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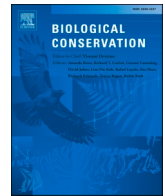
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# Intraspecific variation in sensitivity to habitat fragmentation is influenced by forest cover and distance to the range edge

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## ABSTRACT

The relative effects of habitat loss and fragmentation on biodiversity have been a topic of discussion for decades. While it is acknowledged that habitat amount can mediate the effects of habitat fragmentation, it is unclear what other factors may drive inter- and intraspecific variation in fragmentation effects and their implications for conservation. We tested whether the effects of forest fragmentation on 362 bird species' occurrence in the Atlantic Forest of Brazil are mediated by distance to geographic range edge and habitat amount, and whether these effects explain intraspecific variation across populations. Using a single binomial linear mixed effects model, we found that fragmentation had mostly negative effects on occurrence probability up to 1080 km from the species' range edge, independent of habitat amount. We also show that above this distance, fragmentation has predominantly positive effects, more accentuated in deforested landscapes. We demonstrate that fragmentation effects can be both positive and negative, indicating that different populations of the same species can respond differently depending on distance to range edge and local forest cover. Our results help clarify one of the drivers of contradictory results found in the fragmentation literature and highlight the importance of preventing habitat fragmentation for the conservation of endangered populations. Conservation initiatives should focus on minimising fragmentation closer to range edges of target species and in regions where species range edges overlap.

## 1. Introduction

We are currently undergoing a biodiversity loss crisis, with extinction rates estimated to be greatly elevated compared to long term averages from the fossil records (MEA et al., 2005). These extinctions, which are primarily driven by land-use change (MEA et al., 2005; Sala et al., 2000), continue to increase with the current rising deforestation rates (Global Forest Review, 2020). Though habitat change affects biodiversity through many mechanisms, its effects can broadly be split into three processes: habitat loss, habitat fragmentation and habitat degradation (Newbold et al., 2015; Banks-Leite et al., 2020), which have to be taken into account when determining local conservation targets.

While there is reasonable agreement on the negative effects of habitat loss to biodiversity as a whole, there is an ongoing debate on the effects and relative importance of habitat fragmentation (Fahrig, 2003; Arroyo-Rodríguez et al., 2009; Hanski, 2015; Fahrig, 2017; Fletcher et al., 2018a, 2018b; Fahrig, 2019; Fahrig et al., 2019; Riva and Fahrig, 2023), a term defined in this paper as the breaking apart of continuous habitats transforming them into isolated smaller patches (Fahrig, 2017).

The uncertainty surrounding the effects of habitat fragmentation was first introduced by Fahrig (2003), who described fragmentation as having highly variable effects on species' responses, with habitat loss always having negative effects. In the following decade, evidence accumulated to both support (Fahrig, 2013; Arroyo-Rodríguez et al.,

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2009; Watling et al., 2020) and refute (Didham et al., 2012; Hanski, 2015; Haddad et al., 2015) this assessment. The debate further developed when Fahrig (2017) showed the effects of fragmentation on species to be mostly positive, a review which was received with criticism by some (Fletcher et al., 2018a, 2018b; Püttker et al., 2020). The fragmentation debate continues to this day, with one side arguing that fragmentation has overwhelmingly positive effects on species (Fahrig et al., 2019; Arroyo-Rodríguez et al., 2020; Riva and Fahrig, 2023), and the other arguing the effects are mostly negative (Fletcher et al., 2018a, 2018b; Chase et al., 2020).

One of the reasons why such large inconsistencies may arise between studies is because the effects of fragmentation on species' occurrence (and other response variables studied in the literature) vary across space. The effects of fragmentation range from weak (i.e. species are not sensitive to fragmentation; effects are not significant) to strong (i.e. species are highly sensitive to fragmentation; effects are significant), with habitat amount being so far one of the best studied mediators of these effects (Villard and Metzger, 2014). The link between fragmentation and habitat amount was first made by Andrén (1994), who suggested that the effects of connectivity and landscape configuration on species sensitivity were stronger in landscapes with <30 % suitable habitat. In contrast, Pardini et al. (2010) showed that species' responses to fragmentation in the Atlantic Forest were strongest in landscapes with 30 % forest cover. They found that species' responses to fragmentation were non-significant in more deforested landscapes (10 % forest cover) and in more forested landscapes (50 % forest cover) due to isolation between patches being too large in the former and too small in the latter. More recently, other studies showed that the effects of fragmentation were instead stronger in landscapes with 50 to 100 % (Herse et al., 2020) and 60 to 100 % (Püttker et al., 2020) forest cover: as those areas still retain the most sensitive species. The sheer variety of findings and contingencies in studies demonstrates why the effects of fragmentation are so contentious and highlights the importance of better understanding how habitat amount could mediate the effects of fragmentation.

In addition to habitat amount, range-edge effects are a long-standing (Henle et al., 2004) but lesser-studied mechanism that could also be driving some of this variability in the observed effects of fragmentation on biodiversity (Banks-Leite et al., 2022). Range-edge effects refer to changes in population size or viability that occur near the species' geographic range edge (Busch et al., 2011; Pironon et al., 2017), but also, populations' higher sensitivity to habitat change when they are located near their species' range edge (Anjos et al., 2010; Orme et al., 2019). Orme et al. (2019) showed that within species, populations are more likely to be negatively affected by habitat loss when occurring near their species' range edge, and positively affected when occurring at large distances from range edges. These results show that even habitat loss, which supposedly only has negative effects on species (Fahrig, 2003), can have both positive and negative effects on different populations of the same species. These studies raise the question as to how distance to range edge may interact with habitat amount to mediate the effects of habitat fragmentation, and potentially help explain why fragmentation is such a contentious topic.

Here, we aim to contribute to the fragmentation debate by investigating distance to range edge as a potential driver for such high variability in how species respond to habitat fragmentation. Using presence-absence data for 362 species of birds (see Table S1.3 for a list of the species used) from five fragmentation studies conducted in different regions of the Atlantic Forest of Brazil, we first test whether the effects of fragmentation on local bird occurrence (i.e. the average intraspecific response across species) change with distance to the geographic range edge and local habitat amount. We then use the presence-absence model derivative to obtain a measure of sensitivity to fragmentation to explore patterns of intraspecific species responses, that is, the variation in responses between populations of the same species across the geographic range.

## 2. Methods

### 2.1. The Atlantic Forest

The Atlantic Forest, located along the coast of Brazil, is the second largest tropical forest in South America ranging from 3°S to 30°S, covering approximately 1,482,000 km<sup>2</sup> before European settlement (Metzger et al., 2009). It is considered a 'Biodiversity Hotspot' with around 8723 endemic species, 200 of which are birds, but also including plants, amphibians, freshwater fishes, reptiles and mammals (Goerck, 1997; Mittermeier et al., 1999; Da Silva and Casteleti, 2003). The Atlantic Forest is highly deforested and fragmented, with only 28 % of its original forest cover remaining (Rezende et al., 2018), 80 % of its remnants distributed in patches smaller than 0.5 km<sup>2</sup> and ~50 % within 100 m of a forest edge (SOS Mata Atlântica, 2020).

### 2.2. Species data

To assess bird species' responses to fragmentation and distance to range edge, we used five published datasets from five independent studies located as far as 2000 km apart (Fig. 1) conducted between 1997 and 2017 in the Brazilian Atlantic Forest (see Table S1.1). All five studies were situated in fragmented landscapes near large forest remnants. The main objective of these studies was to investigate the effects of habitat fragmentation on local bird communities. Therefore, the datasets were collected in forest patches (134 sites) that varied in size, proximity to neighbouring patches and matrix features which included pasture, silviculture and agriculture land-use types. All five datasets contain bird data sampled using a point-count method in each site. Within datasets the same time was spent in each forest fragment (site) ensuring standardised sampling effort across sites in each study. The sampling effort did vary between datasets though we account for this variation with dataset level effects in our mixed-model structure (i.e. random effect). In total, the presence-absence of 362 bird species (Table S1.3) across 134 sites was recorded (for more details on the data collection of each dataset, please see (Develey and Júnior, 2004; Anjos et al., 2010; Uezu and Metzger, 2011; Morante-Filho et al., 2015; Hatfield et al., 2020).

### 2.3. Fragmentation metrics and forest cover

We calculated summary statistics for habitat fragmentation and forest cover at each sampling site using the package *landscapemetrics* (Hesselbarth et al., 2021) and the packages *raster* (Hijmans et al., 2021) and *sf* (Pebesma et al., 2021) were used for geoprocessing in R v.4.1.0 (R Core Team, 2021). We assessed fragmentation using two distinct metrics: the number of forest patches and forest edge density. Both gave qualitatively similar results so we present the results for forest edge density in the main text (see discussion and supplementary information for results for number of patches). Both fragmentation metrics were extracted from 30-m resolution 85 % accurate land-cover maps of the Atlantic Forest provided by MapBiomas (2020). MapBiomas provides annual cover for the entire territory of Brazil from 1985 onwards, which allowed us to choose one map per dataset based on their data collection period (see Table S1.1). The definition of forested areas used to measure fragmentation was based on category 3 ("Natural Forest Formation") of MapBiomas, and all other categories were classified as matrix. The South America Albers Equal Area Conic projection (<https://epsg.io/102033>) was used for all calculations.

For each of the 134 sampling sites, we calculated the total number of patches, forest edge density and forest cover within a buffer of 600 m around each site (median nearest neighbour distance between patches within the same landscape was 1409 m). This buffer was selected based on results from a sensitivity analysis presented in Orme et al. (2019) using the same dataset.



**Fig. 1.** Example of distances measured to the nearest continental edge of a hypothetical species' geographic range. The points on the map show the location of each of the five datasets, and the lines connected to them show each respective distance to the nearest continental range edge (dashed line), the dark grey bold line is the coastal range edge which was excluded from analyses, the lighter grey filled area from the dashed line to the bold line represents a hypothetical geographic distribution and the darker polygon underneath shows the extension of the Brazilian Atlantic Forest. The map of South America (with its country boundaries) appears in the background in light-grey.

#### 2.4. Distance to range edge and species range maps

Distances to the species' range edge for all populations were obtained from Orme et al. (2019) who used the same datasets to analyse intraspecific variability in the effects of habitat loss with range data from BirdLife International (following BirdLife International checklist version 2; BirdLife International, 2020). The distances to the range edge were measured to the nearest continental edge of each species' range (Fig. 1), thereby excluding the Atlantic Ocean as a range edge from the analysis. This was done because a hard edge like a coastal line is not a useful indicator of biotic or abiotic range limitations, other than habitat availability (see Orme et al., 2019 and Banks-Leite et al., 2022 for more details). In some cases, the straight line distances might cross over the ocean (for example see SP1 and SP3 in Fig. 1), but this is still likely to reflect turnover in factors such as biogeographic conditions (ie. climate) and community turnover that may affect species sensitivity to fragmentation.

#### 2.5. Statistical analysis

All statistical analyses and visualisations were performed using R v.4.1.0 (R Core Team, 2021) and packages *lme4* (Bates et al., 2021), *performance* (Lüdtke et al., 2021) and *tidyverse* (Wickham, 2021).

Firstly, we used a binomial linear mixed effects model with a logit link function to investigate how the effects of habitat fragmentation vary with distance to the range edge and forest cover. The response variable was the occurrence of all species across all 134 sites, and fixed effects included distance to the range edge (DE; square root transformed), fragmentation (FR; z-transformed), forest cover (FC; proportion) and their fully factorial interactions. In this model, we also included a

random effect term allowing both the slope and intercept of fragmentation, forest cover and their interaction to vary between datasets to account for systematic differences in fragmentation and forest cover between datasets. In addition, we included a second random effect term allowing the slopes and intercepts of distance to range edge, fragmentation, forest cover and their interactions to vary between species. The full model structure, shown here in the R package *lme4* syntax, is:

$$\begin{aligned} \text{Occurrence} \sim & \text{DE} + \text{FR} + \text{FC} + \text{DE} : \text{FR} + \text{DE} : \text{FC} + \text{FR} : \text{FC} + \text{DE} : \text{FR} \\ & : \text{FC} + (\text{FR} + \text{FC} + \text{FR} : \text{FC} \mid \text{D}) + (\text{DE} + \text{FR} + \text{FC} + \text{DE} \\ & : \text{FR} + \text{DE} : \text{FC} + \text{FR} : \text{FC} + \text{DE} : \text{FR} : \text{FC} \mid \text{S}) \end{aligned}$$

where colons indicate the set of variables in interaction terms, and brackets and the vertical lines indicate groups of terms in random effects conditioned on indicator variables showing dataset (D) and species (S) identity.

The fixed effect terms capture the average intraspecific response to the local landscape (FR and FC) and distance to range edge (DE), while the random effects yield the species-specific estimates. We used  $n\text{AGQ} = 0$  in model fitting to reduce fitting time. We checked for multicollinearity among variables, all VIF values were low (i.e. ranging from 1.14 to 1.38 for standalone terms - for all VIFs see Table S2.2).

We also calculated a metric,  $\Delta FR$ , based on the parameter estimates of the binomial mixed effects model described above (see full derivation in Supplementary Information Formula S1.1). Briefly, this measure is defined as the partial effect of fragmentation in the model and obtained by taking the derivative of the linear model with respect to fragmentation. The metric captures the change in occurrence (specifically the change in log-odds) to an increase in fragmentation given the forest cover and distance to range edge. The metric is defined by the following

equation in mathematical notation:

$$\Delta FR = \frac{dI}{dx_{FR}} = \beta_{FR} + \beta_{DE:FR}x_{DE} + \beta_{FC:FR}x_{FC} + \beta_{DE:FR:FC}x_{DE}x_{FC}$$

where  $\beta$  and  $x$  are the coefficients and predictor variables indicated by the subscript respectively.

The  $\Delta FR$  metric has several advantages: (1) it allows us to evaluate both the sign and magnitude of the effects of fragmentation for a given distance to the range edge and forest cover. Values of  $\Delta FR > 0$  indicate that fragmentation has a positive effect on species occurrence and values of  $\Delta FR < 0$  indicate that fragmentation has a negative effect. (2) Larger values indicate that fragmentation has a greater impact (i.e. the average probability of occurrence changes more for a given change in fragmentation) than values close to zero. (3) The  $\Delta FR$  metric allows us to identify critical distances to the range edge at which the effects of fragmentation change sign (i.e. from positive to negative effects or vice versa). (4) We can apply this metric to either: a) the fixed effect parameter estimates from the model, giving the average intraspecific sensitivity across all species in the study or b) the conditional species-specific parameter estimates (obtained from the random effects) allowing us to examine patterns of variation in responses of individual species to fragmentation across different landscapes.

### 3. Results

#### 3.1. Fragmentation, distance to range edge and forest cover alter birds' average probability of occurrence

The binomial mixed effects model showed that habitat fragmentation (i.e., forest edge density, see Supplementary Information Table S3.2 for results on number of patches), distance to range edge, forest cover, and all their interactions were significant ( $p < 0.05$ ; Table S2.2) except the interaction between fragmentation and forest cover ( $p = 0.250$ ) (Fig. 2, Fig. S2.1 and Table S2.2).

The fixed effects estimates showed that the average probability of occurrence across species varied depending on the local landscape and its position in the geographic range. The average probability of occurrence increased with distance to range edge ( $\beta_{DE} = 0.052$ ,  $p < 0.001$ ), a result that was stronger at higher levels of fragmentation and lower forest cover. The average probability of occurrence decreased at higher levels of fragmentation close to the range edge (i.e., when  $DE = 0$ ,  $\beta_{FR} = -0.891$ ,  $p < 0.05$ ). However, at larger distances from the range edge, the effects of fragmentation on the average probability of occurrence

became positive ( $\beta_{DE:FR} = 0.027$ ,  $p < 0.001$ ). The effects of fragmentation were independent of forest cover at the range edge (as indicated by the non-significant  $\beta_{FR:FC}$  interaction term; Fig. 2) but became positive at higher distances (i.e., higher forest cover reduces the negative effects of fragmentation further from the range edge;  $\beta_{DE:FR:FC} = -0.022$ ,  $p < 0.01$ , Fig. 2).

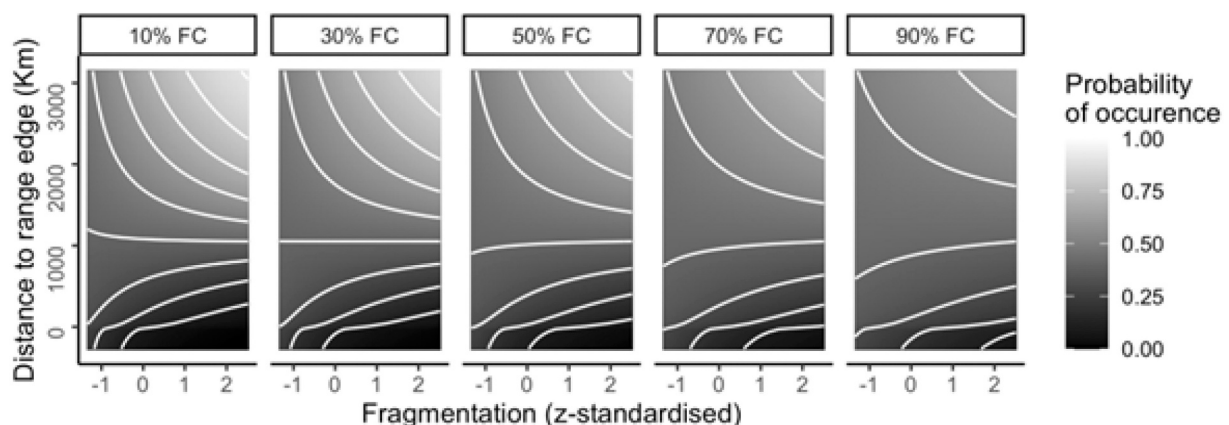
#### 3.2. Variation in intraspecific responses to fragmentation

The  $\Delta FR$  metric shows how responses to fragmentation both across and within species vary depending on forest cover and distance to range edge (Fig. 3). Looking at the average intraspecific response (thick line, Fig. 3), the metric mirrors the results showing in Fig. 2.  $\Delta FR$  is negative near the range edge and positive at further distances from the range edge with the strength of this interaction becoming weaker with increasing forest cover (Fig. 3). The critical distance at which the effects of fragmentation change in sign from negative to positive was estimated as ~1080 km (1028–1266 km, depending on the local forest cover, Fig. 3).

The species-specific  $\Delta FR$  estimates obtained from the random effects (thin lines, Fig. 3) show the variation around the average in intraspecific responses. At lower levels of forest cover (10–30 % FC), most species followed the average across-species trend (i.e. response to fragmentation becomes more positive with increasing distance to range edge) and the variation around the mean response is relatively small. At higher levels of forest cover, (50–100 % FC), individual species responses became increasingly variable and the effect of distance to range edge on sensitivity to fragmentation overall became weaker.

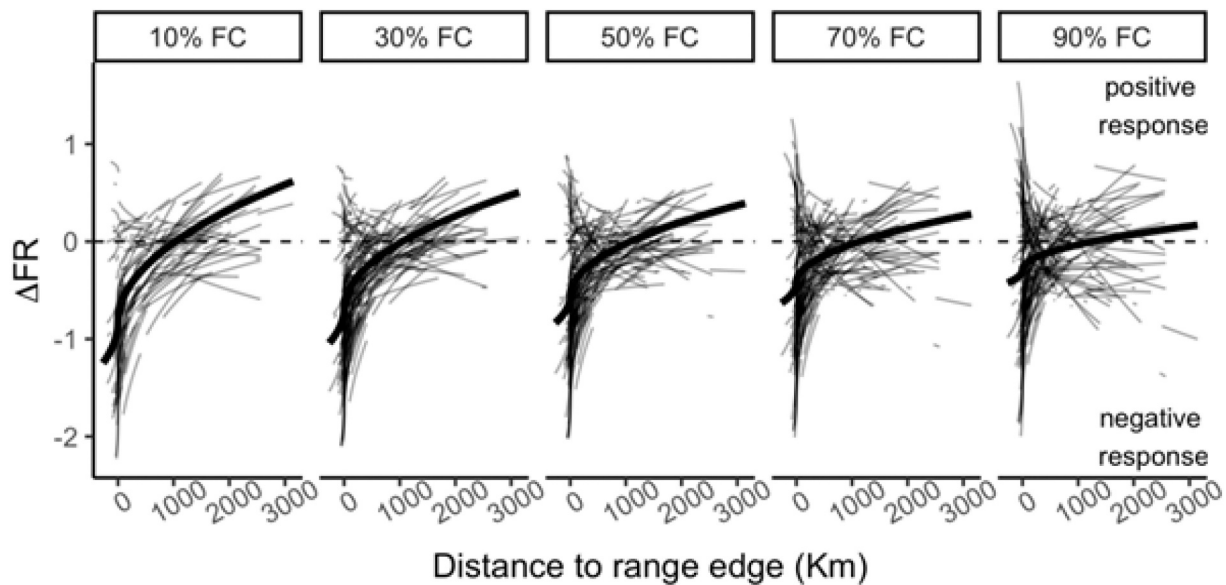
### 4. Discussion

Our results suggest that habitat fragmentation has highly variable effects on species. We show that species responses to fragmentation are mediated by the location of the population within its range, and that this relationship varies depending on local forest cover. These results are important because, to our knowledge, it has not yet been shown how the position of a population in the geographic range affects sensitivity to fragmentation, despite evidence showing that not all populations of a species respond to habitat fragmentation in the same way (Ries and Sisk, 2004; Schneider-Maunoury et al., 2016). This means that two different researchers each conducting a study with the same question and same experimental design but in different locations within a species' range could obtain contrasting results regarding the effects of habitat fragmentation. Our results are also relevant for conservation as our methodology can generate quantitative targets and aid in prioritisation



**Fig. 2.** Probability of occurrence for the average intraspecific response as a function of distance to range edge (y-axis), forest edge density (x-axis) and forest cover (FC, different panels). Average probability of occurrence is represented by the change in shading from low occurrence (black) to high occurrence (white). The white lines show how the average probability of occurrence changes with the interaction between distance to range edge and fragmentation. The bottom half of each panel shows negative responses to increasing fragmentation (e.g., grey shading becomes darker along the x-axis). At around a critical distance of 1080 km, species responses to fragmentation become positive (e.g., grey shading becomes lighter along the x-axis). This pattern is more accentuated at lower levels of forest cover.





**Fig. 3.** Change in species' responses to fragmentation is mediated by distance to range edge and forest cover. Thick black lines show how the average across-species response to fragmentation (y axis) changes with distance to the range edge (x axis) at each forest cover (panels 10 %, 30 %, 50 %, 70 % and 90 % FC). Thin lines represent the trajectory for individual species ( $n = 362$ ) to highlight the variation in intraspecific sensitivity for each species. The dotted line shows the point where responses to fragmentation change from positive ( $\Delta FR > 0$ ) to negative ( $\Delta FR < 0$ ) or vice versa. This figure was plotted by taking the derivative of the mixed effects model parameters with respect to fragmentation (Formula S1.1).

mapping of direct use to policymakers and practitioners.

When is fragmentation negative for biodiversity? Our findings show that responses to fragmentation are usually negative when populations are found within roughly 1000 km from the nearest range edge, and this value is relatively independent of habitat amount (Figs. 2,3). Populations near the range edge may be more sensitive to environmental changes because these areas are associated with the limits of species' ecological niches (Hargreaves et al., 2015; Lee-Yaw et al., 2016; Orme et al., 2019). These populations are likely to be under higher stress from pressures such as extreme temperature, moisture (Moore, 2013), and less suitable vegetation and soil conditions (Cumming et al., 2014) than populations further from the range edge. In addition, populations near the range edge might have a higher probability of local extinction because they have fewer populations surrounding them which facilitates source-sink dynamics (Angert, 2009; Torrenta et al., 2022). These factors may be particularly important in modulating responses to fragmentation (as opposed to other landscape features such as habitat amount) if they affect processes such as dispersal which are known to be important in ensuring population persistence in fragmented landscapes. While there is evidence to suggest that these populations may evolve strategies to adapt to poorer local conditions near the range edge (Pérez-Tris et al., 2000), it is possible that habitat fragmentation would magnify the stress in either additive or synergistic ways (Simmons et al., 2021; Banks-Leite et al., 2022).

When is fragmentation positive for biodiversity? The positive effects of fragmentation were usually found in populations occurring beyond 1000 km from the nearest range edge, and specifically in areas of low forest cover (Figs. 2,3). This is in agreement with previous work showing that some populations can benefit from highly disturbed habitats (Orme et al., 2019). In the specific case of fragmentation, it is possible that these populations reach a high average probability of occurrence in fragmented landscapes because they are at the core of their range. Therefore, these areas present more favourable environmental conditions, and the populations are also more likely to be benefited by source-sink dynamics (Torrenta et al., 2022). Additionally, modelling approaches also show that interpatch distance and the number of fragments increase dramatically below 40 % of habitat amount (Swift and Hannon, 2010). It is possible that species that benefit from these

landscape changes are the ones benefiting from high fragmentation at low forest cover in our study. Regardless of why these populations benefit from habitat fragmentation, these positive effects may not actually translate to positive effects for wider biodiversity if the “winners” are widespread species that contribute to increasing biotic homogenisation in human-modified landscapes (Arce-Peña et al., 2022; Parra-Sanchez and Banks-Leite, 2020). In fact, “losers” are often likely to be localised species who are always close to their range edge, again contributing to biotic homogenisation.

As expected, habitat amount was also found to be an important mediator of fragmentation effects. Whilst most other studies focused on the levels of habitat amount at which the effects of fragmentation become more negative (Andrén, 1994; Pardini et al., 2010; Püttker et al., 2020), our results show that at lower levels of habitat amount, the effects of fragmentation actually become more positive with increasing distance to the range edge (Figs. 2,3). In fact, our results show that the negative effects of fragmentation are not affected by habitat amount, as we observed them at every forest cover percentage near to the range edge. We acknowledge that these results just add further complexity to the role of habitat amount in the fragmentation debate, however we believe that this controversy partially stems from the fact that most studies do not account for range edge effects (Banks-Leite et al., 2022). In this study we did not set out to determine if factors affecting intra-specific variation are different between habitat fragmentation and habitat loss. However, most of the potential explanations should consider the lack or presence of an additional stressor. It has been suggested before that multiple stressors can interact to have antagonistic effects, though the biological mechanisms are not always understood (Orr et al., 2022). Therefore, we encourage future studies to focus on detecting what are these stressors and whether they interact with fragmentation in synergistic or antagonistic ways; or contrasting alternative theoretical predictions.

Our findings also provide a partial resolution to the fragmentation debate, showing how distance to range edge can be a driver of species sensitivity to habitat fragmentation. Although our results indicate that fragmentation can have both negative and positive effects, not all species may show such plasticity. For instance, species with small and narrow ranges will probably only show negative responses to

fragmentation because all their populations potentially occur near the range edge (Banks-Leite et al., 2022). On the other hand, we would probably observe both negative and positive fragmentation effects in species with very large geographic ranges. It is also likely that distance to range edge is not the only factor that drives the variation in sensitivity seen across other studies. A combination of factors like habitat edge effects (Ries and Sisk, 2004; Ries and Sisk, 2010), source-sink dynamics across ranges (Torrenta et al., 2022), climatic and/or habitat suitability (Williams and Newbold, 2020), species traits (Henle et al., 2004; Barbaro and Van Halder, 2009; Bregman et al., 2014), tropical versus temperate species (Betts et al., 2019), dispersal ability (Thompson et al., 2019) and range shapes combine to determine observed species responses. Future research should focus on how and to what extent these other factors affect species sensitivity to fragmentation and how they interact across species' geographic ranges.

Our results could also be particularly relevant in identifying where conservation initiatives should be focused. Broad conservation actions involving several species could have greater impact if decision makers considered whether communities are mainly composed of populations located far or close to their species' range edges. For instance, in areas where target populations are mainly located near range edges (i.e. <1000 km away from a range edge), the focus should be on increasing forest amount in the landscape by planting species with rapid growth and ample canopy, modifying non-forested matrix with forested buffers to reduce forest edge effects (Hatfield et al., 2020) and fencing areas to reduce browsing allowing natural regeneration (Banks-Leite et al., 2020). Specifically for our study sites, Orme et al. (2019) showed that 60 %–80 % of the bird species are close to their range edge in the south-west of the Atlantic Forest, so these populations are more likely to show negative responses to habitat loss and fragmentation. In these areas, we suggest increasing habitat amount and reducing fragmentation by modifying the matrix. Hatfield et al. (2020) showed that forestry land uses can reduce the spillover of non-forest species into forest patches, indirectly benefiting forest species in these areas, thus it is possible that by changing and softening the matrix fragmentation effects could be reduced. In the northeast of Brazil however, where most communities are composed of populations located further than 1000 km from their species' range edge (Orme et al., 2019) and therefore most likely to be positively affected by habitat loss and fragmentation, we suggest targeted activities on specific species of conservation concern, for example targeting habitat quality and connectivity within and around existing strongholds.

In conclusion, the effects of fragmentation on species are highly variable, very complex and while they may appear to be random, they are predictable across space. In tropical regions, fragmentation can further species decline and lead to biotic homogenisation, neither of which have positive impacts on biodiversity. Landscape ecologists should focus on what drives intraspecific variation in the effects of habitat loss, fragmentation and degradation. We suggest that exploring the reasons why fragmentation effects are variable across the geographic range is a reasonable way forward to explain opposing results reported in the fragmentation debate literature. Further research should consider other variables, like the ones mentioned here, that could influence intraspecific variability across the range. Decision makers should consider the composition of communities across a biome, and especially whether populations are far or close from the range edges of their constituent species, to implement conservation and management activities.

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We have permission to use the BirdLife species range polygons.

#### CRediT authorship contribution statement

**Flavia C. Bellotto-Trigo:** Conceptualization, Methodology, Formal analysis, Data curation, Writing – original draft, Writing – review & editing. **Alexandre Uezu:** Investigation, Writing – review & editing. **Jack H. Hatfield:** Investigation, Writing – review & editing. **José C. Morante-Filho:** Investigation, Writing – review & editing. **Luis dos Anjos:** Investigation, Writing – review & editing. **Pedro F. Develey:** Investigation, Writing – review & editing. **Thomas Clegg:** Methodology, Writing – review & editing. **C. David L. Orme:** Conceptualization, Methodology, Writing – review & editing, Supervision. **Cristina Banks-Leite:** Conceptualization, Methodology, Data curation, Writing – original draft, Writing – review & editing, Funding acquisition, Supervision.

#### Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

Cristina Banks-Leite reports financial support was provided by Natural Environment Research Council.

#### Data availability

Bird occurrence datasets and scripts of analyses are available from github. We do not have rights to redistribute the underlying range polygon (BirdLife) data, but these datasets are available for use under licence. Land use rasters are available from <https://mapbiomas.org/>.

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#### Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.biocon.2023.110167>.

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