Populations across species ranges respond differently to habitat loss and fragment

ERICA HASUI (ericahasui@gmail.com)
Universidade Federal de Alfenas (UNIFAL-MG), Instituto de Ciências da Natureza

Alexandre Camargo Martensen
Universidade Federal de São Carlos (UFSCar)

Alexandre Uezu
Instituto de Pesquisas Ecológicas - IPÊ

Rafael Guerra Pimentel
Universidade de São Paulo (USP)

Flavio Nunes Ramos
Universidade Federal de Alfenas (UNIFAL-MG), Instituto de Ciências da Natureza

Milton Cezar Ribeiro
Universidade Estadual Paulista (UNESP)

Jean Paul Metzger
Instituto de Biociências, Universidade de São Paulo (USP), Rua do Matão, Travessa 14, 321, Butantã, São Paulo, SP, 05508-900, Brazil

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Abstract

Context

Conservation strategies assume all species populations respond equally to habitat loss, but we investigated sensitivity patterns and tested two hypotheses: 1) equal sensitivity across the range or environmental suitability, and (2) highest sensitivity in range edge populations or at low environmental suitability. We also evaluated if species traits such as dispersal ability, habitat specialization, and range size were associated with sensitivity responses.

Methods

We studied the Brazilian Atlantic Forest across 179 landscape sites. We used two model types to analyze sensitivity to habitat transformations and performed a PCA and permutational MANOVA framework to link species traits to sensitivity patterns.

Results

Our study shows that populations within a species’ range can have different patterns of sensitivity to habitat transformations. We found four sensitivity patterns, which were not related to species traits. Biogeographic and landscape factors interact to affect population abundances, resulting in antagonistic or synergistic effects. These interactions can change population responses to habitat transformations depending on their range position or environmental suitability.

Conclusions

The study found different patterns of sensitivity to habitat transformation within species. Conservationists should avoid generalizing species sensitivity without considering range position and environmental suitability. Wildlife managers should protect vulnerable areas along the range edge, especially for species sensitive to habitat transformations. For Atlantic Forest endemic species, the vulnerable areas are in the transition region between the Atlantic Forest and the Cerrado.

Highlights

a. Study reveals varying population sensitivities to habitat transformations in 81 bird species across geographic ranges.

b. Four sensitivity patterns identified, including higher sensitivity at range edges and core ranges, and different sensitivity in intermediate range positions.

c. Dispersal ability, habitat specialization, and distribution range do not fully explain sensitivity patterns.

d. Importance of considering biogeographic and landscape factors on population abundances, highlighting need for conservation strategies that account for population variations.

Introduction

The health and sustainability of populations are heavily reliant on the quantity, quality, and distribution of their native habitats (Fischer and Lindenmayer 2007; Haddad et al. 2015; Flesch 2017). Habitat loss, fragmentation, and degradation are typically accompanied by a decrease in habitat quality, leading to an increase in isolated patches and a decrease in patch size (Haila and Hanski 1983; Arroyo-Rodríguez and Dias 2010). These changes (habitat transformation, sensu Millennium Ecosystem Assessment 2005) can exacerbate edge effects and inter-patch distances, resulting in detrimental effects on ecological processes such as reproduction, dispersal, and mortality, as well as species interactions (Smith et al. 2017). Therefore, the preservation and restoration of native habitats should be prioritized in conservation efforts to ensure the continued abundance and persistence of populations in fragmented landscapes.
Recent research in macroecology has shed light on the potential for spatial variation in populations’ responses to habitat transformations across a species’ geographic range (Banks-Leite et al. 2022). Traditionally, it has been assumed that all individuals within a species’ range respond equally to habitat changes, but this assumption may not always hold true. Two main mechanisms that may influence spatial variation in response to habitat transformations are distance to the geographic range edge and environmental suitability. The center-periphery hypothesis suggests that populations are more abundant at the center of a species’ range, gradually declining towards the edge, as the center represents the most favorable environmental conditions for the species (Brown 1984; Sagarin and Gaines 2002). Habitat transformations can amplify the negative effect on species abundance at the range edge. Orme et al. (2019) provided evidence to support this hypothesis, showing that populations are more sensitive to habitat transformation at the range edge.

In turn, the physiological tolerance hypothesis proposes that a species’ tolerance to environmental factors, such as temperature and precipitation, can vary across its range, leading to differences in responses to habitat disturbances (Banks-Leite et al. 2022). Populations located near their physiological limits are likely to be more sensitive to habitat transformation than those living in areas with optimal conditions (Williams and Newbold 2021).

While the center-periphery hypothesis and physiological tolerance hypothesis are important factors, recent evidence shows that the relationship between geographic distance and environmental gradients is not always straightforward (Pironon et al. 2015; Santini et al. 2019). The abundance of species may not necessarily decline in a linear fashion from the center towards the edge of their range, and the interaction between environmental gradients and geographic distance to the range edge may play an important role in determining species’ responses to habitat transformation (Weber et al. 2017; Santini et al. 2019; Williams and Newbold 2021). Therefore, a better understanding of the complex interactions between environmental gradients and geographic range edge may be crucial in comprehending spatial variation in populations’ responses to habitat transformation.

Despite the critical nature of the issue, there has been a lack of attention given to understanding the factors or processes at macroecological scales that influence species’ responses to habitat transformation. However, such an understanding is crucial for conservation proposals (Opdam and Wascher 2004; Jarzyna et al. 2016; Oliver et al. 2016). Failure to comprehend the patterns of abundance could result in ineffective conservation measures. It is essential to recognize how populations respond to habitat transformation across a species’ ranges to develop conservation strategies in the face of severe population declines and the negative cascading effects on ecosystem functioning and services (Ceballos et al. 2017; Betts et al. 2017).

To investigate patterns in population sensitivity to habitat transformation, we tested two hypotheses derived from previous research (Brown 1984b; Safriel et al. 1994; Banks-Leite et al. 2022)(Fig. 1). First, we evaluated the hypothesis of equal sensitivity across the range or environmental suitability. Second, we assessed the hypothesis of highest sensitivity in range edge populations or at low environmental suitability.

To test these hypotheses, we used data from 81 bird species in the Brazilian Atlantic Forest. First, we evaluated the influence of landscape forest cover and fragmentation on species abundances and determined whether these influences were affected by environmental suitability or distance to the geographic range edge. We then compared population responses among species, looking for general sensitivity patterns associated with species traits related to dispersal ability, habitat specialization, and range extension. We predicted that species with higher dispersal ability, lower habitat specialization, or continuous habitat distribution would exhibit equal sensitivity to habitat transformation across their range, while species with lower dispersal ability, higher habitat specialization, or disjunct habitat distribution would be more sensitive to habitat transformation. We also predicted that range edge populations or those at low environmental suitability would exhibit the highest sensitivity to further habitat transformations. These predictions are based on previous research that suggests populations at the range edge may be more sensitive to habitat disturbance due to less favorable environmental conditions and lower genetic diversity, while populations under optimal conditions may have a higher
sensitivity due to a difference in selective pressures (Maurer and Taper 2002; Vucetich and Waite 2003; Angert 2006; Bell and Gonzalez 2011; Orme et al. 2019; Banks-Leite et al. 2022).

Methods

1. Study area

Our study was conducted in 179 landscapes spanning the Brazilian Atlantic Forest, which encompasses diverse biogeographical subregions, including Bahia Coastal Forests, Serra do Mar Coastal Forests, Araucaria Moist Forests, and Bahia Forests, as described by Silva et al. (2004). In addition, we included transitional landscapes between the Atlantic Forest and the Cerrado, as shown in Fig. 2 and Table S1.

The Atlantic Forest has undergone significant degradation, and its forest cover has been reduced to a mere 28% of its original extent, consisting mostly of small fragments (< 50 ha) scattered throughout the region, as reported by Ribeiro et al. (2009) and Rezende et al. (2018). These fragments are typically surrounded by pastures or croplands such as sugarcane, corn, coffee, and citrus, as well as Pinus and Eucalyptus forests (Souza et al. 2020).

3. Species traits

To identify predictors of species sensitivity to fragmentation, we compiled six biogeographical and ecomorphological traits from published datasets (Stotz et al. 1996; Olson et al. 2001; Claramunt et al. 2012; Rodrigues et al. 2019; Tobias et al. 2022). These traits were previously suggested by Henle et al. (2004) as good indicators of species sensitivity to fragmentation, as they capture various dimensions of ecological niche, including spatial distribution, habitat preference, and dispersal ability.

The six traits we examined include geographic range size, habitat specialization (number of habitats, forest dependence, versatility index), and morphological traits related to flying ability (body mass, hand-wing index). Table 1 provides detailed information on each trait.
Table 1
Legend of morphological and biogeographical traits of bird species used as a proxy for dispersal ability, habitat specialization, and spatial distribution.

<table>
<thead>
<tr>
<th>Class of traits</th>
<th>Traits</th>
<th>Scale</th>
<th>Description</th>
<th>Ecological meaning</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Geographic range size</td>
<td>Extent of occurrence (breeding resident, km²)</td>
<td>Continuous</td>
<td>Total range size in km²</td>
<td>Extent of occurrence can be used as a surrogate to dispersal ability of the bird species (Paradis et al. 2009). Higher values indicate higher dispersal ability. Maps from BirdLife International and NatureServe, 2012. (<a href="http://datazone.birdlife.org/home">http://datazone.birdlife.org/home</a>)</td>
<td></td>
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<tr>
<td>Habitat specialization</td>
<td>Number of Habitats</td>
<td>Continuous</td>
<td>Number of habitat types used the species</td>
<td>Number of habitats can be used as a surrogate to specialization degree for habitat trait</td>
<td>Stotz et al., 1996</td>
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<tr>
<td>Forest dependence</td>
<td>Categorical Forest dependency (category = High, medium and low)</td>
<td>Categorical</td>
<td>Forest dependency</td>
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<td>(<a href="http://datazone.birdlife.org/home">http://datazone.birdlife.org/home</a>)</td>
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<tr>
<td>Versatility index</td>
<td>Continuous</td>
<td>Continuous</td>
<td>Number of ecoregions within the distribution range of species</td>
<td>Versatility index can be used as a surrogate to specialization degree for ecoregion traits. An ecoregion as defined as a &quot;large unit of land or water containing a geographically distinct assemblage of species, natural communities, and environmental conditions&quot;</td>
<td>Olson et al. 2001</td>
</tr>
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### Table

<table>
<thead>
<tr>
<th>Class of traits</th>
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<th>Scale</th>
<th>Description</th>
<th>Ecological meaning</th>
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<tr>
<td>Dispersal ability</td>
<td>Body mass median (g)</td>
<td>Continuous</td>
<td>Median body mass (g)</td>
<td>1. Large species need more resources, and probably need to move at greater distances to explore them. 2. As body size is correlated with a wide range of ecomorphological traits, we expected body size to be significantly correlated with dispersal distance and anticipated the need to correct for body size in our analyses (Paradis et al. 1998).</td>
<td>Rodrigues et al., 2019</td>
</tr>
<tr>
<td></td>
<td>Hand wing index (HWI)</td>
<td>Continuous</td>
<td>100 x (WL – SL) / WL</td>
<td>Hand wing index can be used as a surrogate to flight and dispersal ability of the bird species (Dawideit et al., 2009, Claramunt et al. 2012). Species with highest values tend to have the ability to move further than the smallest values species.</td>
<td>Sheard et al. 2019; Claramunt et al. 2012; Smith et al. 2017</td>
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### 4. Species abundance

We obtained abundance data for 81 bird species from the Atlantic-Bird database (Hasui et al. 2018). The database contains a total of 33,119 abundance records collected using various sampling methods such as mist-nets, point counts, and line transects. We selected only mist-net data with detailed information on sampling location (coordinates) and sampling effort. To standardize effort among sites, we included only unique individuals captured per 100 net-hours (1 net-hour = 1 mist-net open for 1 hour) and excluded repeat captures of individual birds. We required robust sampling effort and only included species sampled in at least 15 landscapes (within a circular buffer of 1000 m radius), based on the number of variables included in the models and the gradient of abundance across the species’ geographic range. We limited our analysis to data collected between 1990 and 2016 from study sites that were natural habitats and had remained unchanged for over 20 years, allowing for standardization of vegetation structure and successional stage. We excluded sites located within urban landscapes to avoid the influence of strong anthropogenic factors. A summary of the selected species and study sites is provided in Table S1.

### 6. Predictor variables

We selected five predictor variables to examine intraspecific variation in habitat transformation response due to biogeographic factors. These variables included two biogeographic factors (environmental suitability index and distance
from the nearest range-edge) and three landscape metrics (percentage of forest, clumpiness index, and patch cohesion index; see Table S1).

6.1. Biogeographic factors. Previous studies have used distance from the nearest range edge (Orme et al., 2019) or environmental suitability (Godsoe et al. 2017; Williams and Newbold 2021) as proxies for a species' position within geographical or environmental space forms (environmentally-based center, Brown 1984) to explain species abundance. The "abundant center" hypothesis suggests that if there are gradual changes in environmental conditions across a species' distribution range, there is a coincidence between the range edge and the species' niche limit, with the distance to the range core positively correlated with environmental suitability (Sagarin and Gaines 2002). However, due to the complex pattern of environmental distribution, such as coastlines or steep elevational gradients, across the geographic range of species in the Atlantic Forest, our study area, this correlation is difficult to detect (Dallas et al. 2017; Dallas and Hastings 2018). Therefore, we decided to use both biogeographic factors (environmental suitability and distance to the range-edge) to increase the redundancy of environmental suitability's proxies.

6.1.1. Environmental suitability index. We used an environmental suitability index as an operational variable to define the optimal conditions of sites in a species’ geographic range (Illoidi-Rangel et al. 2004). To calculate this index, we used species distribution modeling (SDM) and applied the maximum entropy method (Maxent version 3.3.1, available at: www.cs.princeton.edu/~schapire/maxent/; Phillips et al. 2006). This modeling is rooted in niche theory and infers distribution patterns by relating species occurrences with the environmental conditions in which they were recorded (Guisan and Zimmermann 2000).

*Species occurrences.* We collected occurrence data from the Atlantic-Bird database (Hasui et al. 2018). This database has qualitative data using multiple methods, such as surveys focused on specific taxa or guilds, museum records, online resources, inventories (combining multiple methods), qualitative surveys based on visual and aural detections, or occasional observations. Each species had at least 46 presence records (see Table S2). Previous studies have shown that this method is robust for small samples (~ 10 records; Stockwell and Peterson 2002; Pearson et al. 2007). Therefore, our records (mean = 213 ± 129) were considered suitable for modeling. We also used 10,000 background points to determine the SDM. We calibrated the SDMs using 80% of the occurrence data (randomly chosen) as a training sample and evaluated them with the remaining 20% (test data).

*Environmental predictors.* To build the SDMs, we selected 20 variables under the categories of climate, topography, soil, and vegetation (see Table S3), based on their direct or indirect effects on ecophysiological processes, which can reflect the tolerance limit of bird species or their resources; their act as dispersal barriers for bird species (Austin and Van Niel 2011); their use by other studies to characterize the distribution pattern of forest bird species (De Barros Ferraz et al. 2012; Hasui et al. 2017); and their ability to minimize the correlations between all possible pairs of variables (correlation threshold Pearson's r = 0.7, Hasui et al., 2017). All variables were projected using WGS 1984 and standardized to the same 30" grid resolution (ca. 900 m x 900 m).

*Accuracy evaluation.* To evaluate the accuracy of our model, we employed the methods described by Phillips et al. (2006) to analyze the receiver operator characteristic (ROC) curve using presence/random data. The ROC curve plots sensitivity against 1 minus specificity across a range of thresholds (Pearson 2010) and the area under the curve (AUC) quantifies the model's ability to correctly classify a species as present or absent. An AUC value of 0.5 suggests that model predictions are no better than random guessing, whereas higher values indicate better performance. Although there is no consensus on desirable AUC values in the literature, we evaluated our AUCtest using the following criteria: values below 0.70 indicate poor model performance, 0.70 to 0.8 indicate good performance, 0.8 to 0.9 indicate excellent performance, and values above 0.9 indicate outstanding performance (Pearce and Ferrier 2001).

We excluded species with AUCtest values below 0.70 and evaluated the performance of the remaining models. These models exhibited excellent discriminatory power, with a median AUCtest of 0.8699, a minimum AUCtest of 0.7305, and a
maximum AUCtest of 0.9789 (see Table S2). The models predicted high probabilities of species occurrence in moist forests and mountain areas near the coastline of the Serra do Mar Coastal Forests, with lower probabilities further inland toward the Alto Parana Atlantic Forest. The models also showed a probability reduction toward the Cerrado.

6.1.2. Distance from the nearest range-edge (range-edge distance). To evaluate the range-edge effect, we measured the Euclidean distance (in km) from each sampled landscape to the nearest edge of the species’ geographic range predicted by the models. This metric allowed us to assess whether populations located near the range edges are smaller than those further away (Hardie and Hutchings 2010; Banks-Leite et al. 2022). We calculated these distances using the digital maps of Ridgely et al. (2007).

6.2. Landscape metrics

We analyzed landscape metrics for all 179 study sites using the treecover2000 map produced by Hansen et al. (2013), which was generated from Landsat satellite images in a 30 m cell (reference year 2000) and defined as canopy closure for all vegetation ≥ 5m in height. To classify the map into forest and non-forest, we used a threshold ≥ 50% canopy cover as forest in a 30 m cell, following Hansen et al. (2013). We then calculated landscape metrics within a circular buffer with a radius of 1000 m around each sample site, which is appropriate to evaluate bird assembly responses to landscape structure (Boscolo and Metzger 2009). We focused on three metrics as indices of changes in forest loss, fragmentation, and connectedness among patches in a landscape (Table S1). FRAGSTATS 4.2 was used to calculate these metrics (McGarigal et al. 2012).

The first metric we used was the percentage of forest (PLAND), which is the proportion of landscape (%) occupied by forest and ranges from 0–100%. The second metric was the clumpiness index (CLUMPY), which isolates the configuration component from the area component, thereby giving an effective index of fragmentation that is not confounded by changes in area (Olsoy et al. 2016). CLUMPY ranges from −1 to 1, with −1 representing a maximally disaggregated landscape (greater dispersion), 0 representing randomly distributed patches, and 1 representing maximally clumped patches (greater contagion). The third metric was the patch cohesion index (COHESION), which measures the physical connectedness of the forest patches and correlates well with dispersal success under a variety of conditions. COHESION ranges from 0 to 100 and is proportional to the perimeter-area ratio divided by the shape index (Schumaker 1996).

7. Abundance models

We conducted a study to investigate whether different populations within the same species exhibit varying sensitivity to habitat transformations. To do this, we employed a generalized mixed regression model (Zuur et al. 2009). Specifically, we used an additive model to determine whether the impact of biogeographic and landscape factors on species abundance was independent of each other (Dunne 2010). If this were the case, the effect of habitat transformations on species abundance would be consistent across all sites, irrespective of biogeographic variations. This would support the hypothesis that sensitivity to environmental changes is equal throughout the species’ geographic range.

Alternatively, we used an interactive model to examine the scenario where the effect of habitat transformations on species abundance would be dependent on the magnitude and direction of the biogeographic effect. In this case, we could observe the highest sensitivity in populations located in regions with the highest environmental suitability (i.e., at the core of the geographic range), or the opposite trend, where the highest sensitivity would be in populations located in regions with the lowest environmental suitability (i.e., at the edge of the geographic range).

We identified several types of interactions based on the direction of individual factor effects, such as synergistic and antagonistic interactions (Piggott et al. 2015). Before analyzing the data, we tested for correlations among predictor variables using Pearson’s correlation coefficient and excluded highly correlated variables from the models (with a threshold of r = 0.7). To do so, we performed a Pearson correlation matrix analysis between all possible pairs of variables and excluded any pairwise combination that showed a correlation.
In our study, we tested two types of fits (linear and polynomial) for biogeographic factors, considering theoretical predictions of species abundance distribution in geographical space. Several patterns have been proposed to describe the non-linear distribution of demographic parameters, as reviewed by Pironon et al. (2017). In the classical central-periphery model, low abundance is observed at the extremes of the geographic distribution, while the peak of abundance is in the geographic center, similar to the quadratic fit (Diniz-Filho et al. 2009). However, more complex fits have also been proposed to account for a more complex geographical pattern of the environment. To account for curvilinear relationships between each biogeographic factor and species abundance, we included the possibility of linear or quadratic terms in our analysis. Additionally, we included one landscape variable in our models to explain population responses to habitat transformations (Rivadeneira et al. 2010; Pironon et al. 2017).

To analyze the data, we log-transformed species abundance and fit it with a Gaussian error distribution using the lme4 package (Bates et al., 2015). We included terrestrial ecoregions (Olson et al. 2001) as a random effect to account for the spatial dependence of abundance sampling in each ecoregion. We also incorporated the total sampling effort in each site (total net-hours) as model weights to account for the heterogeneity in sampling effort among landscape sites.

We used multiple criteria to estimate the performance of the models and select the one that best explained species abundance. We considered a model to be valid and with the best performance if it met the following criteria: (1) Had statistical support and the highest level of support based on the smallest values of BIC (Bayesian Information Criterion). We selected the BIC for scoring and selecting the best model because it penalizes the model for its complexity. Therefore, more complex models will have a worse score and be less likely to be selected; (2) Had the highest probability of being selected as the best model among a set of models given by BIC weights (weights > 0.10); (3) Had no residual diagnostic problems, as determined from the visual representation of the residual distribution and the Shapiro-Wilk test. We considered models with a \( \Delta \text{BIC} \leq 2 \) (\( \Delta \text{BIC} = \text{BIC}_i - \text{BIC}_{\text{best model}} \)) to be equally supported. The wi values can be interpreted as the probability that a particular model is the best model in the set.

8. **Classification of species into sensitivity response**

To classify species based on their sensitivity response to forest loss and fragmentation across their geographic range, we first determined if their best model was an additive model, indicating equal sensitivity to habitat transformations across the range, or an interactive model, indicating different sensitivities. For species with interactive models, we used spotlight analysis to examine the interactive effect between landscape and biogeographic factors (Krishna 2016). We decomposed each model interaction into three levels of biogeographic factors, representing the mean level, one standard deviation above and below the mean value of the biogeographic factor. We then calculated the slope of the estimated regression of the relationship between the landscape factor and species abundance for each level and made pairwise comparisons among the slope levels using t.ratio to compute the p-value. If the slope of the lowest level of the biogeographic factor was higher than the highest level, we classified the species as having the highest sensitivity in regions with low environmental suitability or near the edge of the geographic range. Conversely, if the opposite trend was observed, we classified the species as having the highest sensitivity in regions with high environmental suitability or near the core of the geographic range. We used the emmeans package in R to perform these decompositions. Finally, we classified species based on their sensitivity response pattern.

9. **Effect of bird traits on interspecific variation on species sensitivity to habitat transformation**

To investigate whether bird traits contribute to interspecific variation in species sensitivity to habitat transformation, we conducted a principal component analysis (PCA). The PCA allowed us to examine whether species with similar trait combinations exhibit similar sensitivities to habitat transformation across their geographic ranges. If species share similar principal component scores, it may suggest that they face similar limitations to group membership, as demonstrated by other species with equivalent PCA scores (Summerville et al. 2006). To assess the degree to which sensitivity groups
explain trait space variance among species, we employed a permutational multivariate analysis of variance (MANOVA) framework, using the adonis function. To conduct the PCA, we utilized several R packages, including vegan, tidyverse, kableExtra, factoextra, and ggbiplot.

### Results

Our study identified four distinct patterns in population sensitivity to habitat transformations across the range of environmental suitability and distance from range edge, as presented in Figs. 3 and 4 and Table S5. The first pattern is equal sensitivity, observed in 17 species, accounting for 21% of the total species. In this pattern, habitat transformations have the same influence on species abundance, regardless of biogeographic position or environmental suitability (Fig. 3a). For example, *Synallaxis ruficapilla* and *Turdus rufiventris* exhibited the same decline in abundance along the cohesion and forest cover intensity gradients, respectively, regardless of their distance from the range edge or environmental suitability.

The second pattern is the highest sensitivity in populations located at the range edge or those inhabiting at low environmental suitability, found in 11 species, making up 14% of the total species. For instance, *Drymophila ochropyga* and *Xiphocolaptes albicollis* had the highest decline in abundance with the reduction in forest cover intensity at regions with the lowest environmental suitability and with clumpy change nearest to the range edge, respectively (Fig. 3b).

The third pattern is the highest sensitivity in populations located at the core of the range or those inhabiting high environmental suitability, observed in nine species, comprising 11% of the total species. For example, *Tangara sayaca* exhibited the strongest influence of clumpy in abundance at the highest environmental suitability, while *Dendrocincla turdina* showed the strongest effects of cohesion far from the range edge (Fig. 3c).

The fourth pattern is that the abundance of populations at both geographic range extremes or environmental suitability responds in the same way, while populations in intermediate positions or suitability levels respond differently. This pattern is observed in 9 species (11%) such as *Elaenia obscura* and *Tolmomyias sulphurescens* (Fig. 4).

The observed patterns of population sensitivity to habitat transformations reflect different types of interactions between predictive variables, as shown in Fig. 5. In the case of equal sensitivity, biogeographic and landscape factors had effect on species abundance (ex. *Philydor atricapillus*). However, in the other patterns, there were interactive effects, which could be either synergistic or antagonistic, depending on whether the two factors acted in the same or opposite directions, respectively (Table 2). In synergistic relationships, the effect of habitat transformations was intensified depending on the geographic position of the populations along their range or level of environmental suitability. For example, *Phaethornis squalidus* exhibited a significant decline in abundance with forest loss in regions closest to their range core, whereas the effect was weaker in populations near the range edge. In antagonistic relationships, the effect of habitat transformation varied in the response direction depending on the geographic position of the populations. For example, *Myiothlypis flaveola* showed a decline in abundance with forest loss in regions located at the range edge, but an opposite trend was observed at the range core.

Table 2. Prevalence of addictive and interactive relationships between biogeographic and landscape factors on bird species abundance. Legend: Percentage of forest = proportion of the landscape occupied by forest class; cohesion index = measures the physical connectedness of the corresponding patch forests; clumpiness Index = is an aggregation index that measures the proportion of like adjacencies involving the forest class from that expected under a spatially random distribution; environmental suitability index = geographic position of site location that was classified according to the environmental suitability; range edge distance = distance from the nearest edge of species geographic range. The darker green indicates a higher number of species with this type of relationship than the lighter ones.
Based on the results of the PCA and PERMANOVA analysis (Fig. 6), it appears that there is not a strong relationship between sensitivity response groups and species traits related to dispersal ability, habitat specialization, and range extension. While the PCA captured a significant amount of variation in species traits (first and second components accounting for 57.3% of the total variation), the lack of significant differences among the sensitivity response groups suggests that the variation in traits is not strongly associated with sensitivity patterns (PERMANOVA, $R^2 = 0.089, F_{3,45} = 1.37, p = 0.16$; Fig. 6). Instead, there appears to be more variation in traits within sensitivity groups, which could suggest that other factors beyond these traits are driving the observed sensitivity patterns.

### Discussion

Our study on 81 bird species highlights the need to investigate how populations across a species’ geographic range respond to habitat transformations. The study identifies four sensitivity patterns, including higher sensitivity at range edges, equal sensitivity, higher sensitivity at core ranges, and different sensitivity in populations at intermediate range positions or suitability levels. These patterns cannot be explained by dispersal ability, lower habitat specialization, or extension distribution range, suggesting that other factors are driving the observed sensitivity patterns. Our findings underscore the importance of considering the interactions between biogeographic and landscape factors on population abundances, which can result in either antagonistic or synergistic effects. These interactions can change the strength and direction of populations’ responses to habitat transformations depending on their biogeographic position or environmental suitability. It is important to note that these results are specific to the dataset and analysis methods used, and further research may be needed to fully understand the relationship between species traits and sensitivity to environmental stressors. Nevertheless, our study provides valuable insights into how different populations of a species may respond to habitat transformations, highlighting the need for conservation strategies that take into account the varying sensitivities of different populations.

Henle et al. (2017) and Banks-Leite et al. (2022) propose biological mechanisms to explain the contrasting patterns of genetic diversity and differentiation observed in species across their ranges. These patterns can be influenced by multiple factors, including environmental suitability, dispersal capacity, and biotic interactions. The interaction of these drivers determines the extent to which a species can retain or lose its genetic diversity under habitat transformations or range shifts. When a species expands into naturally fragmented habitats or experiences slow natural habitat loss and fragmentation, the resulting environmental pressures may select for different beneficial alleles in different populations, leading to increased genetic diversity. However, when habitat transformation occurs rapidly due to human activities, such as deforestation or urbanization, genetic adaptation may not occur fast enough, resulting in decreased genetic diversity.

Moreover, the biotic interactions among species vary across their ranges, indirectly impacting genetic variability, genetic differentiation, and population sensitivity across a species’ geographic range. The drivers influencing genetic diversity and
differentiation may act synergistically or independently. Thus, a comprehensive understanding of the complex interaction among multiple factors is crucial to predict the consequences of habitat transformations and range shifts on genetic diversity and differentiation of species.

However, our study did not support the commonly assumed link between dispersal capacity and sensitivity pattern. Most species distribution models and predictions of extinction risk assume equal sensitivity to habitat transformations across geographic range or environmental suitability (Henle et al. 2004; Valladares et al. 2014; Boakes et al. 2018), but few studies have provided evidence to support this assumption. Valladares et al. (2014) simulations suggest that equal sensitivity among populations could occur when all populations of a species have the same magnitude of phenotypic plasticity and unlimited dispersal ability, resulting in higher gene flux across the distribution range (Vucetich and Waite 2003). Some evidence of genetic homogeneity across the distribution range supports this explanation (Johannesson and André 2006; Eckstein et al. 2006).

The highest sensitivity of range edge populations (or at the lowest environmental suitability) has distinct biological reasons for this pattern. For instance, it may arise from less suitable and lower-quality habitat available toward the range edge or may increase due to higher environmental instability along the geographic gradient (Holt and Keitt 2000, 2005; Hardie and Hutchings 2010). Under these stress conditions, populations should adapt less to new environmental changes (low resilience) due to lower genetic variability and stronger effects of genetic drift (Sagarin and Gaines 2006; Henle et al. 2017; Macdonald et al. 2017; Prieto-Ramirez et al. 2020). Therefore, populations at the range edge should be more sensitive compared to the range core. If habitat transformations interact synergistically with environmental suitability or biogeographic position, the decline in population size intensifies (e.g., Drymophila ochropyga and Xiphocolaptes albicollis, Fig. 3).

The highest sensitivity of core populations, as shown in Fig. 3c, may be due to their pre-adaptation to survive in harsh and spatially-temporally stochastic environments. This pre-adaptation is thought to result from selective pressures that vary across geographic ranges or environmental conditions. These pressures arise from trade-offs in resource allocation, conservation, and constraints imposed by resistance mechanisms, as predicted by theoretical models such as those developed by Safriel et al. (1994b) and Hoffmann and Blows (1994). Populations at the range edges or in habitats with lower environmental suitability are subject to extreme and variable environmental conditions, which create selection pressures for resistance to these stresses. This results in increased genotypic and phenotypic variation among the populations. These adaptations for resistance may improve the response of species to habitat transformations, as seen in the case of Tangara sayaca in Fig. 3c. There is growing evidence of adaptive evolution in sink habitats and genetic differentiation towards the range edge, supporting this explanation. For example, studies by Holt and Keitt (2005), Eckert et al. (2008) and Gaston (2009) have shown that range edge populations can differ in phenotypic characters and genetic structure. In some cases, they exhibit higher levels of individual fitness and phenotypic plasticity than most core populations, as demonstrated by Yakimowski and Eckert (2007) and Valladares et al. (2014).

Habitat transformations can have varying effects on environmental stress conditions, depending on the type of interactions (synergistic or antagonistic) and habitat preferences of species. For example, forest specialist species with lower dispersal ability, such as Drymophila ochropyga and Antilophia galeata, have shown a synergistic decline in abundance due to habitat transformations (Warren et al. 2001; Holt and Keitt 2005). However, for other species, such as Myioborus flaveola, Myarchus ferox, and Phaethornis squalidus (Fig. 3c, Table S6), the landscape effect has opposite directions depending on their biogeographic position or environmental suitability. This opposite effect may seem contradictory to the expectation that individuals always select optimal habitat conditions to achieve the highest fitness performance (i.e., highest environmental suitability or lowest habitat transformations). However, when considering biotic interactions in habitat selection, suboptimal habitats may sometimes be the best choice to avoid intra- or interspecific competitors (Jacob et al. 2018; Banks-Leite et al. 2022) Thus, the effects of habitat transformations on species abundance and distribution are complex and depend on a variety of factors, including species’ habitat preferences, biotic interactions, and the type of
interactions between environmental stressors. Understanding these complex interactions is critical for effective conservation and management of biodiversity in the face of ongoing habitat transformations.

Previous studies have attempted to predict which species are most vulnerable to habitat transformations by analyzing morphological and biogeographical traits (Henle et al. 2004; Hatfield et al. 2018; Boakes et al. 2018). However, contrary to expectations, none of these traits tested in the present study, proved to be a reliable predictor of sensitivity to habitat transformations. It is possible that our approach, which used species-averaged traits to link with sensitivity groups, is not the most effective method for evaluating this relationship. Banks-Leite et al. (2022) suggest that a more promising approach is to examine population-level traits and how they vary across environmental gradients, as well as how they interact with habitat transformations. Another approach, proposed by Henle et al. (2004), is to evaluate trait interactions to better understand species’ sensitivity response. In our study, we only tested the additive effect of these traits, but it is important to recognize that traits can also act synergistically or antagonistically on species sensitivity (Davies et al. 2004). Therefore, we recommend that future studies fill this knowledge gap by testing trait interactions to better understand the sensitivity response of species to habitat transformations.

Implications of sensitivity variation to habitat transformations

The varying responses of species to habitat transformations have significant implications for conservation strategies. Current conservation programs often implement uniform measures over a wide geographic range or avoid range-edge areas. However, our findings indicate that such strategies may not be effective for 36% of species due to the interactions between biogeographical and landscape factors that can alter the strength and direction of habitat transformation effects. This means that the minimal amount of habitat or landscape connectivity required to maintain viable populations will vary depending on the spatial position of the populations within a species’ geographic range. Therefore, we recommend that species sensitivity to habitat transformations should not be extrapolated from one region to another without testing the effect of biogeographic range position on species abundance. We also urge wildlife managers to focus on protecting and restoring land along the range edge where several species have populations that are more sensitive to habitat transformations. In the case of Atlantic Forest endemics, these vulnerable areas are mainly in the transition region between the Atlantic Forest and the Cerrado.

Overall, our findings suggest that conservation strategies should be tailored to the specific needs of each species by considering their spatial position in the geographic range and the interactions between biogeographical and landscape factors. By doing so, we can ensure that conservation efforts are targeted and effective in protecting the most vulnerable populations of species.

Conclusion

In conclusion, our study shows that the sensitivity of bird species to habitat transformations varies across their geographic ranges and environmental suitability. We identify four sensitivity patterns, including higher sensitivity at range edges, equal sensitivity, higher sensitivity at core ranges, and different sensitivity in populations at intermediate range positions or suitability levels. Furthermore, we found that biogeographical and ecomorphological traits were not good predictors of species sensitivity to habitat transformations, and suggest that future studies focus on examining population-level traits and interactions between traits to better understand species sensitivity. Our findings have important implications for conservation strategies, highlighting the need for tailored approaches that take into account the spatial position of populations within a species’ range and the synergistic or antagonistic effects of biogeographical and landscape factors on species sensitivity to habitat transformations. We recommend increasing protection and restoration efforts in vulnerable areas along the range edge, particularly in transition regions between different ecosystems.

Declarations
Ethical Approval

Our research does not require ethical approval.

Competing interests

We have no competing interest.

Author Contributions

The contributions to the study conception and design were made by Érica Hasui, Alexandre Camargo Martensen, Alexandre Uezu, Rafael Guerra Pimentel, Milton Cezar Ribeiro, and Jean Paul Metzger. Material preparation, data collection, and analysis were performed by Érica Hasui and Rafael Guerra Pimentel, and Milton Cezar Ribeiro. The first draft of the manuscript was written by Érica Hasui, Rafael Guerra Pimentel, and Flavio Nunes Ramos and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

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Data Availability

The datasets generated during and/or analyzed during the current study are available in the support information Table S6.

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Figures
**HYPOTHESES**

**Equal sensitivity to habitat transformation across distribution range.** Species with higher dispersal ability, lower habitat specialization, or continuous habitat distribution would exhibit equal sensitivity to habitat transformation across their range.

**Highest sensitivity to habitat transformation at low environmental suitabilities or at edges of geographic range.** Species with lower dispersal ability, higher habitat specialization, or disjunct habitat distribution would be more sensitive to habitat transformation.

**Figure 1**

Theoretical predictions regarding the response of species to habitat transformation, such as habitat loss, fragmentation, and degradation, can vary among populations within a species’ geographic range as well as among species. The response of populations to habitat transformation may differ depending on their proximity to regions with high or low environmental suitability indexes, or whether they are located near the core or edge of the species’ geographic range. To illustrate this point, red lines indicate the response of populations in regions with high environmental suitability or near the core of the geographic range, while blue lines depict the response of populations in regions with low environmental suitability or near the edge of the geographic range.
Figure 2

This map depicts 179 landscape study sites, primarily located in the southeastern region of the Brazilian Atlantic Forest biome. These sites span across four biogeographical sub-regions, including two centers of endemism (Bahia Coastal Forests and Serra do Mar Coastal Forests), two transitional regions (Araucaria Moist Forests and Bahia Interior Forests), and a few sites situated in the transitional zone between the Atlantic Forest and the Cerrado.
Figure 3

This graph represents the varying responses of species to changes in the landscape across their geographic range. Some species exhibit uniform responses to habitat transformation, while others (represented in Figures b and c) display differing responses among populations located in regions with varying levels of environmental suitability. In Figure b, species show a higher sensitivity to habitat transformation in regions with low environmental suitability or near the edge of the geographic range, as indicated by steeper slope levels. In Figure c, species exhibit higher sensitivity to habitat transformation in regions with high environmental suitability or near the core of the geographic range. To visualize the relationships between the predictive factors (biogeographic factors such as range edge distance and environmental suitability index) and response variables, the factors were grouped into three levels. The graphs show the 95% confidence intervals as shaded areas. The legend provides definitions for various terms used in the graphs, such as log bird species abundance, clumpiness index, percentage of forest cover, cohesion index, environmental suitability index, and nearest distance. The bird photos used in the legend are licensed under CC BY-NC-SA 2.0 or CC BY-SA 2.0.
Figure 4

It illustrates how two species respond to habitat transformation across their geographic range. Both species display no significant difference between low and high levels of the biogeographic factor, with the difference occurring at the medium level of pairwise comparison. The shading represents the 95% confidence intervals. The legend provides definitions for various terms used in the graphs, such as log bird species abundance, percentage of forest cover, and cohesion index. The bird photos used in the legend are licensed under CC BY 2.0 or CC BY-NC-ND 2.0 and depict "Elaenia obscura" by Ron Knight and "Tolmomyias sulphurescens" by Erick Houli.
Figure 5

This figure shows a graphical representation of how species respond to habitat transformation across their geographic range. Some species exhibit (a) additive effects between biogeographical and landscape factors. In interactive models, the strength and direction of population responses to landscape change can vary due to synergistic (b) or antagonistic (c) interactions between biogeographical and landscape factors. To visualize the three model terms (two predictive factors and the response variable) in the graphs, the range edge distance variable and environmental suitability index were grouped into three levels. The 95% confidence intervals are shaded. The legend explains the variables used in the graph, such as Log_abundance (log bird species abundance/100net-hours), percentage of forest (the proportion of landscape (%) occupied by forest and ranges from 0% ≤ to ≤ 100%), cohesion index (measuring the physical connectedness of corresponding forest patches), environmental suitability index (a measure of the habitat suitability for a given species based on habitat attributes), and nearest distance (the distance from the nearest edge of the species' geographic range, log of distance). The bird photos used in the figure are Philydor atricapillus by nickathanas (licensed under CC BY-NC-SA 2.0), Phaethornis
This figure presents a PCA biplot with confidence ellipses for the sensitive response of 46 bird species to biogeographic and landscape variables. The plot includes information on several species traits, such as forest dependence (FD), hand wing index (HWI), number of habitat types used (NH), extent of occurrence (EO), versatility index (VI), and median body mass (BM). PCA axes 1 and 2 explain 57.3% of the variation observed. The response groups are as follows: 1) species with the highest sensitivity in regions with high environmental suitability or near the core of the geographic range; 2) species with equal sensitivity to forest loss and fragmentation across their geographic range; 3) species with the highest sensitivity in regions with low environmental suitability or near the edge of the geographic range; and 4) species with non-significant differences between the lowest and highest biogeographic levels, but with significant differences between the medium level of pairwise comparisons.

**Supplementary Files**

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