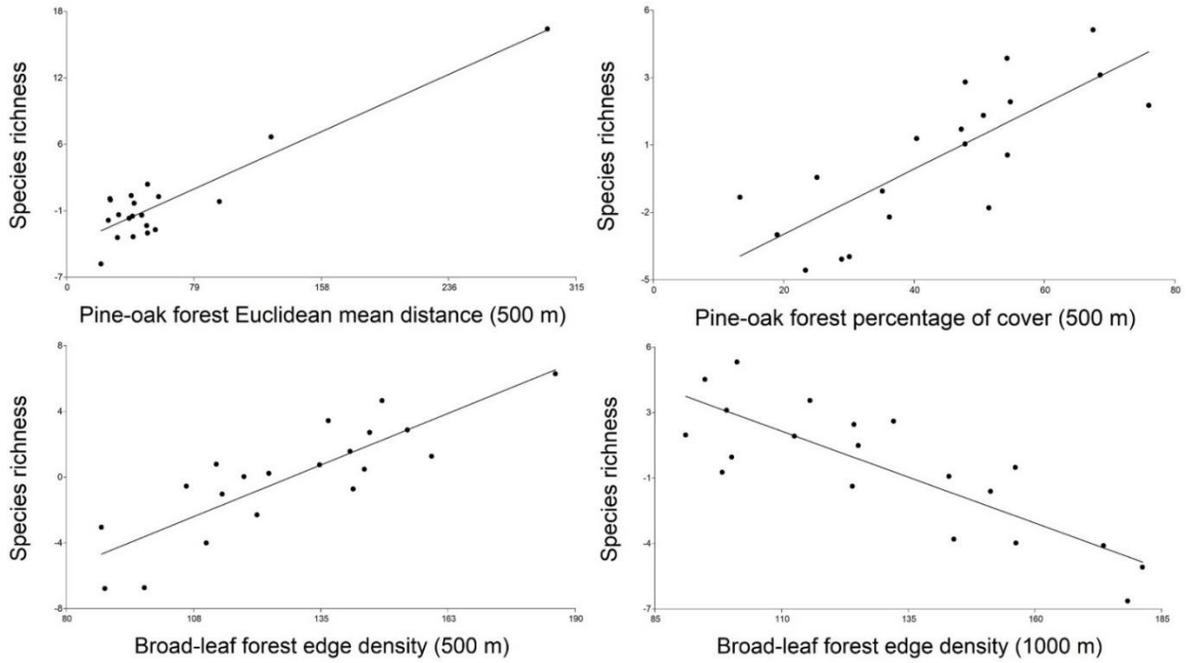


Figure 3
Scatter plots depicting partial regressions of significant relationships between bird species richness and landscapes variables. Scale at which metrics were calculated is within parenthesis

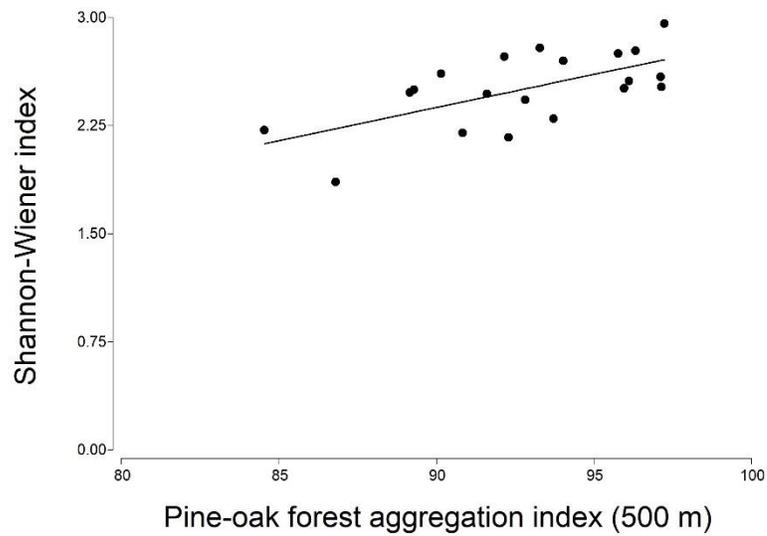


Figure 4
Scatter plot depicting the significant relationships between bird Shannon-Wiener index and Pine-oak aggregation index at 500 m scale

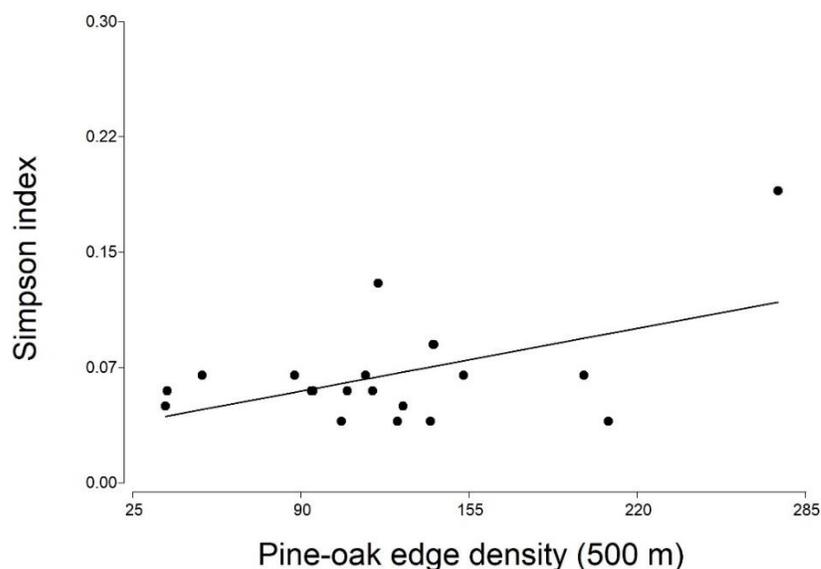


Figure 5

Scatter plot depicting the significant relationships between Simpson index for birds and Pine-oak edge density at 500 m scale

Relationships between birds preferred habitat and landscape metrics

In this analysis, we found significant relationships between the abundance of birds of specific feeding guilds. We found significant relationships between the abundance of birds of specific habitat preference and all nine landscape metrics at the four scales. The scales at which metrics better predicted changes in bird abundance were 500 m, except for highland forests specialist birds which only responded to landscape configuration at 300 m scale. At a 500 m scale, forest generalists were positively related to the number of patches and edge density of pine-oak forest and patch richness and negatively to the pine-oak forest aggregation index. Highland forests generalists were positively related to the percentage of pine-oak forest cover, edge density of pine-oak forest and aggregation index, and percentage of broadleaf forest cover, and were negatively related to LSI and broadleaf forest edge density (Table 4).

Table 4

Significant relationships between bird abundance per habitat preferences and landscape metrics. HFS= Highland forests specialists, HFG= Highland forests generalists, FG= Forests generalists, G= Generalists. ED= Edge density, PLAND= percentage of the landscape of patch type, NP= number of patches, PR= patch richness, SHDI= Shannon’s diversity index, AI= Aggregation index, LSI= Landscape shape index, ENN_MN= Euclidean mean distance, CONTAG= Contagion index

Level	Metrics (scale in m)	Metric type	Habitat preferences			
			HFS	HFG	FG	G
Class	Pine-oak forest ED (100)	Composition		0.0088		
Class	Pine-oak forest PLAND (100)	Composition		0.0049	0.0014	

Class	Broad-leaf forest PLAND (100)	Composition		0.0012	
Class	Pine-oak forest NP (100)	Configuration		0.0421	
Class	Broad-leaf forest NP (100)	Configuration		0.0161	
Landscape	PR (100)	Composition	0.0234		0.0226
Landscape	SHDI (100)	Composition	0.0328		
Landscape	SHDI (300)	Composition	0.0005		
Class	Broad-leaf forest PLAND (300)	Composition		0.0161	
Class	Pine-oak forest PLAND (300)	Composition	0.0007		0.0038
Class	Broad-leaf forest AI (300)	Configuration	0.0119	0.0059	
Class	Pine-oak forest AI (300)	Configuration	0.0302		
Landscape	LSI (300)	Configuration			0.0318
Landscape	PR (300)	Composition		0.0093	
Landscape	PR (500)	Composition		0.0034	
Landscape	LSI (500)	Configuration	0.0094		0.0061
Class	Pine-oak PLAND (500)	Composition	0.0001		
Class	Pine-oak forest NP (500)	Configuration		0.0303	
Class	Broad-leaf ED (500)	Configuration	0.0327		
Class	Pine-oak forest ED (500)	Configuration	0.0197	0.0079	
Class	Broad-leaf forest ENN_MN (500)	Configuration			0.0248
Class	Broad-leaf forest AI (500)	Configuration			0.0089
Class	Pine-oak forest AI (500)	Configuration	0.0484	0.0286	
Class	Pine-oak forest ED (1000)	Configuration		0.0020	
Class	Broad-leaf forest ED (1000)	Configuration	0.0135		
Class	Pine-oak forest NP (1000)	Configuration		0.0005	
Class	Pine-oak ENN_MN (1000)	Configuration		0.0002	
Class	Broad-leaf forest ENN_MN (1000)	Configuration		0.0029	
Class	Pine-oak forest AI (1000)	Configuration		0.0091	

Landscape	CONTAG (1000)	Configuration	0.0006	0.0023
Landscape	SHDI (1000)	Composition		0.0165

Relationships between birds' feeding guild and landscape metrics

In this analysis, we found significant relationships between the abundance of birds of specific feeding guilds and all nine landscape metrics at the four scales. The scales at which metrics better predicted changes in bird abundance were 1000 and 500 m (Table 5). Frugivores, omnivores and nectarivores better responded to landscape pattern than insectivores. At a 1000 m scale, frugivores were positively correlated to patch isolation and cover percentage of broadleaf forest and percentage of pine-oak forest cover but negatively associated with the number of patches and edge density of the broadleaf forest, and with Shannon diversity index of patches and with landscape shape index. Nectarivores were negatively associated with edge density and cover percentage of broadleaf forest. Omnivores were positively associated with pine-oak forest and broadleaf forest patch isolation but negatively with edge density of the pine-oak forest. At a 500 m scale, frugivores responded positively to broadleaf forest patch isolation and edge density and Shannon diversity index of patches, and negatively to edge density of the pine-oak forest, the number of patches of broadleaf forest, and to contagion index. Nectarivores were positively correlated with the Shannon diversity index of patches and patch richness but negatively to the percentage of pine-oak forest cover. Finally, omnivores were positively correlated with edge density of pine-oak forest and contagion index but negatively to patch isolation of pine-oak and broadleaf forest (Table 5).

Table 5

Significant relationships between birds' guild and landscape metrics. Fr= Frugivore, In= Insectivore, Om= Omnivore, Ne= Nectarivore, Gr= Granivore

Level	Metrics (scale in m)	Metric type	Feeding guild				
			Fr	In	Om	Ne	Gr
Class	Pine-oak forest PLAND (100)	Composition				0.0006	
Landscape	PR (100)	Composition	0.0011			0.0066	
Landscape	CONTAG (100)	Configuration	0.0250				
Class	Broad-leaf forest PLAND (100)	Composition				0.0006	
Class	Pine-oak forest NP (100)	Configuration					0.0127
Class	Broad-leaf forest PLAND (300)	Composition	0.0047				0.0063
Class	Broad-leaf forest NP (300)	Configuration		0.0186			

Class	Pine-oak forest NP (300)	Configuration				0.0047
Class	Broad-leaf forest ED (300)	Configuration		0.0142		
Class	Pine-oak forest ED (300)	Configuration		0.0259	0.0378	
Landscape	Broad-leaf forest AI (300)	Configuration	0.0342			0.0394
Landscape	CONTAG (300)	Configuration	0.0121	0.0177	0.0109	
Landscape	SHEI (300)	Composition	0.0316			0.0086
Landscape	SHEI (500)	Composition	0.0057			0.0098
Landscape	PR (500)	Composition				0.0015
Class	Broad-leaf forest NP (500)	Configuration	0.0459			
Class	Pine-oak forest PLAND (500)	Composition				0.0034
Class	Broad-leaf forest ED (500)	Configuration	0.0147			
Class	Pine-oak forest ED (500)	Configuration	0.0012	0.0064		
Class	Broad-leaf ENN_MN (500)	Configuration	0.0007	0.0032		
Class	Pine-oak forest ENN_MN (500)	Configuration		0.0071		
Landscape	CONTAG (500)	Configuration	0.0315	0.0219	0.0254	0.0061
Class	Broad-leaf forest AI (1000)	Configuration				0.0052
Class	Pine-oak forest ENN_MN (1000)	Configuration		0.0005		
Class	Broad-leaf forest ENN_MN (1000)	Configuration	0.0001	0.0075		
Class	Pine-oak forest ED (1000)	Configuration		0.0081		
Landscape	Broad-leaf ED (1000)	Configuration	0.0001			0.0367

Class	Broad-leaf forest NP (1000)	Configuration	0.0071		
Class	Broad-leaf forest PLAND (1000)	Composition	0.0233		0.0019
Class	Pine-oak forest PLAND (1000)	Composition	0.0001	0.0442	
Landscape	LSI (1000)	Configuration	0.0001		0.0053
Landscape	CONTAG (1000)	Configuration	0.0001	0.0316	0.0447
Landscape	SHEI (1000)	Composition	0.0003		

Discussion

Vegetation

Except for studies conducted on the MCNP, the floristic composition of El Salvador's pine-oak forests is poorly studied. However, some studies have reported *Pinus oocarpa* and *Quercus elliptica* as abundant species (Murillo-Contreras, 2002; PRISMA, 2005). Cardoza-Ruiz (2011) found that *P. oocarpa*, *Q. segoviensis* and *Q. elliptica* were the three most ecological relevant species in the pine-oak forest of MCNP according to the Importance Value Index (IVI) (which was based on abundance, frequency, and basal area). Our results agree with these findings since *Q. elliptica* and *P. oocarpa* were the most abundant species across our study regions. We also found a greater species richness in the Montecristo and Miramundo regions located at higher altitudes (nearly 800 m higher than El Manzano and Morazán) and have a steeper topography than the El Manzano and Morazán regions. Diversity of vegetation decreases linearly with elevation (Gentry, 1993); however, in pine-oak forests, Siles *et al.* (2017) found greater species richness in vegetation plots at higher altitudes in the pine-oak forests of Nicaragua compared to those at lower elevations. Differences in elevation and topographic features across our study regions can partially help explain differences in vegetation; however, other factors can also influence these differences, such as the fact that Montecristo holds a protected area (the MCNP), anthropogenic fires (Lineal & Laituri, 2013), soil differences between regions, as soils in Montecristo are not the same as in Morazán (Vogt, 1946) and soil use, in previous decades, for productive activities (i.e., agriculture & mining) (Masin, 1963).

Bird communities in highland forests of El Salvador

More than 50% of the total birds recorded across our study regions were insectivores. The fact that pines (*Pinus* sp.) and oaks (*Quercus* sp.) are the most common trees found in our study area and that these species lack any fleshy fruit could explain the dominance of insectivorous birds. Martin & Karr (1986) found evidence that indicated that the presence of insectivore and frugivore birds in forest gaps was driven by resource availability. Other studies have suggested that tree species might provide different food resources for birds, determining certain species' presence or abundance (Balda, 1969; Holmes & Robinson, 1981). The majority of the birds we found were generalist (i.e., birds that can be found in any habitat) and highland forest specialists (i.e., birds that inhabit only in a specific highland forest), among generalist birds, resident species included the golden-olive woodpecker (*Colaptes rubiginosus*), house wren (*Troglodytes aedon*) and great-tailed grackle (*Quiscalus mexicanus*), while migratory species

included Wilson's warbler (*Cardellina pusilla*), Tennessee warbler (*Leiothlypis peregrina*) and western tanager (*Piranga ludoviciana*). Migratory species are known to use a wide range of habitats in their wintering grounds (Terborgh, 1980); however, both residents and migratory species we found are known to be frequent in a variety of ecosystems, such as coffee plantations, urban and open areas and even in pine-oak forests (Vannini, 1994; Komar, 2002; Pablo-Cea *et al.*, 2018), some of these ecosystems were present in our study areas. Almazán-Núñez *et al.* (2018) found similar results in a study conducted in pine-oak forests in México. As expected, several of the highland forest specialists that we recorded are characteristic of the pine-oak forests, such as painted warbler (*Myioborus pictus*), Grace's warbler (*Setophaga graciae*), olive warbler (*Peucedramus taeniatus*), yellow-backed oriole (*Icterus chrysater*), and brown creeper (*Certhia americana*) (Komar, 2002; Herrera-Serrano & Domínguez-Miranda, 2020).

Differences in species richness and composition were found between regions. Both Montecristo and Miramundo have cloud forests in the surrounding landscapes (Daugherty, 1973; Komar, 2002), which explains a greater highland bird's diversity (Watson & Peterson, 1999). The greater richness of generalist bird species in El Manzano and Morazán, characterized by higher heterogeneity, may be compensatory dynamics, where extinction of specialist species is masked by the colonization of better-adapted species (Supp & Ernest, 2014); therefore, species richness might not be a good indicator of habitat quality (Ernst & Brown, 2001). Environmental variables can also help explain the similarity and differences between regions; there is evidence that elevation range, climatic diversity, and population isolation play an essential role in determining changes in bird species richness across topographic reliefs (Janzen, 1967; Ruggiero & Hawkins, 2008). Hernández-Baños (1995) identified pine-oak forest types based on humidity patterns, recognizing humid pine-oak and arid pine-oak forests; our study sites at the four regions may fit well in these categories, being Montecristo and Miramundo regions humid pine-oak and El Manzano and Morazán arid pine-oak, and thus, having differences in species composition, which is reflected in the species composition analysis. Also, the relative arid conditions, vegetation, and altitude might explain the lower highland forest specialist's species richness and dominance of generalist birds in El Manzano and Morazán. However, the lack of information in these regions restricts our ability to make more interpretations.

Surrounding landscape and bird species diversity and composition

We did not find any significant relationships between bird's abundance, richness, and diversity with local vegetation structure; these findings agree with studies that have found that landscape structure is more important in determining bird community characteristics (Morante-Filho *et al.*, 2021). Similarly, Miller & Chambers (2007) found few significant relationships between the bird community and local vegetation variables of a pine-oak forest in Mexico; neither species richness nor abundance was correlated with vegetation variables. Evidence suggests that significant relationships with local vegetation become visible when studying interactions with species and are hardly visible at the community level (Ueze & Metzger, 2011).

Bird communities responded to landscape metrics, particularly to configuration rather than composition metrics. Forest's configuration has been considered of lesser importance (in comparison with landscape composition) in shaping birds' community in both temperate and neotropical landscapes (Fahrig, 2003; Zurita & Bellocq; 2010; Carrara *et al.*, 2015; De Camargo *et al.*, 2018; Shoffner *et al.*, 2018; Gonçalves-Bonfim *et al.*, 2021). However, few studies have been conducted in the Neotropics in comparison with temperate areas. Neotropical birds have a different evolutionary history than temperate birds, differing in climate adaptation, sedentarism,

biological interactions, among others (Janzen, 1967; Skutch, 1985; Marra & Remsen, 1997; Tobias *et al.*, 2013), which could make them more sensitive to forest's fragmentation (Stratford & Robinson, 2005; Cerezo *et al.*, 2010; Bregman *et al.*, 2014). For example, pine-oak specialist birds like the brown creeper (*Certhia americana*) are sensitive to edge effects (Poulin & Villard, 2011) and require dead trees for nesting and large-diameter trees for foraging (Pouling *et al.*, 2008; Geylese *et al.*, 2016), and though little is known about the ecology of many bird species in the CAPOE, the sensitivity of highland specialist bird species to forest fragmentation might occur in this region. Moreover, highland birds are restricted in their spatial distribution by altitudinal limits, which make them more sensitive to forest isolation (i.e., fragmentation) (Kattan *et al.*, 1994) in addition to habitat loss (i.e., deforestation).

Surprisingly, we found a significant and positive relationship between species richness and pine-oak Euclidean mean distance (ENN_MN) and broadleaf forest edge density at the 500 m scale (Table 8). ENN_MN is a metric of patch isolation that reflects the lack of habitat around the patch (Farigh, 2003). This Euclidean mean distance only reflects the geographical distance between patches and does not provide information about the matrix around patches, which directly influences patches (Stouffer & Bierregaard, 1995; Antongiovanni & Metzger, 2005; Bender & Fahrig, 2005). The matrix around our study areas comprises croplands and broadleaf forests patches, which might be suitable for some generalist species that could penetrate pine-oak forest patches. The spillover effect, which is the exchange or movement of organisms from natural habitat to matrix areas or vice versa (Blitzer *et al.*, 2012; Frost *et al.*, 2015), can help explain this positive relationship. Most of the species we found were generalist birds, which can be the result of species venturing into isolated pine-oak forest patches from adjacent habitats to take advantage of resources, increasing species richness at pine-oak forest patches. The spillover effect could also help explain the positive relationship of SR with broadleaf forest edge density at 500 m and 1000 m scale. This effect is amplified in fragmented and heterogeneous landscapes, where interaction between native habitat and the matrix is more frequent (Blitzer *et al.*, 2012; Boesing *et al.*, 2017; van Schalkwyk *et al.*, 2020), being the matrix where generalist bird species are most frequently found.

Forest generalists were associated positively with edge density and patch numbers of pine-oak forests, but negatively with the pine-oak aggregation index. Forest edge has been associated with adverse effects (Laurence *et al.*, 2002; Banks-Leite *et al.*, 2009), but other studies also have found positive edge relationships with forest birds (Carrara *et al.*, 2015). More patches mean more edges, and complex fragments might ease colonization due to patch shape complexity (Ewers & Didham, 2006). Forest generalists and other species can use patches as steppingstones (Gillies & St. Clair, 2010). On the other hand, highland forest generalists increased with more coverage of pine-oak and broadleaf forests, more of these forests implies more suitable habitat (Fahrig, 2003); but responded negatively to edge related metrics, which is not strange, given their forest dependence and sensibility to fragmentation (Kattan *et al.*, 1994; Devictor, 2008).

Generalist birds tend to be reduced with forest amount (Carrara *et al.*, 2015; Morante-Filho *et al.*, 2016). Aggregated patches can indicate more forest and, in the context of our study areas (which are relative forested), isolated patches might be surrounded by other types of forest. This could also help to explain the negative relationship of generalist birds with the number of patches at 1000 m since more patches in our study areas might be due to fragmented patches of forests. Generalist birds tend to use resources from different habitats (Devictor, 2008) and inhabit less specialized communities (Julliard *et al.*, 2006), an increase in forest amount might reduce these resources (Morante-Filho *et al.*, 2016), leading to a decrease in generalist birds.

Concerning birds' feeding guilds, nectarivores, granivores, and omnivores did not show a clear pattern of relationships with landscape metrics; overall, they were positively associated with edge and isolation-related metrics at both 500 and 1000 m scale. Species and these guilds use diverse resources (Pineda-Diez *et al.*, 2012) and might benefit from a diverse matrix where edges and diverse habitats are frequent (Gray *et al.*, 2007; Bregman *et al.*, 2014). Frugivores, in turn, showed a more robust negative response to edge density of both pine-oak and broadleaf forests and were positively associated with pine-oak and broadleaf forest cover. Broad-leaf Forest might provide more resources for frugivorous birds in pine-oak forests since fruit is common in broadleaf forests, especially secondary forests (Leck, 1987; Levey, 1988), but also, frugivorous birds can be affected by an increase of edges (Gray *et al.*, 2007). The frugivores species we found, like the northern emerald-toucanet (*Aulacorhynchus prasinus*) and collared trogon (*Trogon collaris*), might use resources from both broadleaf and pine-oak forests such as fruits and snags (usually dead pines) that provide nesting holes since these species are cavity nesters (Skutch, 1956; Riley, 1986). Furthermore, frugivorous with a large body mass (especially toucans & guans) are vulnerable to fragmentation (Kattan *et al.*, 1994; da Silva & Tabarelli, 2000); therefore, frugivorous in the pine-oak forest might be affected by edges and loss of both pine-oak and broadleaf forests.

Contrary to our expectations, we found few significant relationships between landscape metrics and insectivores. Evidence suggests that landscape fragmentation significantly affects insectivores (Canaday, 1997; Lindell *et al.*, 2007; Sekercioglu *et al.*, 2002; Bregman *et al.*, 2014). We found them to be positively correlated with the contagion index, broadleaf forest number of patches but negatively with pine-oak cover. Insectivorous birds such as foliage gleaners and bark foragers have been related to vegetation structures such as DBH, number of stems, and basal area (i.e., spatial variation at fine-scale) (Castaño-Villa *et al.*, 2014). We found a dominance of pine trees (*Pinus* spp.), which can be interpreted as structurally homogeneous vegetation at the study sites, requiring insectivorous birds to use broadleaf forest resources. King & Rappole (2000) found flocks of pine-oak insectivores like grace warbler (*S. graciae*), olive warbler (*P. taeniatus*), slate-throated redstart (*M. miniatus*), and black-throated green warbler (*S. virens*), which were common in our study, associated to open-canopy pine forest, or in some cases with deciduous forest, suggesting that insectivores in these types of habitats move through a gradient of vegetation, and do not adhere strictly to the pine-oak ecosystem.

Scale

We found that bird SR, SWI, and SI responded mostly to landscape configuration metrics within a 500 m radius. King & Rappole (2000) estimated 9.6 ha as minimum home ranges (175 m of radio assuming circular home ranges) for flocks of insectivorous birds at the CAPOE (for *C. americana* has been estimated 10 ha in North America (Pouling *et al.*, 2008)), similar findings have been found in the region by Carrara *et al.* (2015) and Cerezo *et al.* (2010). Our results indicate that the landscape structure affects pine-oak bird communities at larger scales than their home range sizes, suggesting that management decisions based solely on local-scale information might not be the most effective (Drapeau *et al.*, 2000). The scale of effect (i.e., the spatial extent or scale at which environmental variables are considered biologically or statistically significant) can be affected by dispersal, species traits, landscape, abundance variables, or even regional context (Jackson & Fahrig, 2012; Miguet *et al.*, 2016). In our relatively forested study sites, dispersal distances may be more significant since habitat cover and habitat aggregation facilitate movement (Miguet *et al.*, 2016), and thus being affected forest fragmentation occurring at larger scales than the estimated home range.

Our key findings are that 1) bird communities that inhabit pine-oak forests are affected by both habitat loss and habitat fragmentation, 2) broadleaf forests in the vicinity of pine-oak forest patches might be critical for some species, and 3) edge effect might be negatively affecting birds at the pine-oak forests (specially frugivores and insectivorous birds). In addition to reduce habitat loss, increasing the number of good quality forest patches might promote the conservation of bird communities persisting in these landscapes. Conservation practitioners and stakeholders must reduce shape complexity by stopping forest fragments' deforestation and increasing patch size to enhance core areas (Ewers & Didham, 2008). Of all pine-oak forests in El Salvador, only 1170 ha are being officially protected (1000 ha in MCNP and 170 ha in La Ermita Protected Natural Area (Komar, 2002; MARN, 2016). The effectiveness of traditional conservation approaches such as natural protected areas might be debatable or even controversial in some regions of Mesoamerica (Harvey *et al.*, 2008; Ramírez-Albores *et al.*, 2020); in the case of the MCNP seems to protect these otherwise endangered ecosystems within El Salvador. However, with a shifting view to landscape restoration nationwide (Patel, 2021), it is important to explore alternative conservation options that can guarantee the persistence of pine-oak forests. Forest community management implemented at El Manzano and other areas in Chalatenango and Morazán seem to provide feasible alternatives for sustainable pine-oak management. Further studies should explore the efficiency of these approaches independently or in combination.

Our data and few other studies conducted in Miramundo (Mertens, 1952) suggest that this area is critical for highland forest specialist birds and biodiversity in general. However, the Miramundo area is not under any protection and faces various threats derived mainly from agricultural expansion in this region; species like northern pygmy-owl (*Glaucidium gnoma*), unspotted saw-whet owl (*Aegolius ridgwayi*) seems to be restricted to this region (and to the nearby mountain of El Pital). Meanwhile, El Manzano region holds habitat for the globally endangered golden-cheeked warbler (*S. chrysoparia*) (Bolaños, 2009), so further studies will likely unveil other species of conservation concern that persist in this region. Finally, even though we found fewer bird species and highland forest specialists in the Morazán region, recent studies conducted in this region have revealed its importance for biodiversity (Argueta-Rivera *et al.*, 2020; Funes & Pocasangre-Orellana, 2020; Morales-Rivas *et al.*, 2020), and locally endangered species such as King Vulture (*Sarcorhampus papa*), Bat Falcon (*Falco rufigularis*) and Northern Barred-Woodcreeper (*Dendrocolaptes sanctithomae*) have been recorded in this area (MARN, 2015; eBird, 2021). Large parts of Morazán (and other northern forests) have been little explored; thus, we urge more systematic and long-term studies to be conducted across the Miramundo, El Manzano, and Morazán regions. Among the limitations of our work is that our bird samples were only in pine-oak forests and not in other areas with other land cover or uses. Our analysis focused on the community-level, missing possible relationships at species-level with the landscape structures. Further studies should focus on species ecology at these forests that help us advance our understanding of species respond to habitat loss and fragmentation and improve conservation policies.

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