



Effects of landscape composition and configuration on Andean birds are influenced by spatial scale

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ABSTRACT

Land use change is impacting biodiversity worldwide with outcomes that may vary according to landscape characteristics which operate on different spatial scales. We evaluated the influence of landscape configuration and composition at scales of 100 and 500 m on bird species richness and occupancy of functional groups (diet, body size, elevational ranges) in the tropical Andes of southern Ecuador. Surveys were conducted at 57 sites with varying degrees of land-use change, and data were analyzed using Bayesian multi-species occupancy models. The results indicate a negative relationship between farmland extent and both bird species richness and the presence of certain functional groups (e.g., frugivores) across spatial scales. The presence of native forest also emerges as a significant predictor of the occupancy of different functional groups, but only at the larger spatial scale. Furthermore, configurational features like density had a positive association with species richness, particularly at the smaller scale. Our research reveals that landscape composition and configuration can positively or negatively influence avian diversity depending on the spatial scale. Understanding how bird diversity and occupancy vary across different spatial scales can offer valuable insights for effective conservation in human-influenced landscapes.

1. Introduction

Human activities are transforming natural landscapes, with widespread impacts on biodiversity (Newbold et al., 2015). Two important characteristics of landscapes that can determine the distribution and abundance of animal species are composition (i.e. types and amount of the different habitat types), and configuration (i.e. the spatial pattern and connectivity of habitat types) of landscape elements (Adler and Jedicke, 2022; Fahrig, 2017; Fahrig et al., 2019; Fletcher et al., 2018; Hadley and Betts, 2016; Uemaa et al., 2009). Despite significant progress made in understanding how these landscape characteristics impact biodiversity patterns (Adler and Jedicke, 2022; Hadley and Betts, 2016; Uemaa et al., 2013, 2009), substantial knowledge gaps still remain, particularly in species-rich ecosystems like the tropical Andes, where decades of land use change have profoundly altered landscapes (Loughlin et al., 2018).

Birds are particularly sensitive to changes in landscape composition

and configuration (Adler and Jedicke, 2022; Uemaa et al., 2009). For instance, the diversity of habitat types in a landscape (measure of landscape composition) can increase the types of resources available for birds, by positively influencing bird diversity (Estrada-Carmona et al., 2022; Martínez-Núñez et al., 2023). Furthermore, landscape connectivity (a measure of landscape configuration) can influence bird biodiversity; landscapes with high connectivity can facilitate bird movements among patches, which results in higher biodiversity levels compared to landscapes with lower connectivity (Herrera et al., 2018). However, comprehensive studies that elucidate the role of landscape characteristics in biodiversity in the tropical Andes remain limited (Lisón et al., 2022; Sevillano-Ríos and Rodewald, 2021; Tinoco et al., 2018), and existing studies on this subject in the region have often employed spatially limited data or insufficient sampling intensity, which highlight the need for more thorough research.

The sensitivity of bird biodiversity to landscape composition and configuration depends on the spatial scale (Bailey et al., 2007; Duro

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et al., 2014; Morelli et al., 2013; Schindler et al., 2013). At small scales, habitat vegetation type (i.e. its composition) can determine biodiversity patterns by influencing resource availability and environmental conditions. In contrast, fragmentation is recognized as a large landscape-scale phenomenon (Fahrig, 2017, 2003), where the connectivity among different landscape components is a critical factor that influence biodiversity. Another outcome of fragmentation at the landscape-scale is the increase in edges, a factor that can have either negative or positive effects on biodiversity (Pfeifer et al., 2017). Therefore, attention needs to be paid when drawing conclusions about biodiversity responses across spatial scales, and understanding the appropriate spatial scale is essential for devising effective conservation plans (Bailey et al., 2007; Duro et al., 2014; Hadley and Betts, 2016; Morelli et al., 2013; Schindler et al., 2013).

When assessing the relationship between landscapes and birds, species richness is often used as the primary indicator of biodiversity responses (Adler and Jedicke, 2022; Fletcher et al., 2018). However, taxonomic richness can mask biodiversity changes that are highly relevant for ecosystem functioning and conservation (Fletcher et al., 2018). Notably, the effects of land use change may differ among either distinct functional guilds (Bregman et al., 2016; Harms et al., 2017; Herrera et al., 2018; Lisón et al., 2022; Mayer and Cameron, 2003) or species with different morphological traits (Santillán et al., 2019; Tinoco et al., 2018). Particularly, body mass has been identified as a significant factor, because it increases sensitivity of species to land-use change (Tinoco et al., 2017). The species situated at the edges of their ranges may also exhibit increased susceptibility to land-use change compared to those closer to the center of their range. The species that inhabit the edges of their ranges are usually located at the threshold of abiotic and biotic conditions that can support populations, and modifications to these conditions driven by land-use change can substantially impact these populations (Anjos et al., 2010; Burner et al., 2020; Kattan et al., 1994; Neate-Clegg et al., 2021; Orme et al., 2019). However, it has been shown that functional traits for specific guilds can vary in their sensitivity to land use, depending on the landscape scale (Tinoco et al., 2017).

In Andean landscapes, bird biodiversity can be positively influenced by both, compositional characteristics, such as the extent of remaining native forest (Lisón et al., 2022; Sevillano-Ríos and Rodewald, 2021; Tinoco et al., 2018), and configurational characteristics, like edge density (Estrada-Carmona et al., 2022). Can some of these relationships be scale-dependent? To explore this question, we examined the influence of landscape characteristics on bird biodiversity at two scales, utilizing data collected in human-modified landscapes located in the southern Andes of Ecuador. We used spatial covariates related to landscape composition and configuration to evaluate their effects on the avian community richness and occupancy of functional guilds. Our objectives were to (1) determine the influence of spatial scale on the responses of bird richness to landscape characteristics; (2) evaluate the relative importance of landscape composition and configuration on the occupancy of distinct avian guilds. We suspect that bird richness responses may vary according to scale, with composition being more influential at small scales and configuration at larger scales. We expect certain landscape elements, such as native forests, to be more important for some specific guilds that require certain habitat characteristics, and configuration to have a significant impact on shaping the response of those associated with vulnerability to fragmentation, such as species with a large body size and those at the edge of their altitudinal range. Understanding how bird richness and occupancy differ among spatial scales can provide useful information for improving the effectiveness of management strategies and for prioritizing conservation actions.

2. Materials and methods

2.1. Study area

This study was conducted in montane landscapes located between

3000 and 3500 m.a.s.l. in the western Andes of the Azuay province, southern Ecuador. This region has a mean annual precipitation ranging from 1100 to 1800 mm, and the monthly mean temperatures range from 5 to 12°C (Celleri et al., 2007). The main rainy season extends from February to May, followed by a dry season from June to September, and a weak second rainy season from October to January (Celleri et al., 2007). The landscapes in the region form a mosaic of vegetation types dominated by cattle pastures and agricultural lands, intermixed with pine and eucalyptus plantations, private smallholder residences, and native forests primarily confined to protected areas like the Cajas National Park, and on steep slopes and along streams (White and Maldonado, 1991).

2.2. Study design

We chose three inter-Andean valleys with an area of 2000 ha across a gradient of natural habitat remnants and fragmentation levels in our study area (Fig. 1). In each valley, we delineated 100 grids of 200 m² and randomly selected 57 grids as survey sites (19 in each valley) to capture all the landscape heterogeneity. The selected grids were located at least 1 km away from another grid. The long history of anthropogenic disturbance in the region means that it is not possible to perfectly distinguish independent landscape composition and configuration effects. However, our sampling design, with several survey sites and sampling space that incorporate landscape heterogeneity, helped us to quantify for the habitat composition and habitat configuration effects (Fahrig, 2017; Hadley and Betts, 2016).

2.3. Bird surveys

One 200 m-long transect was established at each survey site (n=57). Birds were sampled over four sampling periods that cover distinct rainy seasons: the secondary wet season (sampled between October and December in 2017 and 2018) and the main rainy season (sampled between May to June in 2018 and 2019). Each transect was visited 3 times during each sampling period, and we ensured a minimum of a two-week interval between visits within the same sampling period to ensure adequate temporal spacing. In total, there were 12 survey replicates to each transect.

All surveys were conducted from 06:00 a.m. to 10:00 a.m. During each visit, an observer walked the transect at a constant pace and recorded all the birds seen or heard within 30 m at both sides of the transect, for 20 min. Two observers conducted all the surveys in this study. The observer and starting time were alternated across the visits of each transect to avoid any bias related to observer experience and time of day. We excluded large raptors, aquatic birds, and birds flying over the transect to avoid bird richness overestimation.

2.4. Functional groups

Data about ecological traits of birds from a variety of datasets were collated (Supplementary Table S1). The included traits were primary diet, body mass (in g.), and elevational range. Birds were grouped by diet based on the proportional use of different food types and were classified as insectivores, nectarivores, frugivores, granivores, carnivores, or omnivores. A species was assigned to a specific dietary guild if its diet included more than or equal to 40% of a particular food type (Santillán et al., 2019; Wilman et al., 2014). Birds were classified into different body size groups: small (3–15 g.), middle (16–85 g.), and large (>86 g.).

To examine whether the species at the limits of their elevational ranges are more sensitive to land-use change, each species was assigned to one of the following categories: (1) Edge of range, (2) Interior of range. To classify species into these categories we measured the difference between the mean elevation of our study area (3250 m.a.s.l) and the closest limit (upper or lower) of the elevational range of a species. A

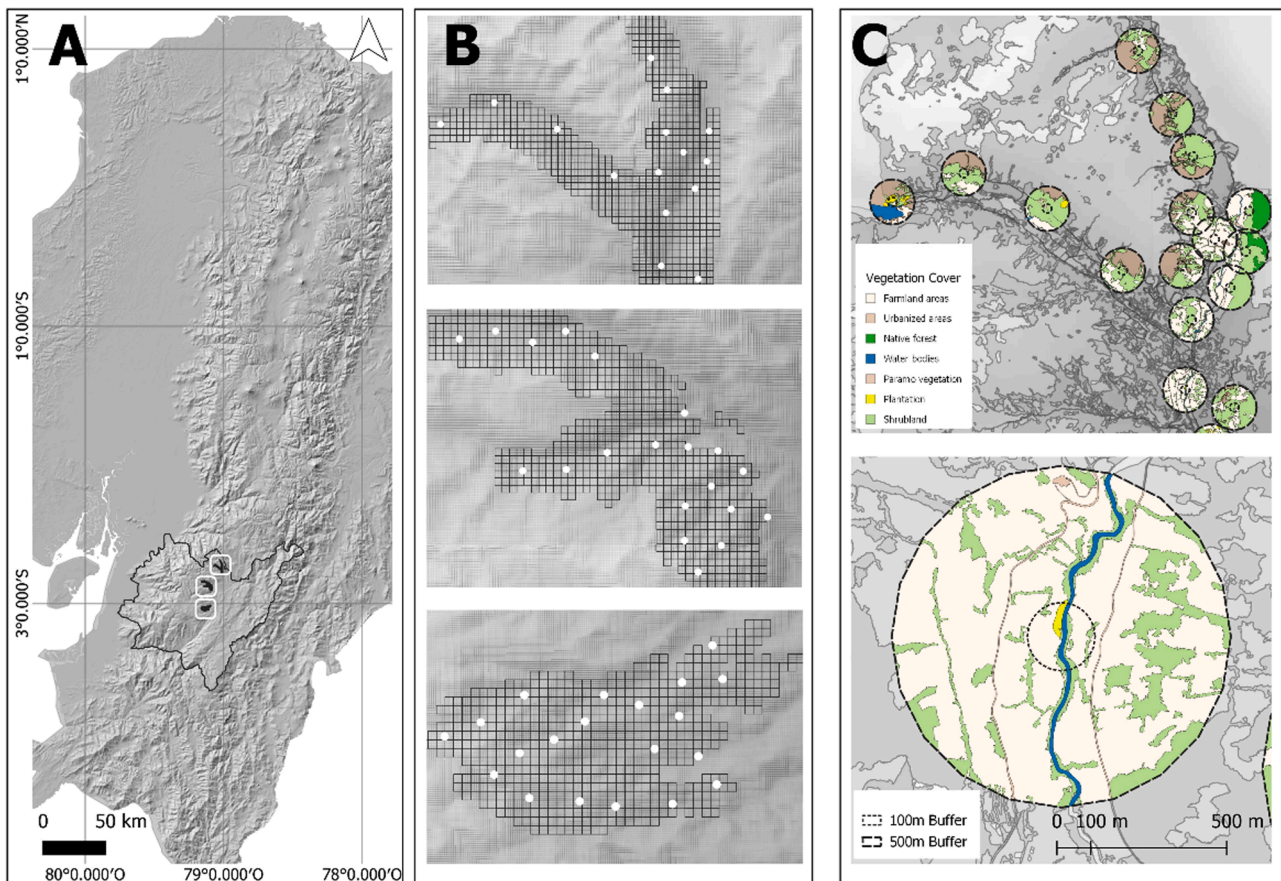


Fig. 1. Map of the study area (A) located in the western Andes of the Azuay province in southern Ecuador that contains our (B) 2000 ha grid systems in the three inter-Andean valleys and the (C) location of survey sites showing the two spatial scales (plots of 100 m and 500 m radius) outlined by black circles showing the landscape attributes measured in our study [figure in color].

species was considered to be at the edge of its range if the difference between our study area and the limit of its elevational range was $\leq 20\%$ of its total elevational range (Supplementary Table S1) (Anjos et al., 2010). For instance, consider a bird species that ranges from 1800 to 3300 m.a.s.l, our study area is located at 50 m of that upper limit, which represents 3% of the total elevational range of that species, and will be classified as on the edge of its range species.

2.5. Landscape metrics

The landscape was characterized using both composition and configuration metrics of a regional map: “Map of Vegetation Cover and Land Use of the province of Azuay, scale 1: 5.000” (Tenesaca, 2017). From this map, a layer was created that consisted of seven land cover classes: (1) Native forests, (2) shrubland, (3) farmland areas, including cattle pastures areas (4) pine and eucalyptus plantation, (5) urbanized areas, including buildings and roads, (6) paramo vegetation (dominated by tussock grasses) and, (7) water bodies such, as ponds and streams. Patch Analyst extension in ArcGIS® (Elkie et al., 1999; ESRI, 2016), version 2.0, was used to quantify the different landscape metrics. Then, we obtained metrics related to the composition and configuration at two different spatial scales, using radius of 100 m, and 500 m from the centroid of the transect. The chosen minimum scale provides a fine-grained, localized perspective that covers the immediate habitat of a transect, while the larger scale offers a broader range, encompassing all identified coverage types across the landscape and capturing its heterogeneity. A larger scale was not considered due to elevation variations, which would have incorporated vegetation types not included in this study.

We obtained landscape metrics commonly used to describe spatial structure in agriculturally dominated areas, which significantly influence bird communities (Adler and Jedicke, 2022; Fahrig et al., 2011, Uuemaa et al., 2009) and represent a gradient in land use. For landscape composition, the percentage of native forests and farmland areas were calculated. We also obtained two measures of habitat diversity: the number of cover classes (habitat richness) and the Shannon Index (habitat heterogeneity) (Fahrig et al., 2011; Hadley et al., 2014; Herrera et al., 2018; Morelli et al., 2018). For landscape configuration, we combined native forests and shrublands and quantified the total number of patches in the landscape, mean patch size (m^2), and edge density (m/m^2). Pair wise correlations between variables ranged from $r = 0.02$ to $r = 0.63$ (Supplementary Figure S1).

2.6. Data analysis

Two Bayesian multi-species occupancy models were performed (Dorazio and Royle, 2005; Dorazio et al., 2006), one for each of the spatial scales used in this study (i.e., one model for 100 m and one for the 500 m radius). Our models incorporated the spatial covariates related to landscape composition and configuration while accounting for heterogeneity in species detectability. The Bayesian multispecies occupancy model is an extension of the single-species site occupancy model (MacKenzie et al., 2002), incorporating landscape characteristics into the probability of occupancy (Kéry and Royle, 2016). This modeling approach has been applied in occupancy modeling with birds (Zipkin et al., 2009, Jiménez-Franco et al., 2019; Lisón et al., 2022). An analogous model was adopted to estimate the occurrence probability ($\psi_{i,k}$) for species k at transect i by incorporating the above-mentioned

scale-specific metrics related to composition and configuration. Therefore, the probability of occupancy was defined as follows:

$$\text{logit}(y_{i,k}) = (\beta_{0,k} + \beta_{1,k}\text{VAR}_1 + \dots + \beta_{7,k}\text{VAR}_7)$$

where $\beta_{0,k}$ was the occurrence probability for species k at a site with “average” landscape characteristics (species-specific intercept). The coefficients from $\beta_{1,k}$ to $\beta_{7,k}$ were the effects of the 7 landscape variables (VAR_1 to VAR_7) respectively as follows: percentage of native forest, percentage of farmland area, Shannon index, number of cover classes, edge density, mean patch size, and number of patches. Also, since our ability to detect the species could vary along surveys, we considered a total of 12 survey replicates (j) for each sample site. We also included in the model the influence of temporal effects (Julian date) on detectability; such a factor is an important one to be considered when temporal replicates are realized (Kéry et al., 2013; Zipkin et al., 2010). All quantitative covariables were standardized by subtracting the mean and dividing by the standard deviation. The two models were fitted using JAGS (Plummer, 2003), run in R. 4.2.1 (“R Development Core Team,” 2022) with the package jagsUI (Kellner, 2015), using uninformative priors, three chains, 15,000 iterations, and a burn-in of 5000 iterations and a thin rate of 2.

As our Bayesian models facilitate the estimation of the number of species expected to occur at each survey site, we assessed the relationships between species richness along the gradient of compositional and configurational variables by representing smoothing splines and 95% credible interval of these relationships for each spatial scales. Means of estimated occupancy probabilities for each functional group using composition and configuration metrics as predictors were compared between the two spatial scales. Tukey’s Honestly Significant Difference (Tukey’s HSD) was used to test for any significant differences between the mean occupancy probability among the functional groups. All the statistical tests were performed at the 95% confidence level.

3. Results

In total, 13549 observations of 82 bird species were registered (Supplementary Table S1). These species corresponded to 24 avian families, with Trochilidae (hummingbirds) and Thraupidae (tanagers) being the richest families (14 and 13 species, respectively); Trochilidae was also the dominant family in terms of records ($n = 2916$, 21.5% of the total records). The most frequent bird species were *Metallura tyrianthina* ($n = 1345$, 10%), *Myioborus melanocephalus* ($n = 1141$, 8.4%), and *Turdus fuscater* ($n = 1081$, 8%). These birds were also all present in more than 98% of transects. The number of species recorded across the 57 transects ranged from 16 to 48 ((35 ± 7) ; [mean, \pm SD]).

Among dietary guilds, approximately 50% of birds were classified as

insectivores (44 species), 18% as nectarivores (15 species), and 11% as frugivores (9 species). The other dietary guilds were poorly represented (see Table S1 for a species list of all insectivores, nectarivores, frugivores, granivores, carnivores, or omnivores). The number of species classified according to body size classes included 46% small species (38 species), 38% midsize species (31 species), and 16% large species (13 species). The species at the edges of their altitudinal ranges were represented by more than 50% (43 species) of species, while the other percentage (48%) was for birds within their interior range of altitudinal distribution (39 species).

3.1. Estimated species taxonomic richness responses to landscape composition and configuration

The estimated bird richness for each transect ranged from 23.67 to 57.72 at the 100 m spatial scale and from 22.4 to 60.6. at the 500 m spatial scale (see details for each site in Supporting Information Tables S2 and S3). Considering the compositional variables, estimated richness declined with an increasing amount of farmland area at both the 100 m and 500 m spatial scales (Fig. 2). Bird richness was positively related to the Shannon index at the 500 m scale. The configurational variables, edge density, and mean patch size were positively associated with species richness at the 100 m spatial scale. No clear relationships were observed with the other covariables at either the 100 m or the 500 m spatial scales.

3.2. Effect of landscape composition and configuration in functional groups

For the diet groups at the 100 m spatial scale, carnivores responded positively to the percentage of native forest, while at the 500 m spatial scale, this variable also had a positive effect on frugivore and omnivore species (Fig. 3). The percentage of farmland area had a negative effect on frugivore species occupancy, on both the small and large spatial scales. For the configuration variables, at a 100 m scale the number of patches had a positive effect on carnivores and omnivores species occupancy and was also significant for granivores at the larger scale. The mean patch size had a positive effect in frugivores, carnivores, and omnivores, but unlike that observed on the small scale, it had a negative effect on the occupancy of most functional groups.

We did not find any variation in the responses of body-size groups to landscape metrics at the 100 m spatial scale (Fig. 4). At the 500 m spatial scale, larger birds were sensitive to the percentage of native forest and number of patches. Moreover, the birds grouped according to the distance to the edge of their altitudinal distribution showed

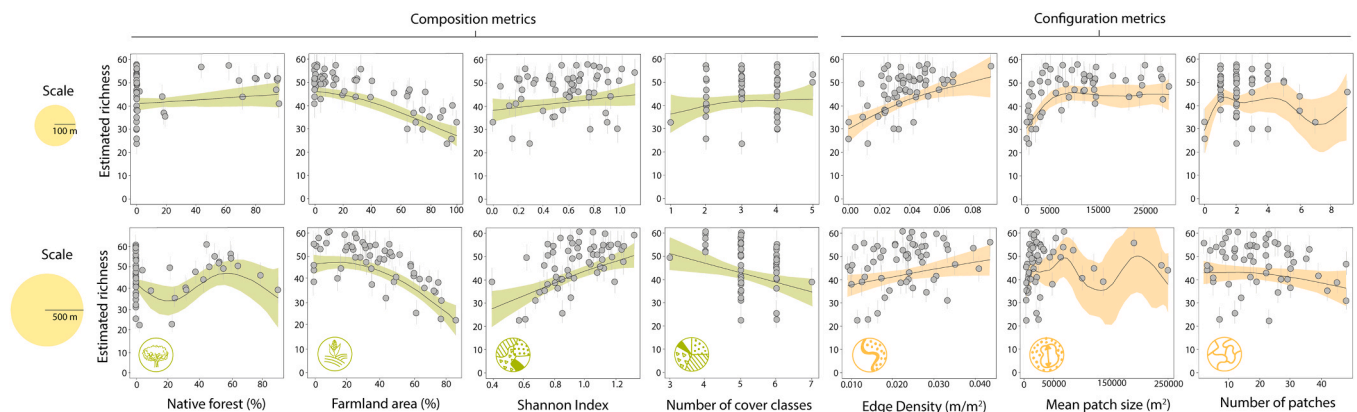


Fig. 2. Relationship between the estimated bird species richness at each site in the western Andes, Ecuador ($n=57$) and (a) Native forest, (b) farmland area, (c) Shannon Index, (d) Number of cover classes, (e) Edge Density, (f) Mean patch size and (g) Number of patches, on the 100 m and 500 m spatial scales. Each point represents the estimated bird species richness and vertical lines represent the 95% credible intervals of the bird species richness estimated with our Bayesian model. The solid black lines represent smoothing splines and the gray shaded area denotes a 95% credible interval.

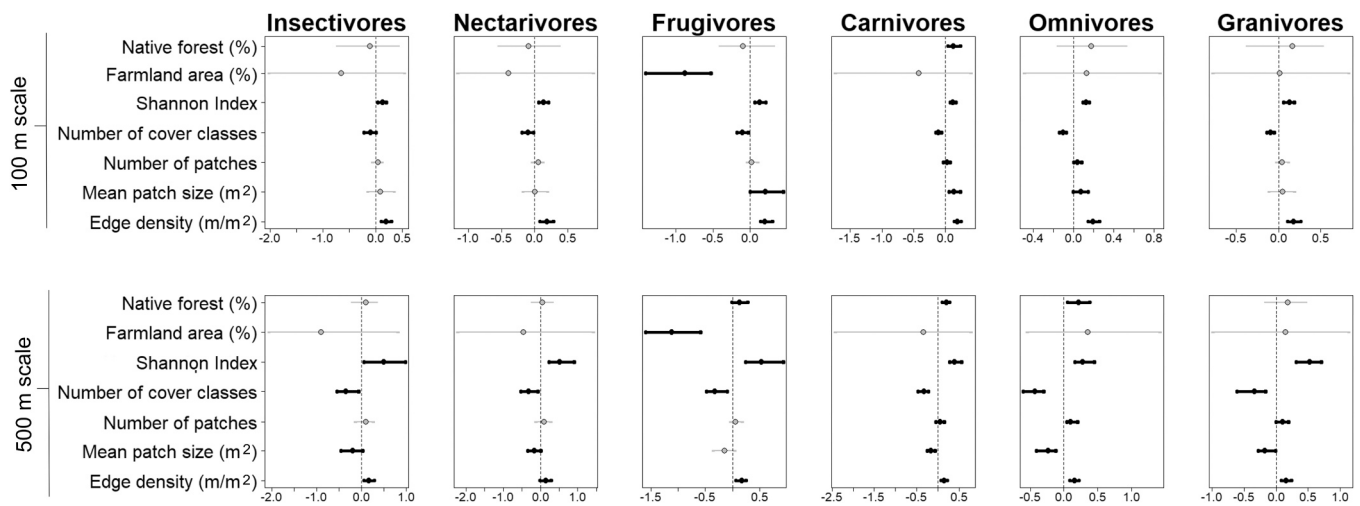


Fig. 3. Importance of landscape variables in the occupancy probability of the bird trophic groups in the western Andes (Ecuador) on 100 m and 500 m spatial scales (upper and bottom panels, respectively). Dots represent the functional group means response and bars indicate the 95% confidence intervals. Significant results are those where the 95% confidence set does not overlap zero.

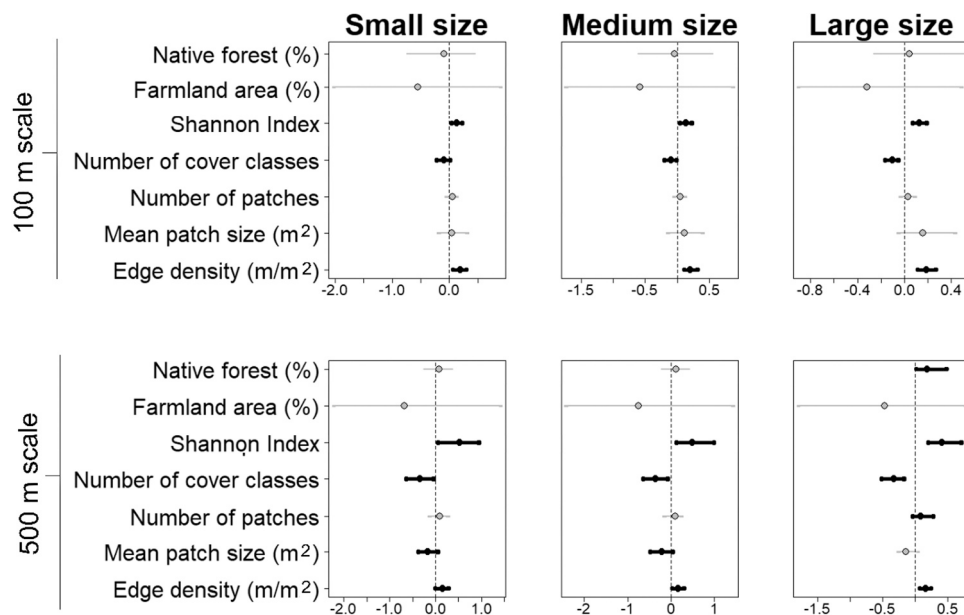


Fig. 4. Importance of landscape variables in the occupancy probability of the bird groups according to size classes on 100 m and 500 m spatial scales (upper and bottom panels, respectively). Dots represent the functional group means response and bars indicate the 95% confidence intervals. Significant results are those where the 95% confidence set does not overlap zero.

significant responses to the Shannon index, number of cover classes, and edge density across scales. We did not find any responses to other landscape covariates related to the distance to the edge of the altitudinal distribution at either the small or large spatial scale (Fig. 5).

Our results indicated a significant influence of the compositional variables on shaping the occupancy probability of all the functional groups, irrespectively of scale: all the functional groups responded positively to the Shannon Index and negatively to the number of cover types (Figs. 3 and 4). The edge density positively influenced the occupancy probability of all the functional groups on both spatial scales. The effects of the percentage of native forest, farmland area, number of patches and mean patch size were scale-dependent with significance varying across the different functional groups (Figs. 3, 4, and 5).

4. Discussion

The relative importance of composition versus configuration has been paid considerable attention in landscape ecology and conservation biology in recent years (Adler and Jedicke, 2022; Fahrig, 2017; Fahrig et al., 2019; Fletcher et al., 2018; Hadley and Betts, 2016; Uuemaa et al., 2009). Here we examined how landscape configuration and composition at spatial scales of 100 m and 500 m influenced the richness and occupancy of Andean birds. Composition-related variables appeared as the primary determinants of diversity regardless of scale, while the influence of configuration depended on the spatial scale of the analysis. We also demonstrate that certain avian groups exhibit varying sensitivity to landscape composition and configuration, with scale playing a key role in the nature of responses. Our results contribute to understand in what circumstances landscape composition and configuration can influence avian diversity positively or negatively, which has significant

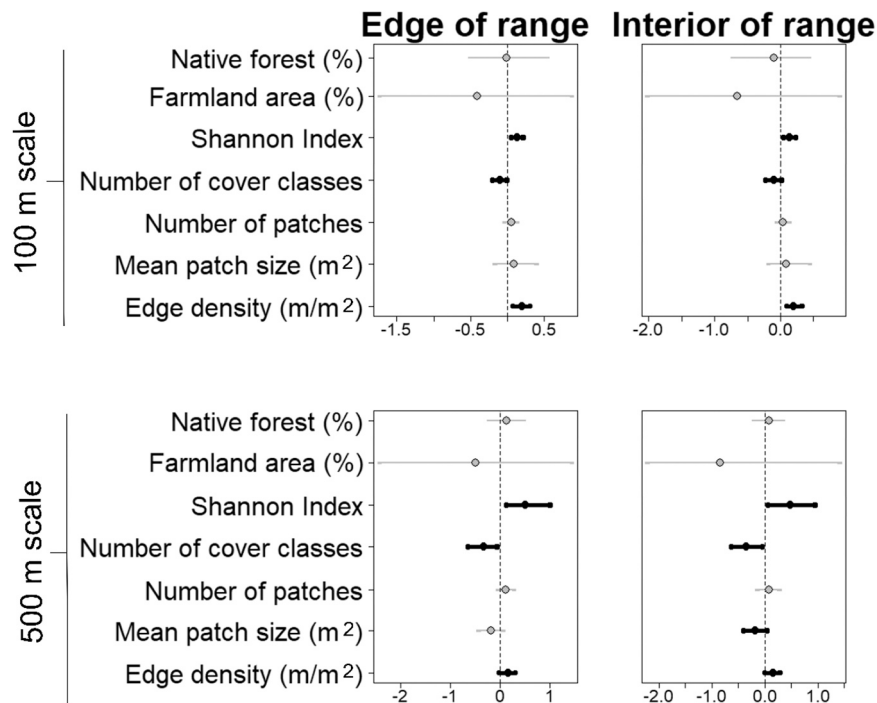


Fig. 5. Importance of landscape variables in the occupancy probability of the bird groups in the western Andes (Ecuador) according to distance to the edge of the altitudinal distribution within 100 m and 500 m landscape scale (upper and bottom panels, respectively). Dots represent the functional group means response and bars indicate the 95% confidence intervals. Significant results are those where the 95% confidence set does not overlap zero.

implications for conservation planning.

4.1. Response of bird species richness to landscape characteristics

The decrease in species richness to increasing farmland area at small and large scales highlights the negative effects of human activities on bird diversity in Andean landscapes and indicates that these effects may be generalized and are not scale-dependent. These results are particularly relevant given the ongoing conversion of mountain forests into pastures in the Ecuadorian Andes (Tapia-Armijos et al., 2015), which continues to impact biodiversity (Santillán et al., 2019; Tinoco et al., 2018). Our findings align with others that show that species richness can be better explained by landscape composition than by spatial configuration (Harms et al., 2017; Lisón et al., 2022; Sevillano-Ríos and Rodewald, 2021; Uemaa et al., 2009). Notably, the Shannon index was another important compositional predictor, with a positive influence on richness at a large scale. A greater combination of habitat types available for animals can provide more resources for wildlife (Estrada-Carmona et al., 2022; Martínez-Núñez et al., 2023), and that heterogeneity of habitat types can positively influence bird richness (García-Llamas et al., 2018). However, this relationship becomes clear when the chosen scale adequately captures the landscape's heterogeneity. Although the number of land cover classes in a landscape can influence species richness (Herrera et al., 2018; Morelli et al., 2018), we did not find this relationship. Therefore, our results suggest that relationships between birds and space should consider not only the number of cover types but also their proportion in the landscape.

Landscape configuration was important only at small scale, as richness was associated with the amount of edge density. Edge density is one of the main drivers of species richness for different biotic groups (Fahrig, 2017). The high food availability (Tschamtker et al., 2008), and the increasing abundance of generalist and opportunist species (Sevillano-Ríos and Rodewald, 2021) on habitat borders, are factors that can promote an increase in species richness. However, edge can exhibit scale-dependent effects (Fletcher et al., 2018), as supported by our results which indicate that edge density was linked with species richness

only at small scales.

Although studies argue that habitat configuration influences biodiversity mainly at large spatial scales (Fahrig, 2017, 2003; Mcgarigal and Cushman, 2016), we did not find this result. Our findings may be attributed to several factors in the Andean landscape context. Centuries of land use have molded the Andean landscape into a complex mosaic of habitat types (Loughlin et al., 2018; White and Maldonado, 1991), which potentially leads to uniform landscape configuration across large scales. As a result, the current avian community in our study area might be insensitive to fragmentation effects (Tinoco et al., 2019). Consequently, landscape configuration becomes a less reliable predictor of bird richness in this historically transformed landscape. Finally, it is essential to consider the high bird mobility of birds. The 500-meter radius that we employed for our analysis might not adequately encompass the very long distances that these birds can cover.

4.2. Importance of landscape characteristics in functional groups

We assessed how landscape composition and configuration can influence the occupancy probability of avian functional guilds. Overall, the composition variables related to diversity and heterogeneity, such as the number of cover classes and the Shannon index, or the configurational variables related to edge density, were important predictors for all the different bird groups. However, we found that the importance of some landscape characteristics was scale-dependent.

Frugivores were especially affected by the percentage of farmland area in the landscape at both the small and large scale. This result is consistent with another study (Bonfim et al., 2021) which reported that landscape composition is more important than landscape configuration for tropical frugivores. Habitat loss may reduce the availability and quality of fruit resources (Pessoa et al., 2017a, 2017b), which leads to lower occupancy of frugivore birds in agricultural-dominated landscapes. Our results suggest that the expansion of agricultural activities in the Andes may impose serious threats to this group. In correspondence with this pattern, at the larger scale of our analysis, the amount of native forest positively influenced the occupancy of frugivores, carnivores, and

omnivores. This is a key finding given the widespread changes in tropical Andean landscapes (Tapia-Armijos et al., 2015). Previous studies have highlighted the importance of the native habitat for Andean bird diversity (Sevillano-Ríos and Rodewald, 2021; Tinoco et al., 2018). However, native forest represents a small proportion of the Andean landscape, hence being scarce and unevenly distributed among the selected sample plots, and its significance was observed primarily at larger spatial scales. Our finding highlights the importance of selecting the appropriate scale of analysis when using landscape characteristics to predict or manage bird communities.

We expected birds of varying body sizes to exhibit differing sensitivities to spatial metrics at different scales. Nevertheless, these groups exhibited similar responses, with few exceptions. We specifically found that the percentage of native forest and the number of patches were predictors of larger birds at large spatial scales. Body size is associated with home range size and likely this can result in relatively large-scale movements within the landscape (Concepción and Díaz, 2011; Thorn-ton and Fletcher, 2014). As a result, larger-bodied species are likely to be more sensitive to land-use change at larger scales.

Distance to the edge of their limit of altitudinal distribution was not relevant for bird occupancy. More than 50% of the species in our study are at the edges of their altitudinal ranges, yet they showed the same response to landscape characteristics as those that are in the interior of their range. These results contrast with previous studies (Anjos et al., 2010; Orme et al., 2019) which show how bird populations near their range edges may be more sensitive to deforestation and habitat loss. However, this hypothesis has not been validated in tropical mountainous regions, like Andean landscapes. Recent studies (Freeman et al., 2022, 2019) indicate that biotic interactions, particularly interspecific competition, can play a significant role in shaping the elevational ranges of bird species in tropical mountains. Additionally, elevational limits of birds could be highly dynamic in time, influenced by seasonal changes under abiotic and biotic conditions, or more long-term environmental changes. Consequently, altitudinal range limits alone to predict species sensitivity to landscape characteristics can be limited given the complex underpinnings that determine the elevational distributions of Andean birds (Freeman et al., 2022, 2019; Santillán et al., 2020).

5. Conservation implications

Andean landscapes have a long history of anthropogenic disturbance (White and Maldonado, 1991), with agricultural activities being one of the main drivers of the reduction in native vegetation cover across the tropical Andes (Vina and Cavelier, 1999). Our results showed that the maintenance of native vegetation cover seems to be the best policy for the conservation of Andean birds and for sustaining ecosystem services provided by functional groups, such as frugivores. In these anthropogenically influenced landscapes, it is necessary to incorporate social aspects and implement management actions aimed at protecting vegetation remnants. Therefore, management practices like maintaining native vegetation along rivers, incorporating native vegetation hedgerows (Baudry et al., 2000), and using native plants on fences could be strategies that can significantly contribute to conservation efforts on the bird community.

Although native forest represents a small proportion of the Andean landscape, our study highlights their importance as a habitat for many avian groups. In our study area, large patches of native forest are preserved primarily in protected areas like the Cajas National Park. These findings reinforce the role of protected areas as a key strategy for bird conservation. They also emphasize the need to implement effective management strategies to counteract the impacts of the land-use changes that occur outside these protected areas and prevent the conversion of native forest into other land uses (Tapia-Armijos et al., 2015). However, we caution that significant responses of bird communities to these patchy habitats can be missed at small spatial scales. Decision-makers should consider the difficulty in detecting important

relationships between birds and the non-common cover types in the landscape when developing conservation strategies for bird diversity.

Our research provides information about the nature of the influence of configurational effects associated with fragmentation in the tropical Andes. Specifically, an increase in edge density, as a result of fragmentation, can positively impact the abundance or distribution of certain species (Adler and Jedicke, 2022; Fahrig, 2017, 2003). However, misinterpreting positive edge effects may underestimate their adverse impacts, by fostering the spread of generalist and invasive species and increasing vulnerability to anthropogenic pressures and habitat loss. This emphasizes the need for careful consideration in conservation strategies (Fletcher et al., 2018). Variation in the spatial scale of numerous bird studies poses a challenge to identify the mechanisms behind positive fragmentation effects on species richness (Adler and Jedicke, 2022; Fletcher et al., 2018). We highlight this challenge, emphasizing the need for a more comprehensive understanding of the role of spatial scale in these relationships.

CRedit authorship contribution statement

María Victoria Jiménez-Franco: Supervision, Formal analysis. **Francisco Robledano:** Supervision, Conceptualization. **Omar Stalin Landázuri:** Investigation, Formal analysis, Conceptualization. **Boris Tinoco:** Supervision, Project administration, Methodology, Conceptualization. **Carlos Iván Espinosa:** Supervision, Project administration, Funding acquisition.

Declaration of Competing Interest

I, Omar Landázuri Paredes, declare that I have no conflicts of interest regarding the research, authorship, or publication of the manuscript titled "Effects of landscape composition and configuration on Andean birds are influenced by spatial scale" submitted to Biological Conservation Journal. I affirm that neither I nor any co-authors have financial interests, affiliations, or other connections with any organization or entity that might be perceived as having influenced the content of the manuscript. I hereby confirm that the work presented in the manuscript is entirely original, and I have not submitted it for publication elsewhere.

Data Availability

Data will be made available on request.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.foreco.2024.121960](https://doi.org/10.1016/j.foreco.2024.121960).

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