Imperial College of Science, Technology and Medicine
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The Effects of Distance to Range Edge on Bird Responses to Habitat Change in Tropical Forests

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Abstract

Habitat change is arguably the most important environmental driver of species decline. In spite of this, there is still uncertainty surrounding the mechanisms that mediate species sensitivity when disturbances occur in their habitat. One source of variation in species responses to habitat change is location within their distribution range. In this thesis I attempt to answer some of the questions related to variation in species sensitivity to habitat change across ranges. First I investigate the relative effects of habitat fragmentation on species sensitivity. I reveal that populations within a species can show positive, negative or neutral responses to fragmentation depending on location within the geographic range and the amount of local forest cover. Then I try to detect the more sensitive populations based on phenotype asymmetry due to physiological stress caused by environmental change. The results are inconclusive, which suggest that either these populations are able to implement mechanisms that compensate for asymmetry during development under stress; or that they are not under physiological stress near range edges. Finally, I investigate if variation in trait size across the range change systematically and provide a mechanism to explain sensitivity. I find no consistent pattern of decrease in trait size or increase in variance of trait size near the range edge, with only forest cover amount potentially showing a decreasing trend in trait size with increase of forest cover. Overall my work demonstrates how complex the study of species sensitivity to habitat change across species distribution ranges are, and that species responses cannot always be generalised. In general, future studies should consider including distance to range edge as a predictor variable in analyses, as it might help explain some of the variation in intraspecific responses to environmental change.

Declaration of Originality

I declare that the work in this thesis was performed and prepared by myself under the supervising of Dr Cristina Banks-leite and Dr David Orme. All sources of information are appropriately cited.

Whilst this work is my own, it has been a collaborative effort that could not have been done without the contributions of collaborators and colleagues (as with all science).

Chapter 2 has been written in collaboration with other authors, hence being written in the third person plural. This chapter has been published as an Open Access research paper in the journal Biological Conservation (DOI:10.1016/j.biocon.2023.110167) under the terms of the Creative Commons CC-BY license, and it has been reproduced here. I carried out the bulk of the analysis, model fitting and writing, however, all collaborators gave advice and made comments throughout. Alexandre Uezu, Jack H. Hatfield, José C. Morante-Filho, Luis dos Anjos and Pedro F. Develey generously shared their data to be used in this chapter. Each author's specific contribution has been stated in the article's "CRediT authorship contribution statement".

All trait measurements in **Chapter 3** and tail feather photos were taken by me at the Museu de Zoologia da Universidade de São Paulo in Brazil. The feather growth bars were measured from the photos by the master's student Anna David. All model fitting, analysis and writing were carried out by me. My supervisors and PhD colleagues made suggestions on the writing and analysis.

Chapter 4 used data published in Rodrigues et al. (2019). All model fitting, analysis and writing were carried out by me. My supervisors and PhD colleagues made suggestions on the writing and analysis.

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Not many people know this, but when I arrived in the UK in 2014 I was working in the production line of a factory in Scunthorpe. Now in 2023, I am finishing a PhD. I am proud of myself, but I would never have been able to do this alone. I am so grateful to all the people who helped me along the way.

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I am very privileged for all the people in my life.

"Aerography is like measuring, weighing,

and studying the behaviour of ghosts."

E. H. RAPOPORT

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Chapter 1

Introduction

Biodiversity loss presents a significant crisis. Experts estimate that approximately 37% of species face the risk of extinction or endangerment by the year 2100 (Isbell et al., 2023) and this is predicted to lead to declines in ecosystem functioning, ranging from 10% to 70%. The main drivers of biodiversity loss are land-use change, climate change, and over-exploitation (Sala et al., 2000; Díaz et al., 2019), however these are expected to have different degrees of impact among taxon and ecosystems (Isbell et al., 2023). Understanding what causes the sensitivity of specific species' populations to these drivers is crucial to our ability to predict and mitigate their negative effects. This is especially true in the Neotropics which stand as both some of the most bio-diverse regions on earth and those most under pressure due to human activities (Saatchi et al., 2021). In this thesis, I focus on understanding the effects of habitat change in this region, specifically the Atlantic Forest of Brazil.

The Atlantic Forest is a biodiversity hotspot with around 8723 endemic species (Atlantica, 2020). It is the second largest tropical forest in South America covering approximately 1,482,000 km2 and it shows high levels of variation in habitat fragmentation and loss (Metzger, 2009; Rezende et al., 2018; Rodrigues et al., 2019; Atlantica, 2020). 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, and 50 % within 100 m of a forest edge (SOS Mata Atlantica, 2020). This allows me to investigate species

responses at different levels of disturbance. Being the subject of many studies, there is plenty of information widely available about the Atlantic Forest, including several recently published data-papers with years of data on mammals (Bovendorp et al., 2017; Gonçalves et al., 2018; Souza et al., 2019), bats (Muylaert et al., 2017), butterflies (Santos et al., 2018), birds (Hasui et al., 2018; Rodrigues et al., 2019), amphibians (Vancine et al., 2018), primates (Culot et al., 2019), epiphytes (Ramos et al., 2019), flowers and its pollinators (Iamara-Nogueira et al., 2022), and ants (Silva et al., 2022). In addition to high-resolution landcover maps available annually since 1985 for the Atlantic Forest and all the other Brazilian biomes (MapBiomas, 2020).

Within this geographical area, I focus on bird species and their responses to habitat change. I focus on birds for two reasons. Firstly, birds are important in their direct roles in several ecological processes like seed dispersal (Murray, 1986; Emer et al., 2020; Tsunamoto et al., 2020), pollination (Stiles, 1978; Abrahamczyk, 2019), scavenging (Hewson, 1981; Michel et al., 2020), predation (Göransson et al., 1975; Speakman, 1991; Freeman et al., 2020), and pest control (Railsback and Johnson, 2014; Boesing et al., 2017; Denan et al., 2020). As such, understanding their responses is of vital importance to predicting the effects of habitat change. Secondly, as perhaps the most well-studied taxonomic group, they have the advantage of having well-known taxonomy and high-quality information on geographical ranges widely available (International, 2020). The use of birds to explore a variety of ecological and evolutionary ideas has contributed greatly to our knowledge of species interactions (MacArthur, 1958), island biogeography (MacArthur and Wilson, 1967), speciation (Darwin, 1859; Grant, 1981) among many other topics.

In this chapter, I will give an introduction to the concepts and previous work relevant to this thesis. I will first review habitat and habitat change, its various forms, and the mechanisms through which it affects species' populations. I also introduce the notion of intraspecific variation in sensitivity. I then go on to discuss the potential of the geographic position of populations to influence this sensitivity. I give an overview of species distribution ranges, what they are, and how various features have been used to explain ecological patterns. I give specific attention to their role potentially reflecting the ecological niche of species and how this may help explain variation in sensitivity to habitat change discussed above. Finally, I give an outline of the thesis

and the topics of each chapter.

1.1 Land-use and Habitat Change

The term "habitat" in ecology refers to a diverse set of elements that occur within a defined area (Krausman and Morrison, 2016). These elements collectively provide the necessary conditions for the sustenance and reproduction of a specific species. Essentially, a species' habitat can be viewed as the tangible expression of its ecological niche. In turn, the ecological niche corresponds to the distribution of resources that are accessed and limited by a species. A "type of habitat" categorises environments based on the type of vegetation and climate of a specific landscape, therefore not connected to a specific species but to a group of species who are able to survive in this landscape with similar environmental conditions (Breed and Moore, 2011; Krausman and Morrison, 2016). Habitats can be defined across terrestrial (forest, savannas, grasslands), fresh-water (rivers, ponds and streams), marine (coral reefs, inter-tidal zones, pelagic zones) (Breed and Moore, 2011), and urban areas (parks, gardens, land-fields) (Elmqvist et al., 2008). Within this large variety of habitat-types, some species are able to thrive in several of them, while others require a narrower set of specific conditions, being constrained to a single habitat-type.

Habitat change is the conversion of one type of habitat into another (Gardner et al., 2008). This conversion could be driven by natural factors (i.e. glaciation) and/or anthropogenic activities (i.e. construction of a new road or building, land used for agriculture). Habitat change occurs due to three interrelated processes: habitat loss, habitat fragmentation, and habitat degradation each of which affect populations in different ways (Banks-Leite et al., 2020). The three mechanisms of habitat change are scale and species specific, that is, different species can respond to habitat change in different ways (positively or negatively) and within species we can observe different responses based on local conditions (Banks-Leite et al., 2020).

1.1.1 Habitat Degradation

Habitat degradation encompasses all changes to the quality of a habitat involving its gradual deterioration without any significant changes to its amount or fragmentation (see below) (Banks-Leite et al., 2020). It can be caused directly by processes such as pollution, burning or selective logging, and over-exploitation, or indirectly if species that are vital to maintaining a habitat's integrity are lost (Banks-Leite et al., 2020). The classic tropic cascade in Yellowstone National park is an example of this where the loss of predators lead to increases in herbivore populations and a resultant degradation of forest habitats (as they experience higher herbivory rates) (Fortin et al., 2005). Habitat degradation can have profound impacts on populations and communities that rely on these habitats, reducing its capacity to support them. This subtle process can reduce the abundance and diversity of native species, leading to cascading effects throughout communities and ecosystems (Harrison and Banks-Leite, 2020).

1.1.2 Habitat Fragmentation

Habitat fragmentation is the breaking apart of habitat types into smaller, isolated patches (Fahrig, 2003) due to increased human infrastructure or natural processes. It is widely assumed that fragmented habitats are more likely to be susceptible to disturbances due to proportionally greater edge-area (i.e edge effects), increased contact with human-modified matrix, and higher isolation between patches (Fletcher et al., 2018a). However, this assumption is not free from criticism. There is a long ongoing debate in landscape ecology regarding the independent effects of fragmentation (i.e fragmentation *perse*; Fahrig (2003)), with studies showing that fragmentation might have positive (Grez et al., 2004; Fahrig, 2017, 2019), negative (Andrén, 1994; Pardini et al., 2010; Anjos et al., 2010; Fletcher et al., 2018a,b) or no effects (Fahrig, 2013; Püttker et al., 2020) on species. As most things in Ecology, the effects of fragmentation are context specific (Betts et al., 2019), with sensitivity to fragmentation varying both across and with species (i.e. inter- and intra-specific variation).

1.1.3 Habitat Loss

Habitat loss is considered the main threat to 85% of species classified as Threatened by the IUCN (WWF, 2023). It depicts the reduction of "habitat amount" involving the elimination of suitable habitat-types through land conversion, urbanization, agriculture, and other human activities (MEA et al., 2005). It leads to the decrease in biodiversity at a global scale (Banks-Leite et al., 2020) and often leads to species turnover (Banks-Leite et al., 2012) and local extinction (Hanski, 2015) at smaller scales. Although it has negative effects at both large and small scales, it has been shown that habitat loss can also show positive effects for populations of species located far from the edge of their geographic range (Orme et al., 2019). Investigating the drivers and consequences of habitat loss is essential for crafting effective conservation strategies.

1.1.4 Variation in Responses to Habitat Change

The responses of species to habitat change vary greatly depending on the taxa and types of disturbance considered. This interspecific variation has been the subject of much work in ecology and there are many studies documenting species responses (Bregman et al., 2014; Hatfield et al., 2018c; Williams and Newbold, 2020a; Banks-Leite et al., 2022). In particular many papers try to attribute these responses to features of species or the types of disturbance to try and understand and perhaps predict responses in the future. This work has revealed the role of factors such as species traits (Pigot et al., 2020), history of disturbance (past disruptions or changes to ecosystems)(Betts et al., 2019) and bio-geographical factors (Slatyer et al., 2013) as important in mediating these responses.

More recently, there has been also been research detailing how populations of the same species can respond differently to habitat change (Alice Boyle et al., 2016; Orme et al., 2019). For instance, Anjos et al. (2010) found that populations near their geographic range edge were more vulnerable to forest fragmentation. This illustrates the importance in understanding intraspecific variation in responses to habitat change if we want to predict future responses.

1.2 Species Distribution Ranges

A fundamental concept in biogeography is the geographic range of a species. A species geographic range is an area in time and space where a species can be found. Geographic ranges can be large, medium or small, narrow or long, continuous or broken up (Brown et al., 1996). Several biotic and abiotic factors and their interaction will determine the range of a species which I discuss here.

1.2.1 Features of Geographic Ranges

Biogeographic research focuses on understanding the structure and dynamics of species ranges, including their sizes, shapes, boundaries, overlaps, and locations. It delves into the spatial and temporal patterns of range dispersion, examines the relationships between ranges and phylogenies, and investigates the underlying processes that shape these patterns (Rapoport, 1982). Some researchers concentrate on specific regions, analyzing portions of one or more species' ranges, while others explore the distributions of multiple species, functional groups, or overall species diversity (Sagarin and Gaines, 2002; Camps et al., 2021). These inquiries are also at the core of macroecological research, addressing questions about the distribution, abundance, and factors influencing the geographic ranges of species, encompassing both abiotic and biotic factors.

Range sizes exhibit high variation among individual species (Brown et al., 1996; Orme et al., 2006). Usually, many species have small to medium ranges with fewer species having large ranges (Rapoport, 1982; Brown et al., 1996). In some instances, a species' geographic range closely aligns with the area that an individual organism inhabits, resulting in a single population. In other instances, and more frequently, their geographic range is many orders of magnitude larger than one individual's home range, leading to several populations separated by distance and possibly geographic barriers that hinder dispersal (Rapoport, 1982; Brown et al., 1996). The size of a range might be limited by the area of the continent or island where

the species exists and species with smaller ranges might be more sensitive to disturbances than species with larger ranges (Orme et al., 2006; Anjos et al., 2010). The size of a range is also thought to correlate with the tolerance to abiotic conditions of a species (Slatyer et al., 2013).

In addition to range size, the shape of ranges is also of interest. Range shapes are diverse, even within the same taxon. Some ranges are compact and spherical while others are elongated and linear (Brown et al., 1996). In the same way that range sizes might be constrained by the size of the continent where they exist, range shapes are subject to the same limitations. Another aspect of range shapes is that ranges are not contiguous and can present gaps and fragments of varying sizes. Generally, near the core geographic ranges might be more continuous but become less so as they approach their edges. It is important to note that range shapes are closely related to the degree of accuracy with which they have been drawn. Nevertheless, these fragmented patterns might result from truly ecological factors like vicariance events (i.e. populations separated by a physical barrier), long-distance colonization or expansions and contractions in a species' range over time (Brown et al., 1995).

Range boundaries and its delimitation have also been extensively researched (MacArthur, 1972; Rapoport, 1982; Pérez-Tris et al., 2008; Slatyer et al., 2013; Louthan et al., 2015; Varsamis et al., 2020). As mentioned before, biotic and abiotic factors play an important role in determining the spatial occurrence of local populations across the range. However, these factors might not apply the same amount of stress across different areas of the range (Louthan et al., 2015). A classic idea in the field is that biotic and abiotic factors are limiting at lower and higher latitudes respectively (MacArthur, 1972). Another characteristic of range boundaries is that some boundaries might be more stable (i.e. hard-boundaries like coastlines), while others could be more dynamic (i.e. soft boundaries, like the transition of a tropical forest into a tropical forested savanna) leading to boundary contractions and expansions along these edges (Mislan, 2016) driven by changes in climatic patterns, vegetation, ice cover or anthropogenic activities.

1.2.2 Location Within The Range

The internal structure of a range encompasses considerable variability in species abundance, population size, connectivity and gene flow. In general local abundances of species can vary a lot with some sites within their range having zero abundance. This pattern itself varies a lot between species with the fluctuations in abundance between sites differing between more common or rare species (Brown et al., 1996). This spatial heterogeneity is also usually assumed to be the most pronounced for vagile species (Pironon et al., 2017) at the centre of the species' range, where some sites with the highest concentrations of individuals coexist with sites characterized by the complete absence or scarcity of them (Brown et al., 1996). In contrast, towards the range boundaries, abundance is expected to maintain a consistent low level (Brown et al., 1996), population size and gene flow are expected to be small, and therefore have higher genetic differentiation among populations but lower genetic diversity within populations (Eckert et al., 2008). This is encompassed by an important long-lasting biogeographic hypothesis, the centre-periphery hypothesis.

The centre-periphery hypothesis predicts that the centre of a range holds the ideal conditions for a species to thrive, while these conditions fade towards the periphery (i.e. range edges) (Brown, 1984). Over the time, some studies have found support for the hypothesis while others have not (Sagarin and Gaines, 2002; Pironon et al., 2015, 2017). As it stands, the hypothesis seems not to generalise for every species range, and it fails to account for interactions between geographic, ecological, and historical gradients (Pironon et al., 2017). There are also biases in the classification of what is a real centre or periphery in a given spatial scale (Sagarin and Gaines, 2002; Pironon et al., 2017).

To avoid this problem in defining a single range "center" the distance to a range edge is an alternative metric to account for populations spatial location within the geographic range (Orme et al., 2019; Williams and Newbold, 2020b). This metric measures only the distance from the edge and does not need to explicitly differentiate between peripheral and central populations. Although there are arguments in regards to how accurate range limits can be, the use of distance

to a range edge works as a proxy for biotic and abiotic changes over ranges. It can also allow for the identification of "thresholds" or "turning points" at which other variables might be acting to affect species sensitivity (Orme et al., 2019).

1.2.3 Location In The Range And Sensitivity To Habitat change

If the location of populations within the geographic range is a driving factor in their ecology it makes sense that the sensitivity of populations to habitat change may depend on this factor. As discussed above populations close to their range edge are likely closer to the edge of their niche space, and thus experience more stressful non-optimal biotic and abiotic conditions (Brown et al., 1996). This can be attributed to several interconnected factors with examples including the decrease of climatic suitability towards the range edge (Williams and Newbold, 2020b), the lower ability to disperse in populations near the range edge due to a small number of populations nearby, which can reduce gene flow and potentially lead to smaller population sizes (Torrenta et al., 2022), and the different biotic interactions that populations may be exposed to across the geographic range. Indeed, a large body of research has demonstrated how species occupancy might change depending on where they are located within their geographic range (MacArthur, 1972; Graves, 1985; Thorpe, 1987; Brown et al., 1995; Gaston, 2009; Louthan et al., 2015; Oldfather et al., 2019).

This logic has been applied with success to explain variation in responses to habitat change. Several recent papers have used the metric of distance to a geographic range edge to explore this hypothesis showing how populations are most sensitive to local landscape disturbance at the edges of their geographic ranges (Anjos et al., 2010; Orme et al., 2019). Whilst these results suggest that location in the range may be useful in explaining this variation in sensitivity, questions still exist as to the importance of different types of habitat change and how we can measure these responses.

1.3 Thesis Outline

In **chapter 2** I investigate the effects of habitat fragmentation on species sensitivity modulated by distance to range edge and the amount of forest cover in the local landscape. Using presence-absence data for 362 species of birds from five fragmentation studies conducted in different regions of the Atlantic Forest of Brazil, I first test whether the effects of fragmentation on local bird occurrence change with distance to the geographic range edge and local habitat amount. I then use a metric based on the presence-absence model to obtain a measure of sensitivity to fragmentation to explore patterns of intraspecific species responses across the geographic range. This chapter was published in the journal Biological Conservation earlier this year, therefore it has been written in the third person as it was a collaborative effort of the authors involved.

In **chapter 3** I use two proxies of physiological stress (i.e. fluctuating asymmetry and ptilochronology) to assess the sensitivity of bird populations to habitat loss and how this varies across their geographic range. Using three Bayesian mixed effect models I investigate how local forest cover and spatial position in the geographic range influence bird museum specimens' wings, tarsi and tail phenotype via physiological stress in Brazil. The previously discussed variation in intra- and interspecific response to habitat change across the species geographic range suggests that populations at the range edge should exhibit relatively higher stress responses to disturbances (i.e. habitat loss) and that there should be a positive interaction between the two (i.e. the most stressed are those at the edge with high habitat loss). Therefore I hypothesise that reduced local forest cover and decrease in distance to the range edge cause higher variance in fluctuating asymmetry in tarsus and wings and shorter growth bars in tail feathers.

In **chapter 4** I explore the possibility that changes in species morphological traits across their geographic range influence sensitivity to local habitat loss. I first look at general patterns of change in trait size within species by modelling both the mean and the variance in body mass, wing length, tarsus length and bill length in bird species in Brazil. I then compare this to the estimates of sensitivity of species occupancy found in **chapter 2** to determine if changes in traits are related to population level responses. I expect that mean and variation in trait size

252 are affected by lower suitable conditions near the range edge and that this is mediated by the
253 amount of forest cover in the local landscape.

254 Finally, in **chapter 5** I go on to link these results together and discuss how they improve our
255 understanding of the effects of position within the distribution range on species' populations
256 and the role of forest cover in mediating this process.

Chapter 2

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

2.1 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.

2.2 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 (Sala et al., 2000; MEA et al., 2005), continue to increase with the current rising deforestation rates (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., 2018b,a; 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., 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., 2018b,a; Püttker et al., 2020). The fragmentation debate continues to this day, with one side arguing that fragmentation has overwhelmingly positive effects on species (Fahrig, 2019; Arroyo-Rodríguez et al., 2020; Riva and Fahrig, 2023), and the other arguing the effects are mostly negative (Fletcher et al., 2018b,a; 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 A.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.

2.3 Methods

2.3.1 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 km2 before European settlement (Metzger, 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 and 50 % within 100 m of a forest edge (Atlantica, 2020).

2.3.2 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 (Figure 2.1)

conducted between 1997 and 2017 in the Brazilian Atlantic Forest (Table A.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 A.3) across 134 sites was recorded (for more details on the data collection of each dataset, please see Develey and Motta Júnior (2004); Anjos et al. (2010); Uezu and Metzger (2011); Morante-Filho et al. (2015); Hatfield et al. (2020)).

2.3.3 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 A.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, [n. d.]) was used for all

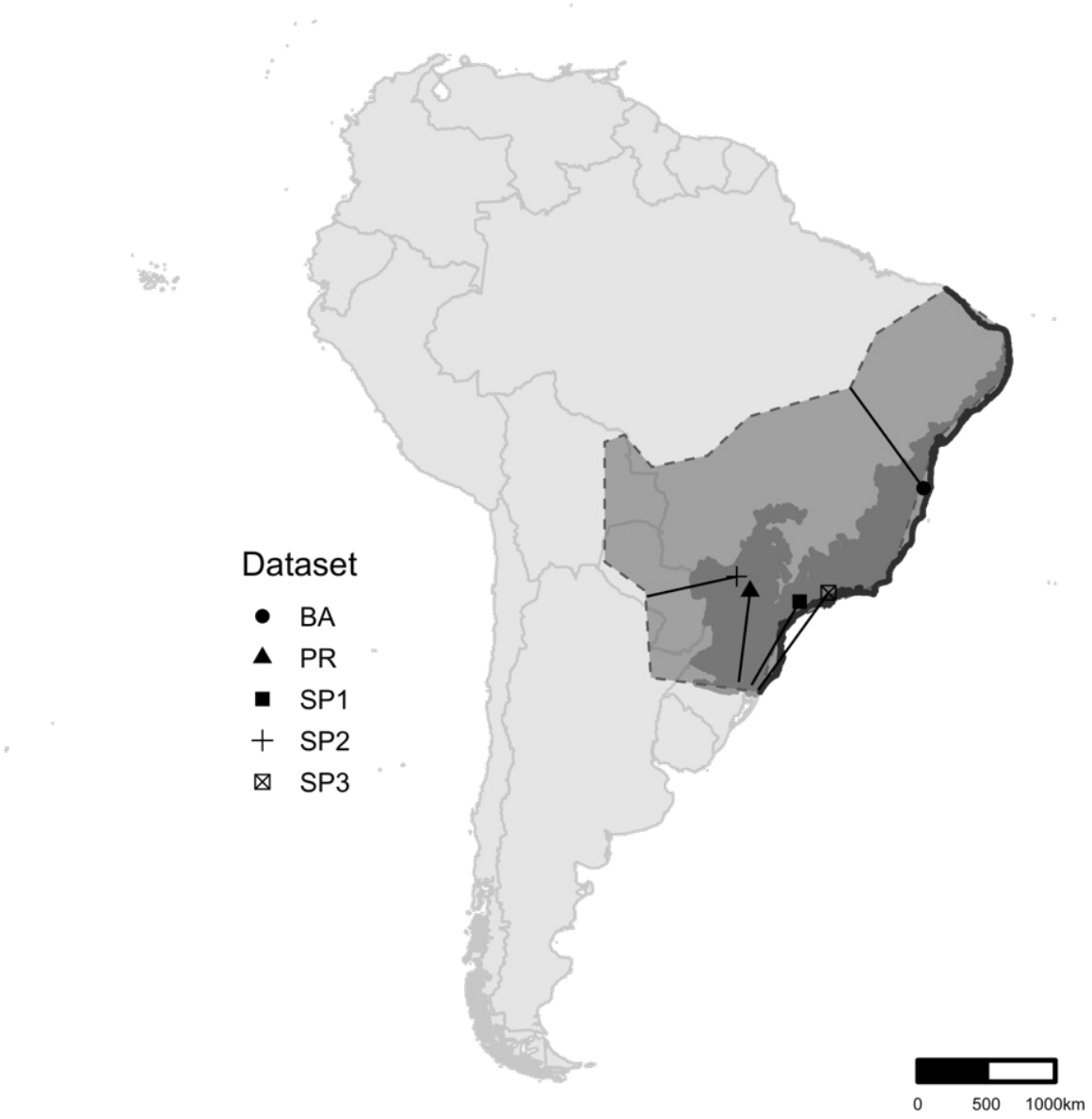


Figure 2.1: Example of distances measured to the nearest continental edge of a hypothetical species' geographic range. The points on the map show the location of each of the five datasets, and the lines connected to them show each respective distance to the nearest continental range edge (dashed line), 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 (figure extracted from Bellotto-Trigo et al. (2023)).

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.

2.3.4 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; International (2020)). The distances to the range edge were measured to the nearest continental edge of each species' range (Figure 2.1), 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 Figure 2.1), 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.

2.3.5 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 (Lüdecke 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:

$$Occurrence = DE + FR + FC +$$

$$DE : FR + DE : FC + FR : FC + DE : FR : FC$$

$$+(FR + FC + FR : FC|D)$$

$$+(DE + FR + FC + DE : FR + DE : FC + FR : FC + DE : FR : FC|S)$$

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 nAGQ = 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 A.6 and table A.7).

We also calculated a metric, ΔFR, based on the parameter estimates of the binomial mixed effects model described above (see full derivation formula in Section A.3). 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:

$$\Delta_{FR} = \frac{dI}{dX_{FR}} = \beta_{FR} + \beta_{DE:FR}X_{DE} + \beta_{FC:FR}X_{FC} + \beta_{DE:FR:FC}X_{DE}X_{FC} \quad (2.1)$$

where β and x are the coefficients and predictor variables indicated by the subscript respectively.

The ΔFR 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 ΔFR >0 indicate that fragmentation has a positive effect on species occurrence and values of ΔFR <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 ΔFR 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.

2.4 Results

2.4.1 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 **Chapter A**, Figure A.10 and Table A.5 for results on number of patches), distance to range edge, forest cover, and all their interactions were significant ($p < 0.05$; Table A.4) except the interaction between fragmentation and forest cover ($p = 0.250$) (Figure 2.2, Figure A.4 and Table A.4).

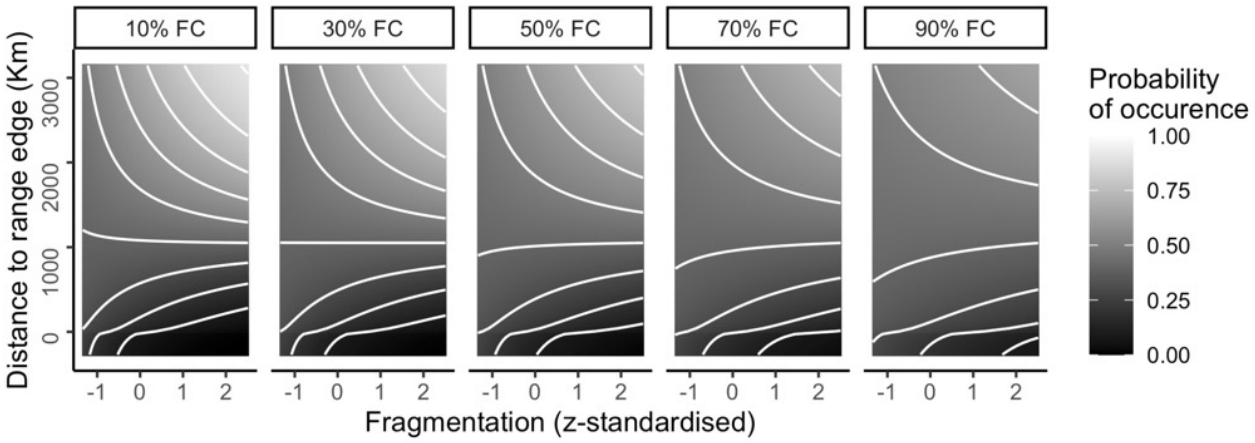


Figure 2.2: Probability of occurrence for the average intraspecific response as a function of distance to range edge (y-axis), forest edge density (x-axis) and forest cover (FC, different panels). Average probability of occurrence is represented by the change in shading from low occurrence (black) to 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(figure extracted from Bellotto-Trigo et al. (2023)).

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 (β_{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 $DE = 0$, β_{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 interaction term $\beta_{FC:FR}$; fig. 2.2) 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. 2.2).

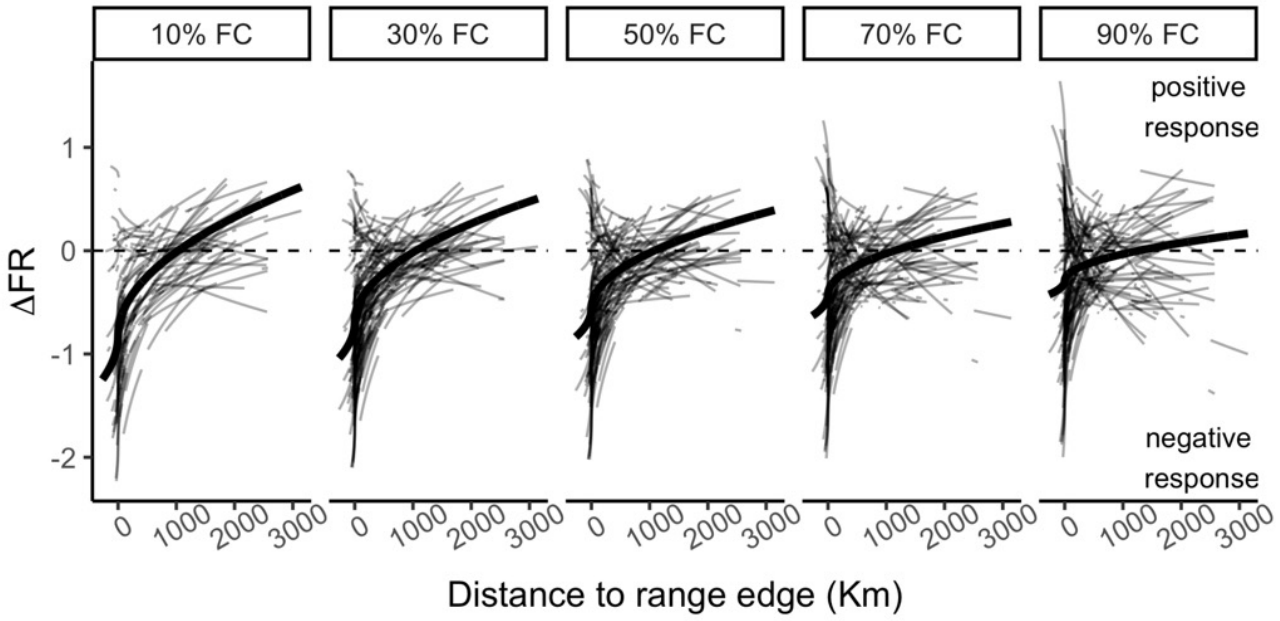


Figure 2.3: Change in species' responses to fragmentation is mediated by distance to range edge and forest cover. Thick black lines show how the average across-species response to fragmentation (y axis) changes with distance to the range edge (x axis) at each forest cover (panels 10 %, 30 %, 50 %, 70 % 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 (ΔFR > 0) to negative (ΔFR < 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)(figure extracted from Bellotto-Trigo et al. (2023)).

2.4.2 Variation In Intraspecific Responses To Fragmentation

The Δ_{FR} metric shows how responses to fragmentation both across and within species vary depending on forest cover and distance to range edge (fig. 2.3). Looking at the average intraspecific response (thick line, fig. 2.3), the metric mirrors the results showing in (fig. 2.2). Δ_{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. 2.3). The critical distance at which the effects of fragmentation change in sign from negative to positive was estimated as $\tilde{1}$080 km (1028–1266 km, depending on the local forest cover, Figure 2.3).

The species-specific ΔFR estimates obtained from the random effects (thin lines, Figure 2.3) 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.

2.5 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 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 (fig. 2.2, fig. 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., 2008), 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 (fig. 2.2, fig. 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 (Parra-Sanches, 2020; Arce-Peña et al., 2022). 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 (fig. 2.2, fig. 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 intraspecific 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, 2010), source-sink dynamics across ranges (Torrenta et al., 2022), climatic and/or habitat suitability (Williams and Newbold, 2020a), 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

588 composition of communities across a biome, and especially whether populations are far or close
589 from the range edges of their constituent species, to implement conservation and management
590 activities.

Chapter 3

Distance to range edge, ptilochronology and fluctuating asymmetry

3.1 Abstract

Anthropogenic habitat change is causing extinctions across the natural world and is a well-known driver of bird species decline. Birds in more deforested areas experience higher stress due to increases in costs of locomotion, decreases in food supply and increases in relative competition for resources. Being able to monitor this stress is important as it lets identify populations most at risk. Identifying phenotypic responses to stress have been suggested as one way to do this, reflecting the stress induced instability of development. Here I use three Bayesian mixed effect models to investigate how local forest cover and spatial position in the geographic range influence museum specimens' wings (n=295), tarsi (n=275) and tail (n=211) phenotype via two proxies of physiological stress, of 20 bird species in Brazil. I hypothesise that reduced local forest cover and decrease in distance to the range edge cause higher variance in fluctuating asymmetry in tarsus and wings and shorter growth bars (i.e. lower growth rates) in tail feathers. I found no significant associations between local forest cover and distance to range edge with any of the stress metrics, although trends follow the expected outcome in terms of direction. The lack of trends suggests these methods may not be suitable for assessment of

609 populations status though additional work is required to make a comprehensive assessment.

3.2 Introduction

Over the past 500 years, 161 bird species have been confirmed extinct and another 22 possibly extinct by the IUCN red list (IUCN, 2020). The hazards propelling bird's extinction rates are diverse but often attributable to human activity. For instance, agriculture, livestock farming, urbanisation and the excessive use of natural resources all drive species declines (International, 2020). Whilst it is important that we identify how populations are under threat from these drivers, it is often not easy. Species vary greatly in their responses to these processes and multiple drivers will often interact to amplify or dampen their effects (Pirotta et al., 2022; Turschwell et al., 2022). It is therefore important that we find ways to identify signs of these impacts on species populations early on so that mitigation action can be established allowing populations to recover (Clarke and Ng, 1995) before they go locally extinct.

One potential tool to assess the status of populations is individual level stress (Leary and Allendorf, 1989). Stress responses refer to the responses of individuals to adverse external conditions which can be both biotic and abiotic in nature (Fujita et al., 2006; Busch et al., 2011). Examples of potential stressors include the presence of predators, poor climatic conditions or the presence of pollutants in the environment (Busch et al., 2011; Coster et al., 2013; Shadrina et al., 2023). It follows that species under threat from anthropogenic disturbances will likely exhibit these stress responses, which may then be a powerful tool to assess population threat status (Lens and Eggermont, 2008; Shadrina et al., 2023).

One common outcome of stress is developmental instability reflected in individual phenotypes (Clarke and Ng, 1995; Clarke, 1998). In birds there are two proxies for stress that can easily be measured by examining phenotype, fluctuating asymmetry and ptilochronology (Anciães and Marini, 2000; Lens and Eggermont, 2008). These measure the differences in traits' symmetry and nutrient intake, respectively (see below). Apart from being easy to observe, these metrics are also low-cost and non-lethal ways to assess stress level of an individual (Lens and Eggermont, 2008) and may therefore provide convenient tools to measure the level of stress across populations.

Fluctuating asymmetry (FA) is the difference in size and shape of bilateral traits (e.g., left and right wings) that arise due to stressful conditions during development (Valen, 1962). Symmetrical bilateral traits are assumed to be optimal morphology for any bilateral organism during development (Polak and Trivers, 1994), as the inability to develop symmetrical traits can cause higher expenditure of energy when trying to compensate for differences between sides (e.g., different wing lengths have higher energy cost during flight - Polak and Trivers (1994)). In fact, many studies show correlations between an increase in FA and environmental stress across diverse groups of vertebrates and invertebrates (Parsons, 1990, 1992; Polak and Trivers, 1994; Lens et al., 1999; Lens and Eggermont, 2008; Maestri et al., 2015; Ivanković Tatalović et al., 2020; Shadrina et al., 2023).

Ptilochronology is the study of feather growth bars (FGB) which can be used to identify the nutritional status of an individual bird (Grubb, 2006). Growth bars can be observed on tail or wing feathers, as alternating light and dark bands. Previous research has shown that one pair of growth bar corresponds to a 24-hour period, where dark bands are formed during the morning and light bands at night (Wood, 1950). These bars are believed to be created by the deposition of nutrients, with longer bars reflecting higher nutrient intake and shorter bars the opposite. Due to the moulting nature of birds, growth bars can inform an individual's intake within the last 6 months or so. Individuals under stressful low nutrient conditions will therefore be expected to have relatively shorter bars (Grubb, 2006).

In this chapter I use these two proxies of physiological stress (i.e. fluctuating asymmetry and ptilochronology) to assess the sensitivity of bird populations to habitat loss and how this varies across their geographic range. Habitat change is a well-known driver of bird species decline (MEA et al., 2005), and birds in more deforested areas are expected to experience increased stress due to increases in costs of locomotion, decreases in food supply and increases in relative competition for resources (Hatfield et al., 2018b; Bennett et al., 2018; Monge et al., 2023). At the same time, the sensitivity of populations to habitat loss is not equal across populations and may be influenced by the position in the geographic range (Orme et al., 2019). Other studies have shown how populations near the edge at high habitat loss are more sensitive to disturbances like habitat fragmentation as they tend to occur only where fragmentation is low

(Bellotto-Trigo et al., 2023). This suggests that populations at the range edge should exhibit relatively higher stress responses to disturbances and that there should be a positive interaction between the two (i.e. the most stressed are those at the edge with high habitat loss). Here I use three Bayesian mixed effect models to investigate how local forest cover and spatial position in the geographic range influence museum specimens' wings (n=295), tarsi (n=275) and tail (n=211) phenotype via physiological stress, of 20 bird species in Brazil. I hypothesise that reduced local forest cover and decrease in distance to the range edge cause higher variance in fluctuating asymmetry in tarsus and wings and shorter growth bars in tail feathers.

3.3 Methods

All data manipulation and analyses were conducted in R (R Core Team 4.3.0, 2023), using packages *tidyverse* (Wickham, 2021), *janitor* (Firke, 2023) and *broom* (Robinson et al., 2023) for a tidy workflow; packages *sf* (Pebesma et al., 2021), *terra* (Hijmans et al., 2023) and *landscapemetrics* (Hesselbarth et al., 2021) for spatial analysis; package *brms* (Bürkner, 2021) for bayesian statistical analysis; packages *ggplot2* (Wickham, 2016), *egg* (Auguie, 2019) and *tmap* (Tennekes, 2018) for data visualization. All spatial calculations were made using maps reprojected from the World Geodetic System 1984 (https://epsg.io/4326, [n. d.]) into the South America Albers Equal Area Conic projection (https://epsg.io/102033, [n. d.]).

3.3.1 Species Data

To select the species used in this study, I chose 24 species of Atlantic Forest birds, which have been shown in previous research to have varying sensitivity to habitat loss with increasing distance to the range edge (Orme et al., 2019).

I measured 480 bird skins from the 24 bird species (see table B.1) from the Ornithology Collection at the Museu de Zoologia da Universidade de Sao Paulo (MZUSP), Brazil. These specimens were collected from 217 distinct locations in Brazil between 1940-2017. Relevant

information on the specimens' tag was documented, which included the museum identification number, species, subspecies, sex (when known), location, GPS location (when known) and date. Specimens missing information on date or location were not measured.

3.3.2 Fluctuating Asymmetry (FA)

To quantify fluctuating asymmetry, I used a 150mm digital slide calliper with 0.1 mm precision to measure the left and right tarsus, and the left and right wings of each bird. Each specimen tarsus and wing were measured three times, alternating left and right to reduce measurement bias, the final measurement being the average of these. For species whose wings were longer than 150mm, a standard 300mm steel ruler was used with 0.1 mm precision.

Tarsus measurements were taken as described by Lens et al. (1999) from the back notch of the intertarsal joint to the corner formed between the tarsus and the toes, when toes were bent to a 90° angle. Some museum specimens were not stuffed with their toes bent to a 90° angle; therefore, these specimens were measured from the back notch of the intertarsal joint to the lowest margin of the last complete scale before the toes diverge (Figure 3.2A). Wing measurements were taken from the wrist joint to the tip of the longest primary feather of a wing in a closed position (Figure 3.2A).

Using these measurements, I calculated FA by taking the difference in left and right measurements $\text{FA} = T_l - T_r$. This metric has a value of 0 when there is no fluctuating asymmetry with negative or positive values indicating a bias towards larger right and left traits, respectively. The degree of fluctuating asymmetry across multiple individuals is therefore measured by the variance in this metric, with the average tending to equal 0 as long as there is no bias in the directionality of asymmetry (i.e. the left or right side should not be systematically larger, as is expected for bird tarsi and wings here).

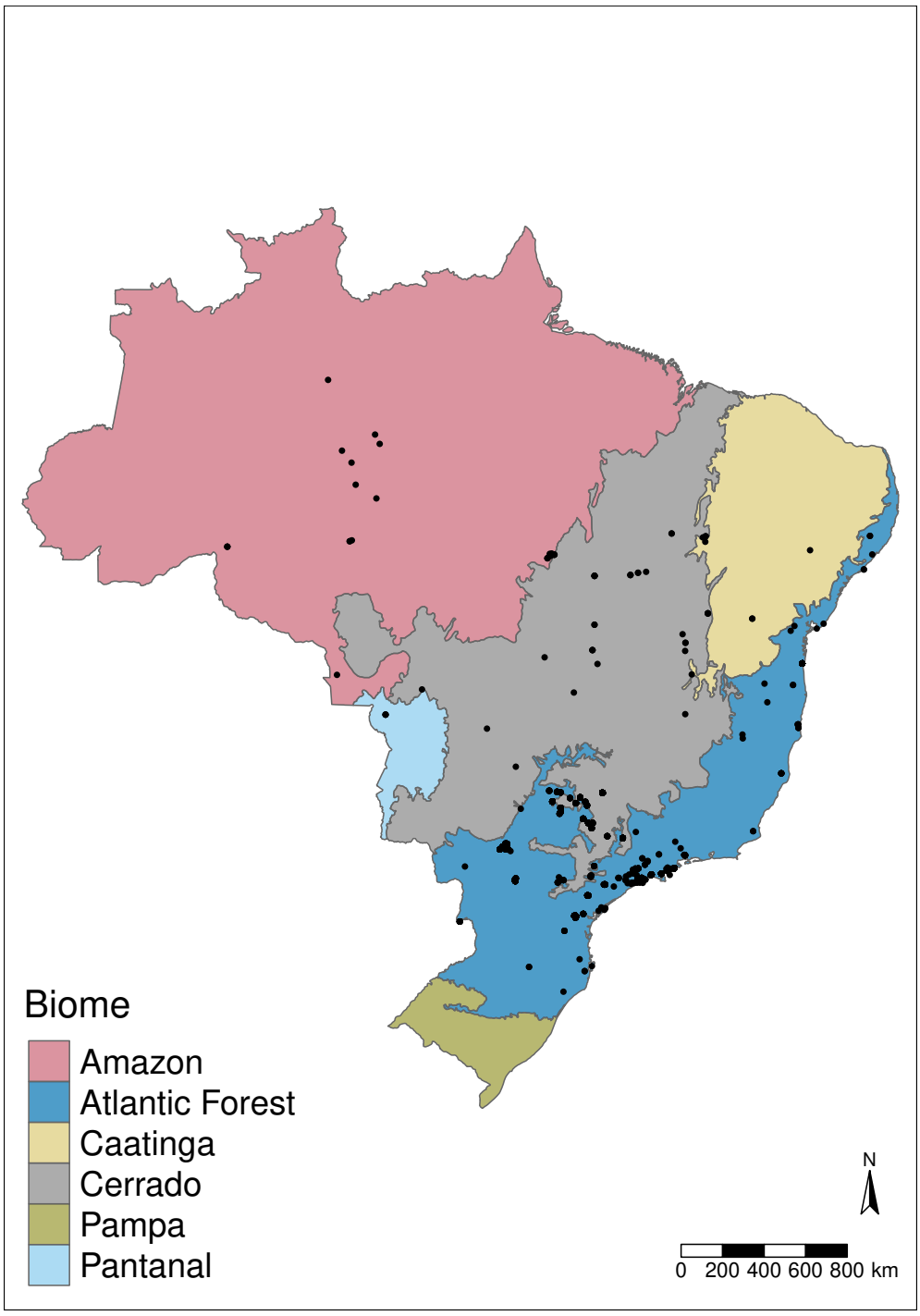


Figure 3.1: Sampling locations of data analysed. Each colour represents a Brazilian Biome and each black dot represents one specimen from which a trait measurement was taken (n=295).

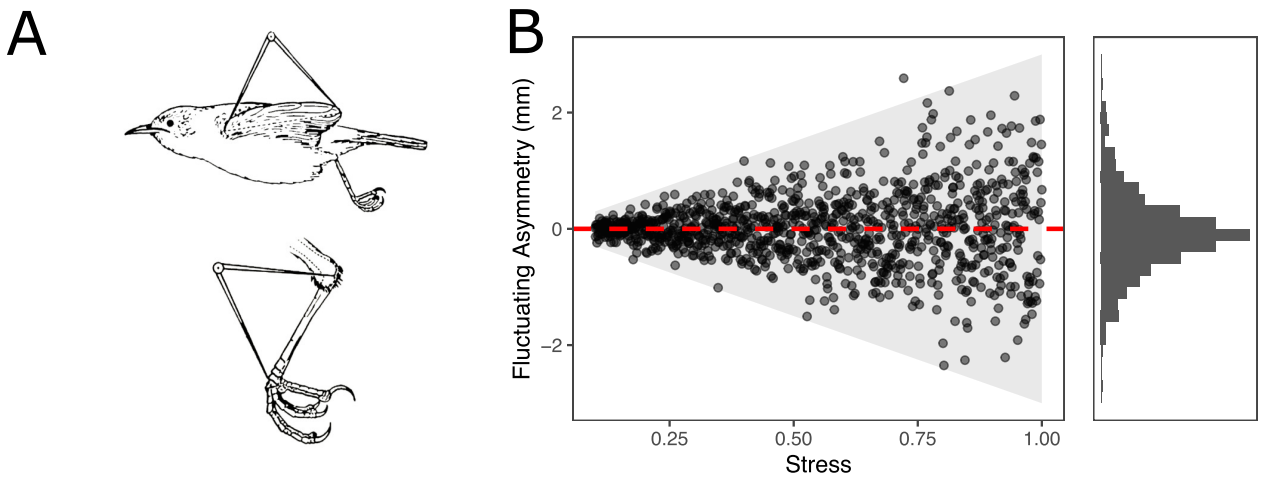


Figure 3.2: Fluctuating asymmetry (FA) as a metric of stress. Panel A shows examples of measurement of wing (above) and tarsus (below). Wing measurements were taken from the wrist joint to the tip of the longest primary feather of a wing in a closed position. Tarsus measurements were taken from the back notch of the intertarsal joint to the corner formed between the tarsus and the toes, when toes were bent to a 90° angle. This figure was extracted and modified from Baldwin et al. (1931). Panel B shows the expected pattern of FA for a trait with increasing stress along the x-axis. The plot shows how whilst the average FA value remains at zero (red line) the variance increases with stress.

3.3.3 Feather Growth Bars (FGB)

To measure FBG, I took pictures of each specimen's outermost right tail feather from a distance of 20cm. When this feather was damaged or bars were not visible, the next feather to the right was photographed. Wing feathers were not used because stuffed birds have rigid wings that cannot be opened. A light source was positioned at a 0° or 45° angle.

Growth bar length was measured from the pictures using the TPSdig software, where length is the distance from the beginning of a dark band to the end of its adjacent light band (Figure B.1). Growth bars which could not be clearly seen were not measured. Out of the 23 original species, only 20 were used due to the unsuitability of pictures to measure ptilochronology. As FGB measurements quantify the growth and thus nutritional intake of birds, larger values indicate low stress due to better conditions.

3.3.4 Distance To Range Edge

Out of the 480 specimens sampled, 222 had spatial coordinates already documented on their museum tags. I obtained the spatial coordinates by feeding detailed descriptions present in their museum tags (e.g., Km 114 Rod. Regis Bittencourt, São Paulo, Brazil) to the function *geocode_OSM* from the package *tmap* to obtain estimates for remaining 258 specimens. I then manually verified all points were within the study area.

I measured the distance of each specimen to the nearest continental edge of their respective species' range 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), Banks-Leite et al. (2022) and Granville (2023) for more details).

3.3.5 Forest Cover

I calculated summary statistics for forest cover for each specimen from 30-metre resolution 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 me to choose one map per biome (Amazonia, Caatinga, Cerrado, Mata Atlantica e Pantanal) per year in which the specimen was collected. The definition of forested areas used to measure forest cover was based on category 3 ("Natural Forest Formation") of MapBiomas, and all other categories were classified as "matrix". For each specimen, I calculated forest cover within buffers varying from 100 m to 1000 m at 100 m increments around each location to check for scale of effect.

3.3.6 Statistical analyses

After the data processing, there were a total of 211 individuals from 17 species with FGB data, 275 individuals from 20 species with tarsus FA data and 295 individuals from 20 species with wing FA data (**??**). I fit three separate Bayesian mixed-effect models to quantify the effects of

forest cover (FC) and distance to range edge (DE) on FA in the wing and tarsus and on the FGB. In all models, I investigate the response of both the mean and variance of the traits to the predictor variables. For FA, this is important as high fluctuating asymmetry is indicated by increased variance in trait asymmetry, not in changes in the mean (which are expected to be zero) fig. 3.2. For FGB, I expect to see shorter growth bars with higher variance in stressful conditions. The models also include a random effect for the slopes and interactions between forest cover and distance to range edge to account for interspecific difference in responses. The model for each trait can be written in the *brms* package syntax as:

$$metric \sim FC * DE + (FC * DE|SP) \tag{3.1}$$

$$\sigma \sim FC * DE + (FC * DE|SP) \tag{3.2}$$

I ran one model per buffer radius varying from 100 to 1000 metres at 100 metres increments to investigate scale of effect.

3.4 Results

The results are presented at the 600 metres buffer, as the model coefficients for both FA and FGB did not change qualitatively between them (see fig. B.2 and fig. B.3). In addition, the 600 metres buffer has been used by other studies conducted with the species used here Lindell et al. (2007); Morante-Filho et al. (2015); Orme et al. (2019); Bellotto-Trigo et al. (2023) and has been chosen because it is a good fit for species with restricted movement Hatfield et al. (2018a).

There was no meaningful response of wing and tarsus FA and FGB to changes in the local forest cover or distance to the range edge. For all model estimates, none fell within the 89% Credible Interval indicating uncertainty in the model fits (see **chapter B**, table B.2 for population-level model coefficients and table B.3 for group-level coefficients).

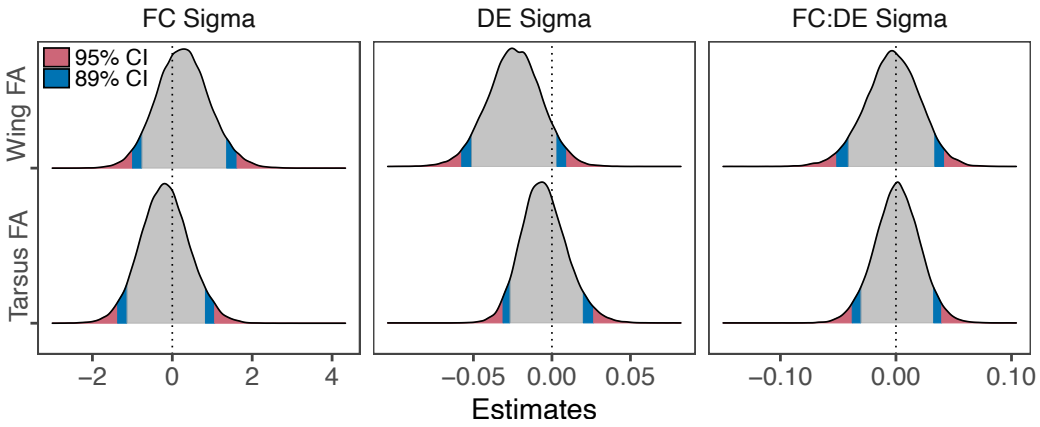


Figure 3.3: Distribution of model estimates for the variance fluctuating asymmetry (wing and tarsus) values. The distributions represents the 2500 posterior draws, which show no responses with respect to forest cover, distance to range edge and the interaction between forest cover and distance to range edge. The distance to range edge panel for wing shows nearly a trend, where the probability of direction of variance in fluctuating asymmetry decreasing with increasing distance to range edge to be 92.13%. The dotted line at zero overlapping the grey area shows the theoretical area of no effect. If the line overlaps the blue area, then the estimated effect falls within the 89% Credible Interval (CI), similarly, if the line overlaps the red area the estimated effect falls within the 95% CI. The first panel shows the coefficient distribution for forest cover proportion (FC), the second panel shows the distribution for distance to range edge (DE), the third panel shows the distribution of coefficients for the interaction of forest cover proportion and distance to range edge (FC:DE), for the variance model (Sigma)

Although no response was above the 89% or 95% CI thresholds, there are a few trends worth noting. For fluctuating asymmetry, the variance model (sigma) for both wing and tarsus were estimated to have very little dependence on forest cover fig. 3.3. For distance to range edge, the variance model (sigma) showed a slight negative relationship as expected with wing (est = -0.02, pd = 92.13%) being stronger than tarsus (-0.0001, pd = 65.39%). The interaction terms were similarly estimated to be almost exactly 0. Although the estimates for the mean were also not above the 89% or 95% CI thresholds, there was a slight positive trend of forest cover for wing (0.41, pd = 77.76%) and tarsus (0.31, pd = 79.38%) and distance to range edge for tarsus (0.01, pd = 90.24%) and a negative interaction for wing (-0.01, pd = 65.14%) and tarsus (-0.01, pd = 69.08%).

For the feather growth bars, forest cover again had little effect whilst distance to range edge has a (slight) positive effect (est = 0.16, pd = 64.92%) fig. 3.5. The interaction between the two was slightly negative (est = -0.21, pd = 84.77%). Though they show high uncertainty, these trends are consistent with the idea that stress is highest at the range edge and at low

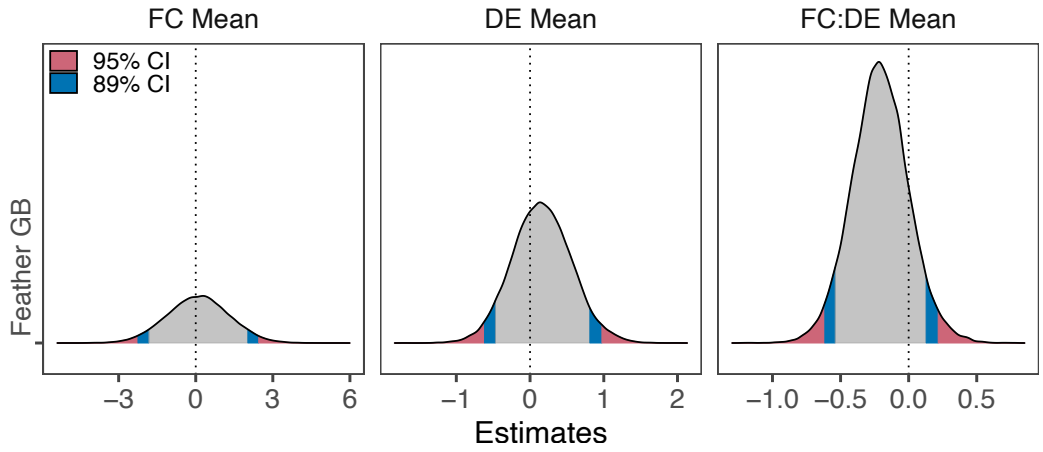


Figure 3.4: Distribution of model estimates for the feather growth bar values. The distributions represents the 2500 posterior draws, which show no responses with respect to forest cover, distance to range edge and the interaction between forest cover and distance to range edge. The interaction between forest cover and distance to range edge panel shows nearly a trend, where the probability of direction of mean feather growth bar decreases with decreasing distance to range and lower forest cover to be 84.77%. The dotted line at zero overlapping the grey area shows the theoretical area of no effect. If the line overlaps the blue area, then the estimated effect falls within the 89% Credible Interval (CI), similarly, if the line overlaps the red area the estimated effect falls within the 95% CI. The first panel shows the coefficient distribution for forest cover proportion (FC), the second panel shows the distribution for distance to range edge (DE), the third panel shows the distribution of coefficients for the interaction of forest cover proportion and distance to range edge (FC:DE), for the mean model (Mean)

783 forest cover. The variance in feather growth bars was estimated to be almost zero for all model

784 predictors.

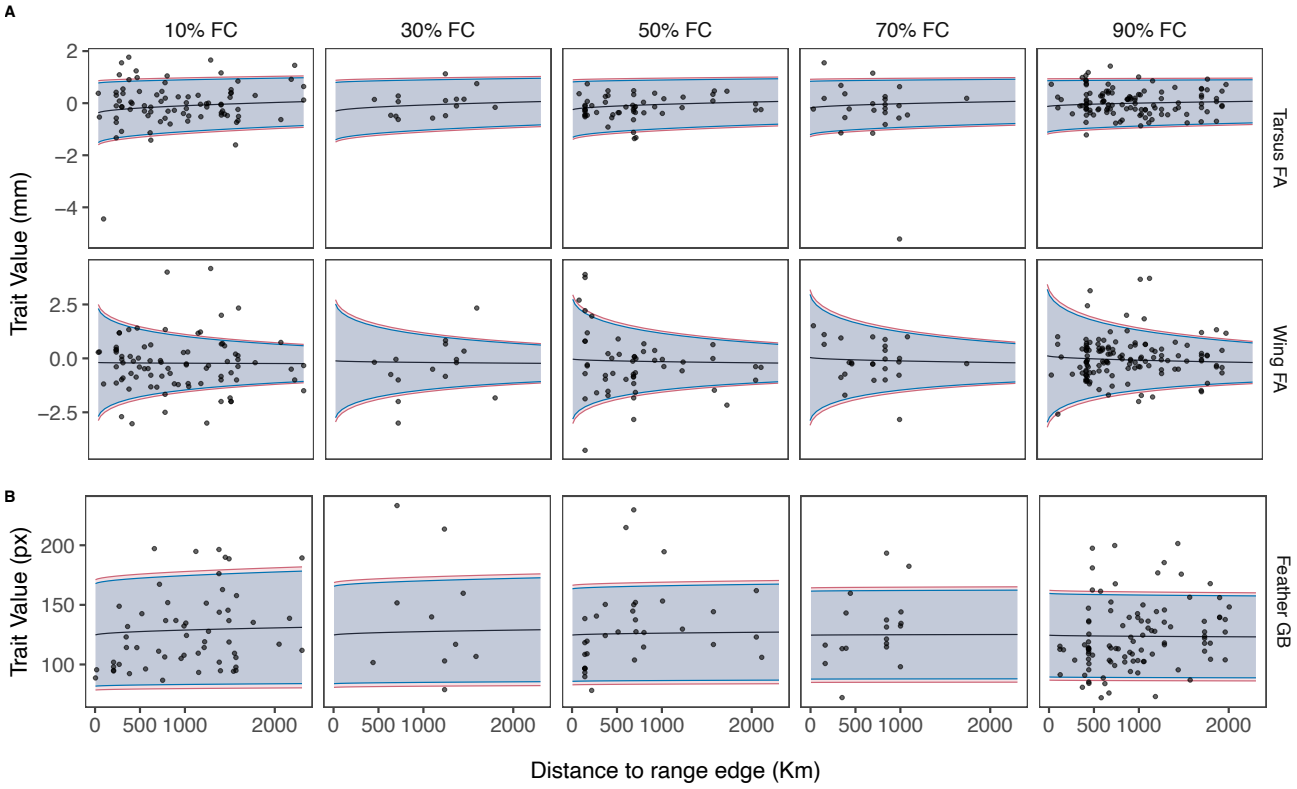


Figure 3.5: Model predictions of mean and variance of trait asymmetry (Wing FA and Tarsus FA) and feather grow (Feather GB) across different percentages of local forest cover (10% to 90% FC) and distances to the range edge (0 to 3500 Km). The black line represents the predicted mean response in trait size from Equation (4.1), while the shaded area shows the predicted variance in trait size from Equation (4.2), with blue and red representing the 89% and 95% Credible Intervals respectively.

3.5 Discussion

Previous research has shown that areas further from the centre of a species distribution present lower population occupancy (Pironon et al., 2017), possibly due to less suitable conditions. Here I explored if this pattern is reflected in individual stress levels using two metrics previously used in birds: fluctuating asymmetry (FA) and ptilochronology (FGB) (Carbonell and Tellería, 1999; Lens and Eggermont, 2008). In general, I was unable to detect an effect of either geographic position or local forest cover on these stress metrics.

There are several explanations for the results I observe here, the first being that the two metrics (FA and FGB) are good proxies for stress but are not affected by forest cover or distance to range edge. Although several previous studies looking at levels of asymmetry across populations has found expected responses to biotic and abiotic stressors (i.e. increasing stress leads to greater asymmetry) (Leary and Allendorf, 1989; Kieser and Groeneveld, 1991; Murphy and Lovett-Doust, 2004; Turmukhametova, 2020; Shadrina et al., 2023) this is not always the case. Indeed, some other studies have also not found effects of forest cover or distance to range edge on FA (Gavrikov et al., 2023) or feather growth bars (Gebremichael et al., 2019). Carbonell and Tellería (1999) did not find differences in either FA or FGB between adult populations of Iberian Blackcaps near or far from their range edge. Similarly, Gebremichael et al. (2019) found no response of FA and FGB when looking at habitat type of bird populations in natural forests and coffee plantations/matrix. Furthermore, a review by Bjorksten et al. (2000) shows that of all studies investigating changes in FA and stress assessed by them, one third found positive relationships, one third found only partial relationships (i.e. specific traits exhibited increasing FA) and the final third showed no response at all. Given this previous work, it may be possible that FA and FGB are unrelated to the stressors I examine here, though further work with larger sample size is needed to test these ideas and identify if general patterns do exist.

Secondly, another possible explanation might be that the metrics themselves are not good indicators of stress. Some experiments show that FA does not arise when we subject individuals to supposedly stressful conditions (Swaddle and Witter, 1994; Kellner and Alford, 2003; Gupta

et al., 2016). This casts doubt on the suitability of FA as an indicator. The tendency of only specific traits to display FA has also been discussed in the literature. For example (Aparicio and Bonal, 2002) tested the idea that the degree of FA exhibited is related to their developmental complexity. That is, complex traits made of many structural units (e.g. a feather) should show lower FA than relatively simpler ones (e.g. a barb) as they have more scope to correct for any developmental instability (Aparicio, 2001). The authors find that asymmetry in bird tail feathers supports this idea. This is a potential explanation for my results, as wing and tarsus are more complex traits which may be able to correct any asymmetry that arises during development.

Whilst to my knowledge FGBs are considered a good indicator of individual growth rate and condition, the lack of clear results may have arisen from other factors determining allocation of resources for feather growth. Terrill (2018) shows that feather growth rate increases with latitude. Likewise, Horák et al. (2022) recently found that feathers tended to grow slower in tropical populations when compared to those in temperate regions of the same species. The authors of these papers suggest these reflect a trade-off in allocation to feather growth versus survival. In tropical regions, the need for rapid feather growth is relatively low due to weak seasonality when compared to temperate regions, where resources are abundant for only short time periods. As the species I focus on here are all tropical, it could be that they have adapted to have constant low allocation to feather growth which is relatively insensitive to stressors such as land use change. This of course would require extensive testing to determine and it is very difficult to test such ideas with observational approaches alone.

Finally, there could be an effect of distance to range edge and forest cover on the FA and FGB metrics but I fail to detect them in my data set. Previous studies have discussed the complexity of measuring fluctuating asymmetry (Lens et al., 2002). Although the conceptual basis and physical measurement of FA are relatively simple it is difficult to test statistically due to the inherently low sample sizes involved. This arises because individual-level FA is effectively an attempt to estimate variance from two data points (i.e. left and right), which causes inherently high sampling variation. That means that detection is always difficult even if stress affects the developmental stability of these traits. Dongen (2007) develop an alternative hierarchical latent

variable Bayesian model which can account for this uncertainty but requires large amounts of data to be used. Unfortunately, the sample size I have here prevents the use of this approach. The fact that my results for FGB are in slightly better agreement with the predictions supports this idea and indicates that FGB may be an easier metric to work with.

In conclusion, my results indicate either that the populations here do not experience greater "stress" near the range edge or at lower forest cover or that FA and FGB are not particularly effective indicators of environmental stress. Although FA and FGB have been found significant as proxies of stress in previous studies, no parameters I measured were responsible for the variation in my analysis. Furthermore, the small sample size might have played a big role on the responses I found. Therefore I caution the use of the results presented here as ground truth to distance to range edge and forest cover not causing stress in populations under unsuitable conditions. I strongly suggest however, to use these results as a starting point (i.e. pilot study) to further data collection and analysis of these proxies/ Future work should aim to use more sophisticated approaches for the analysis of FA (Dongen, 2007) to investigate the effects of stress on populations at varying forest cover proportions and spatial locations within a geographic range.

Chapter 4

Distance to range edge and morphological traits

4.1 Abstract

Species responses to habitat change are context dependent and can be explained by processes occurring at macroecological scales. Within the same species populations are affected by disturbances unequally with some being more sensitive than others. It is not known if and how species traits vary over there gradients and if they could be related to the responses of population performance. Here, I used a linear Bayesian mixed effect model to explore how distance to range edge and forest habitat amount affect mean and variance in trait size (wing, tarsus and bill length and body mass) of 354 species of birds in the Atlantic Forest of Brazil. I show that traits show little general trend and that most patterns of variaion are at the species level. I then compare these species specific estimates of trait change to estimates of population occupancy showing that the two are not related and species that tend to demonstrate similar changes in traits do not also show similar changes in occupancy. My results indicate that at least in tropical birds, variation in traits between populations are not driving the altered sensitivity at the population level. This implies that other factors, such as changes in strength of competition or sub-optimal environmental conditions are responsible for variation in population responses.

4.2 Introduction

Habitat change is one of the largest causes of biodiversity loss (MEA et al., 2005). It acts both by directly affecting species populations and by altering their sensitivity to other drivers (Banks-Leite et al., 2012; Orme et al., 2019), potentially causing local extinctions (Castelletta et al., 2000; Ribon et al., 2003; Haddad et al., 2015). The responses of species to habitat change are not constant across populations and can be explained by processes occurring at macro-ecological scales (Banks-Leite et al., 2022). Previous research and the first chapter of this thesis has shown that populations within the same species can present variable responses to habitat change depending on their location on the species geographic range (Orme et al., 2019; Bellotto-Trigo et al., 2023). This variation in sensitivity may be due to several mechanisms including climatic suitability, evolutionary history, dispersal patterns and biotic interactions (Williams and Newbold, 2020b; Howes et al., 2023; Hatfield et al., 2023).

One potentially important factor in meditating species sensitivity to habitat change is variation in morphological traits. There is a large body of literature studying species-level differences in morphological traits' and how they determine interspecific variation in responses to habitat change. For example, Bregman et al. (2016) demonstrated that the trait composition of frugivorous and insectivorous bird communities was reduced in areas with intense antropogenic land-use, leading to bird communities occupying a distinct region within the trait space. Many studies have used traits to explain variation in responses to habitat change, ranging from a limited set (i.e. focus on body size and/or beak size) to a broader array of traits and single to multiple taxa (Renjifo, 1999; Castelletta et al., 2000; Sodhi et al., 2004; Edwards et al., 2013; Senior et al., 2013; Bregman et al., 2016; Baldwin et al., 2023). The importance of trait differences is explained by their role in determining the ecological niche that individuals occupy and in birds they have been linked to locomotion, flight performance, diet and nesting success (Lack, 1947; Hutchinson and MacArthur, 1959; Norberg, 1979; Leisler et al., 1989; Claramunt et al., 2011).

Though these trait-based approaches have provided insight into interspecific variation in species'

responses, the species-averaged traits they rely on have been criticised. Hatfield et al. (2018c) found that species-averaged traits could not consistently predict species sensitivity to habitat change across datasets despite models fitted to individual studies finding significant relationships. Furthermore these species-averaged approaches are unsuitable if we want to ask questions about intraspecific variation in responses, the difference in responses across populations of the same species. Indeed the inability of the same traits to predict responses by Hatfield et al. (2018c) could be due to variation in actual trait values of the populations in question.

Variation in traits within species is well documented and is caused by an interplay between population structure, genetics and local selection pressure or some level of plasticity (Ives et al., 2007; Moran et al., 2016). When changes to traits are due to heritable causes, these changes will occur at slower rates over generations, but when the variability in traits are due to plasticity then adaptive evolution will be slowed down in the short future (Moran et al., 2016). If populations vary in both their responses to habitat change and morphological traits it follows that intraspecific variation in traits may be one of the causes independent.

In this chapter I explore the potential of changes in species traits over their geographic range to influence sensitivity to local habitat loss. I focus on bird species in the Atlantic forest of Brazil where one of the major anthropogenic pressures causing population declines has been habitat loss (Atlantica, 2020). I first look at general patterns of trait change within species. I model both the mean and the variance in morphological trait size of body mass, wing length, tarsus length and bill length across 354 species and more than 2000 populations in Brazil (Rodrigues et al., 2019). I then compare this to estimates of the sensitivity of species occupancy to the same drivers to determine if changes in traits are related to population level responses. I expect that mean and variation in trait size are affected by lower suitable conditions near the range edge and that this is mediated by the amount of forest cover in the local landscape.

4.3 Methods

All data manipulation and analysis was conducted in R (R Core Team 4.3.0, 2023), using packages *tidyverse* (Wickham, 2021), *janitor* (Firke, 2023), *broom* (Robinson et al., 2023) and *tidybayes* (Kay, 2023) for a tidy workflow; packages *sf* (Pebesma et al., 2021), *terra* (Hijmans et al., 2023) and *landscapemetrics* (Hesselbarth et al., 2021) were used for all spatial analyses; package *brms* (Bürkner, 2021) for bayesian statistical analysis; packages *ggplot2* (Wickham, 2016), *egg* (Auguie, 2019) and *tmap* (Tennekes, 2018) for data visualization. All maps were first reprojected from the World Geodetic System 1984 (https://epsg.io/4326, [n. d.]) into the South America Albers Equal Area Conic projection (https://epsg.io/102033, [n. d.]) before any spatial calculations.

4.3.1 The Atlantic Bird Traits Dataset

To assess bird species trait responses to distance to range edge and forest cover amount, I used the published data set "Atlantic Bird Traits: a dataset of bird morphological traits from the Atlantic Forests of South America" (Rodrigues et al., 2019). This dataset includes 44 morphological trait measurements for 67,197 specimens from 711 bird species across 2790 locations in the Atlantic Forest, but also include records from all the other Brazilian biomes. The measurements were taken from specimens mist-netted in the field (86.5%) or from museums (13.5%) over the period of 198 years (1820 to 2018). I only used measurements from 1985 onwards to match availability of landcover maps, see section Section 4.3.3. See Rodrigues et al. (2019) for more details on the dataset.

4.3.2 Morphological Trait Data

In this study I focus on four morphological traits extracted from the Atlantic Bird Trait Dataset (Rodrigues et al., 2019): Body mass (g), Wing length (mm), Tarsus length (mm) and Bill length (mm). I cleaned the extracted data to tailor it to our analyses aims and availability of data. The

cleaning process included the removal of: a) data from before 1985; b) observations with traits considered to have "low measurement accuracy" by Rodrigues et al. (2019); c) observations without geographic coordinates (i.e. GPS); d) observations without measurements for traits of respective models; e) locations that appear less than five times per species, to guarantee variation of distances per species; and f) species that have less than 20 observations. The final number of species, locations and observations varied per trait, see Table 4.1. The cleaned data includes a total of 50,689 observations from 1985 to 2018, across all Brazilian Biomes, see Figure 4.1.

Trait	N Species	N Locations	N Observations
Body Mass (g)	354	2310	39,655
Wing Length (mm)	330	1786	28,620
Tarsus Length (mm)	327	1803	28,247
Bill Length (mm)	308	1025	26,321

Table 4.1: Total number of species, locations and observations per trait used in each model.

4.3.3 Distance to Range Edge

Distances to the species' range edge were calculated using species' geographic ranges provided by Birdlife International (International, 2020) and GPS locations available from the "Atlantic Bird Traits Dataset" (Rodrigues et al., 2019) for each specimen. The distances were measured in meters from each specimen location to the nearest continental edge of its respective species' range (i.e. excluding the Atlantic Ocean as a range edge). Specimens located outside the range of a species were not included in the statistical analyses.

4.3.4 Forest Cover

Forest cover was calculated as a percentage from 30-m resolution landcover maps of Brazil provided by MapBiomas (2020), which were later transformed into proportions (i.e zero to one) for model fitting purposes. MapBiomas provides annual cover for the entire territory of Brazil from 1985 onwards, which allowed us to choose one map per specimen based on their data collection year (Rodrigues et al., 2019). I used category 3 ("Natural Forest Formation")

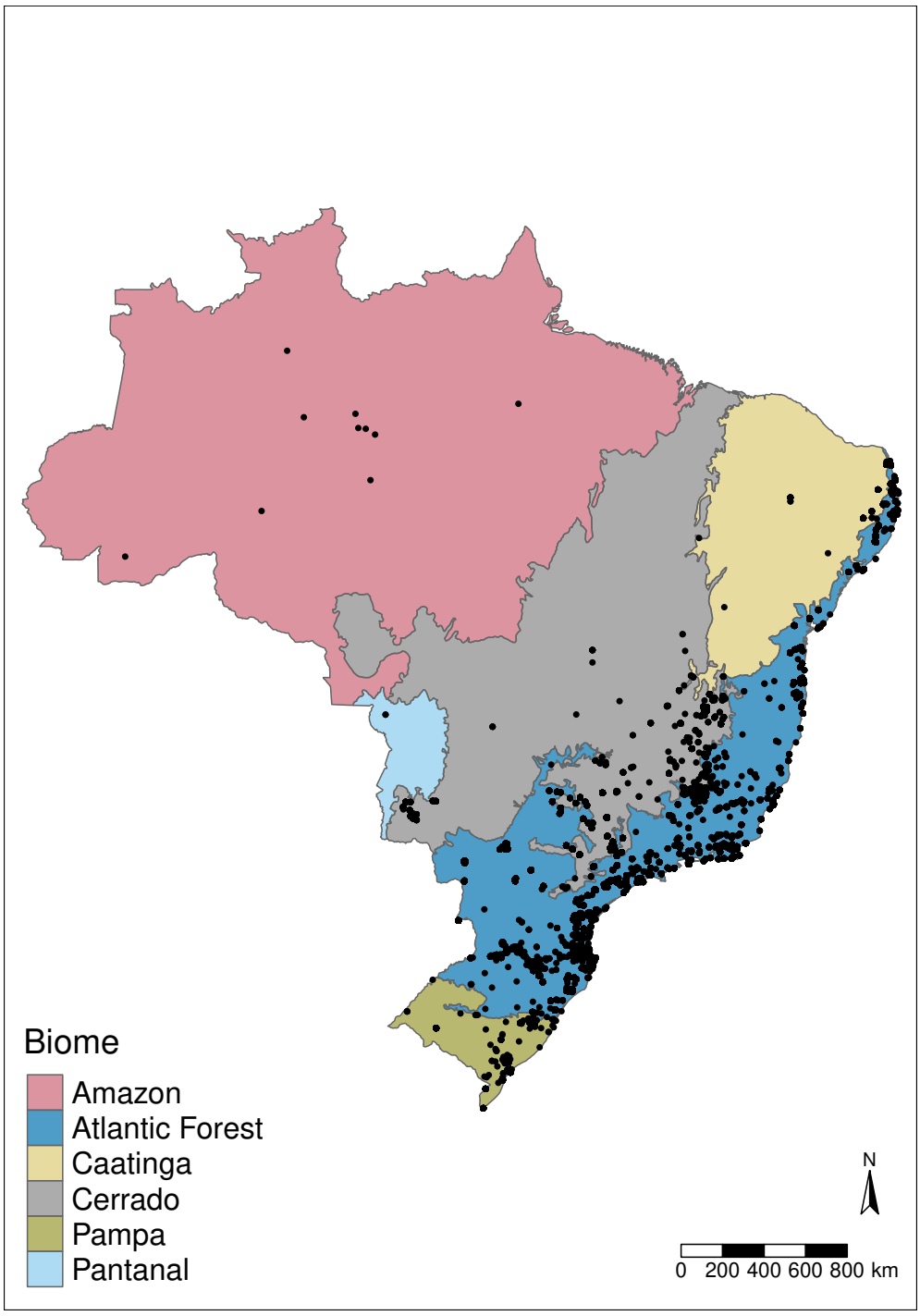


Figure 4.1: Sampling locations of data analysed. Each colour represents a Brazilian Biome and each black dot represents one specimen from which a trait measurement was taken (n=50689).

of MapBiomas for the measurement of forest cover and all other categories were classified as matrix. I calculated the proportion of forest cover within each buffer with radii varying from 100 to 1000 metres at 100 metres increments to account for sensitivity to the scale of effect.

4.3.5 Statistical Analyses

4.3.5.1 Overall species responses

To investigate the effects of distance to range edge and amount of local forest cover in the landscape on traits, I modelled the mean and variance of each trait as a response variable and the explanatory environmental variables using a Generalized Mixed Effect Model in a Bayesian inference framework. Each trait was first log-transformed to adjust to a normal distribution and then z-standardised (i.e. mean of zero and standard deviation of one) to facilitate comparison between models. For the fixed effects, I used distance to the range edge (de), proportion of forest cover (fc) and their fully factorial interactions. These explanatory variables were also z-standardised. To account for the effects of age, sex and status (i.e specimen was live or dead when measured) on trait size, I also included these as categorical fixed effects. In this model I also included a random effect term allowing both the slope and intercept of distance to range edge, proportion of forest cover and their interaction to vary between species (sp) to account for systematic differences in forest cover at different distances to range edge between species. In addition, I included a second random effect term allowing the intercept of the responsible for data collection (m) to vary, to account for measurement repeatability. The model structures, for both mean (μ) and variance (σ), are shown here in the R package *brms* syntax:

$$trait \sim fc * de + sex + age + status + (fc * de|sp) + (1|m) \tag{4.1}$$

$$\sigma \sim fc * de + sex + age + status + (fc * de|sp) + (1|m) \tag{4.2}$$

In this framework, it is possible to estimate predictor terms for all parameters of the response

distribution (i.e the mean and variance). This is in contrast to approaches normally used by frequentist statistics which assume variance is constant across observations. I included soft priors for all parameters, which had a normal distribution ($\beta_0, \beta \sim N(\mu = 0, \sigma = 0.5)$) to ensure that values are biologically coherent. My models were run using four independent MCMC chains, with 10000 iterations (5000 for the warm-up period) in each chain. I show the results with both 89% and 95% credible intervals (McElreath, 2016). I also report the probability of direction (pd; as a percentage), which gives the probability a parameter is strictly above or below zero based on the posterior distribution.

The results are presented at the 600 metres buffer, as the model coefficients for both FA and FGB did not change qualitatively between them (see Figure B.2). In addition, the 600 metres buffer has been used by other studies conducted with the species used here Lindell et al. (2007); Morante-Filho et al. (2015); Orme et al. (2019); Bellotto-Trigo et al. (2023) including the other chapter in this thesis and has been chosen because it is a good fit for species with restricted movement Hatfield et al. (2018a).

4.3.5.2 Species-specific responses

To investigate patterns in intra-specific responses and test the idea that changes in morphological traits are related to broader population performance I compare the responses of morphological traits here with the sensitivity of occupancy from **chapter 2**. For the trait responses I extract the species-specific coefficients for forest cover, distance to range edge and their interaction for the mean and variance of each four traits. Combined this gives a set of 24 values for each species defining the response of their traits to these factors. I do the same for the occupancy models from **chapter 2** giving a 3 values describing their response to forest cover and distance to edge. Filtering for species that overlap in the datasets results in a set of 227 species with information for both.

After extracting the species-specific responses I calculate the correlation between responses using a mantel test. I first z-transformed the coefficients and constructed distance matrices using euclidean distances for the both datasets giving the distance between species in their occupancy and trait responses. I then run the mantel test (9999 permutations) using Pearson's

correlation. Overall this approach measures the correlation between species occupancy and trait responses. A strong correlation would indicate that species that tend to respond similarly in one way also respond similarly in the other, that is, if a species that changes in occupancy along the geographic range also demonstrates changes in trait size along the range.

4.4 Results

4.4.1 Overall Species Responses

My results show no consistent response among traits, both for the mean (Equation (4.1)) and variance (Equation (4.2)) models.

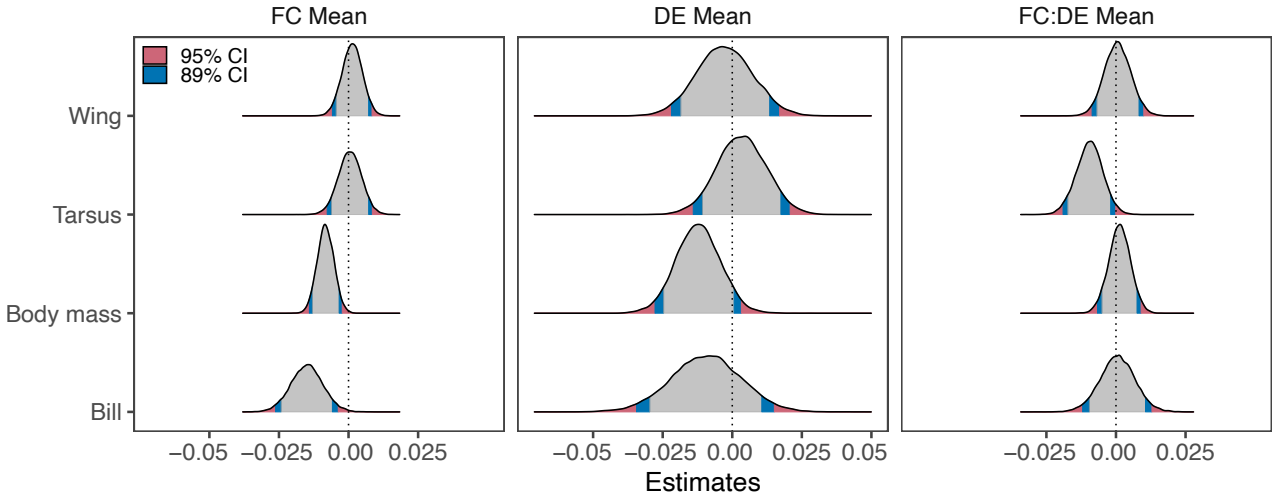


Figure 4.2: Distribution of model estimates for the mean trait (wing length, tarsus length, body mass, bill length) values. The distributions represents the 2500 posterior draws, which show small responses for body mass and bill length with respect to forest cover, and for tarsus with respect to the interaction between forest cove and distance to range edge. The dotted line at zero overlapping the grey area shows the theoretical area of no effect. If the line overlaps the blue area, then the estimated effect falls within the 89% Credible Interval (CI), similarly, if the line overlaps the red area the estimated effect falls within the 95% Credible Interval (CI). The first panel shows the coefficient distribution for forest cover proportion (FC), the second panel shows the distribution for distance to range edge (DE), the third panel shows the distribution of coefficients for the interaction of forest cover proportion and distance to range edge (FC:DE), for the mean model (Mean).

Mean trait size does not change consistently with distance to range edge, or their interaction (Figures 4.2 and 4.3). Mean wing length (est = 0.00 [89% CI = -0.0001:0.01], pd = 64.24%)

and mean tarsus length (0.00 [-00.1:0.01 89% CI], 54.77%) showed no response to forest cover whilst mean body mass (-0.01 [-0.01:-0.0001 95% CI], 99.64%) and mean bill length (-0.01 [-0.03:-0.0001 95% CI], 99.56%) showed a very small negative response (Figure 4.4. Distance to range edge showed an even weaker effect, with all traits effects falling within the 95% quantiles. Body mass did however exhibit a very slight negative response (-0.01 [-0.01:0.00001 89% CI], 94.12%). The interaction between forest cover and distance to range edge was only non-zero for mean tarsus length (-0.01 [-0.02:-0.0001 95% CI], 97.67%) which showed a slight negative response. This is seen in the predictions where mean tarsus length increases marginally as we move from the range edge at low forest cover and decreases at high cover (Figure 4.4).

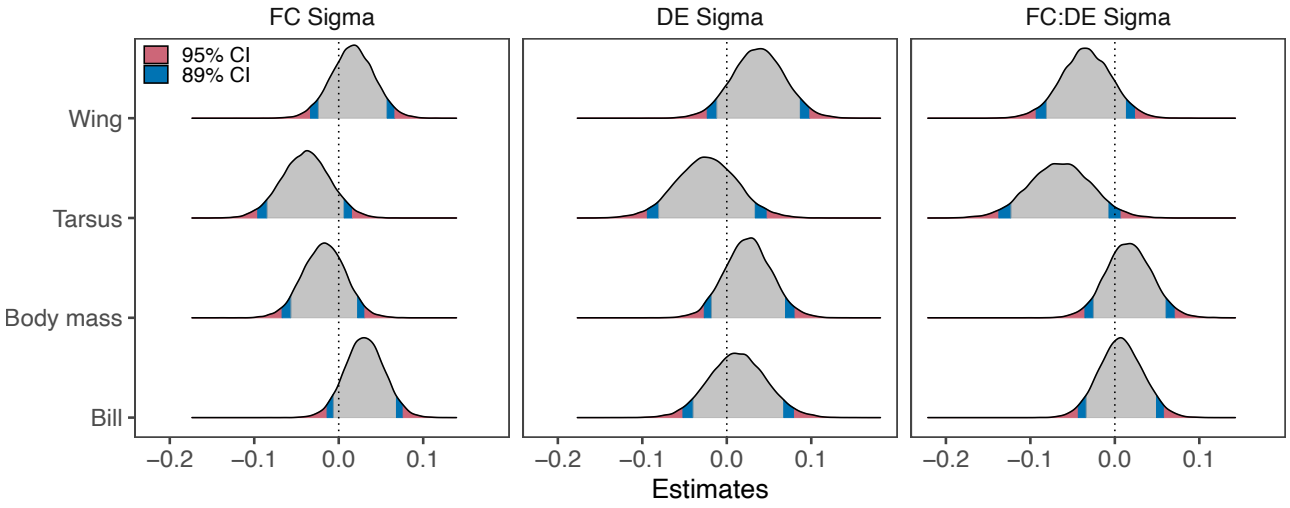


Figure 4.3: Distribution of model estimates for variation in trait (Wing length, Tarsus length, Body mass, Bill length) values. The distributions represents the 2500 posterior draws, which only shows a small response of tarsus for the interaction between forest cover and distance to range edge. The dotted line at zero overlapping the great area shows the theoretical area of no effect. If the line overlaps the blue area, then the estimated effect falls within the 89% Credible Interval (CI), similarly, if the line overlaps the red area the estimated effect falls within the 95% Credible Interval (CI). The first panel shows the coefficient distribution for forest cover proportion (FC), the second panel shows the distribution for distance to range edge (DE), the third panel shows the distribution of coefficients for the interaction of forest cover proportion and distance to range edge (FC:DE), for the sigma model (Sigma).

In general the modeled trait variance was more responsive to predictors than the mean but most estimates were still not distinguishable from zero. The modeled trait variance did not change with forest cover amount although results suggest a relatively high probability of tarsus length decreasing (pd = 91.97%) and bill length increasing (pd = 90.83%) with forest cover proportion (Figure 4.3, FC Sigma). Distance to range edge did not influence variance in trait

size either, with wing showing the highest probability of presenting a positive response (pd = 88.60%). Only the variance in tarsus length showed a non-zero estimate for the interaction term(-0.06 [-0.12:-0.01 89%CI], 96.24%). This suggests that the variance in tarsus length increases slightly with distance to range edge at low forest cover (Figure 4.4, Tarsus 10% FC), but decreases with distance to range edge at higher forest cover proportion (Figure 4.4, Tarsus 50% to 90% FC).

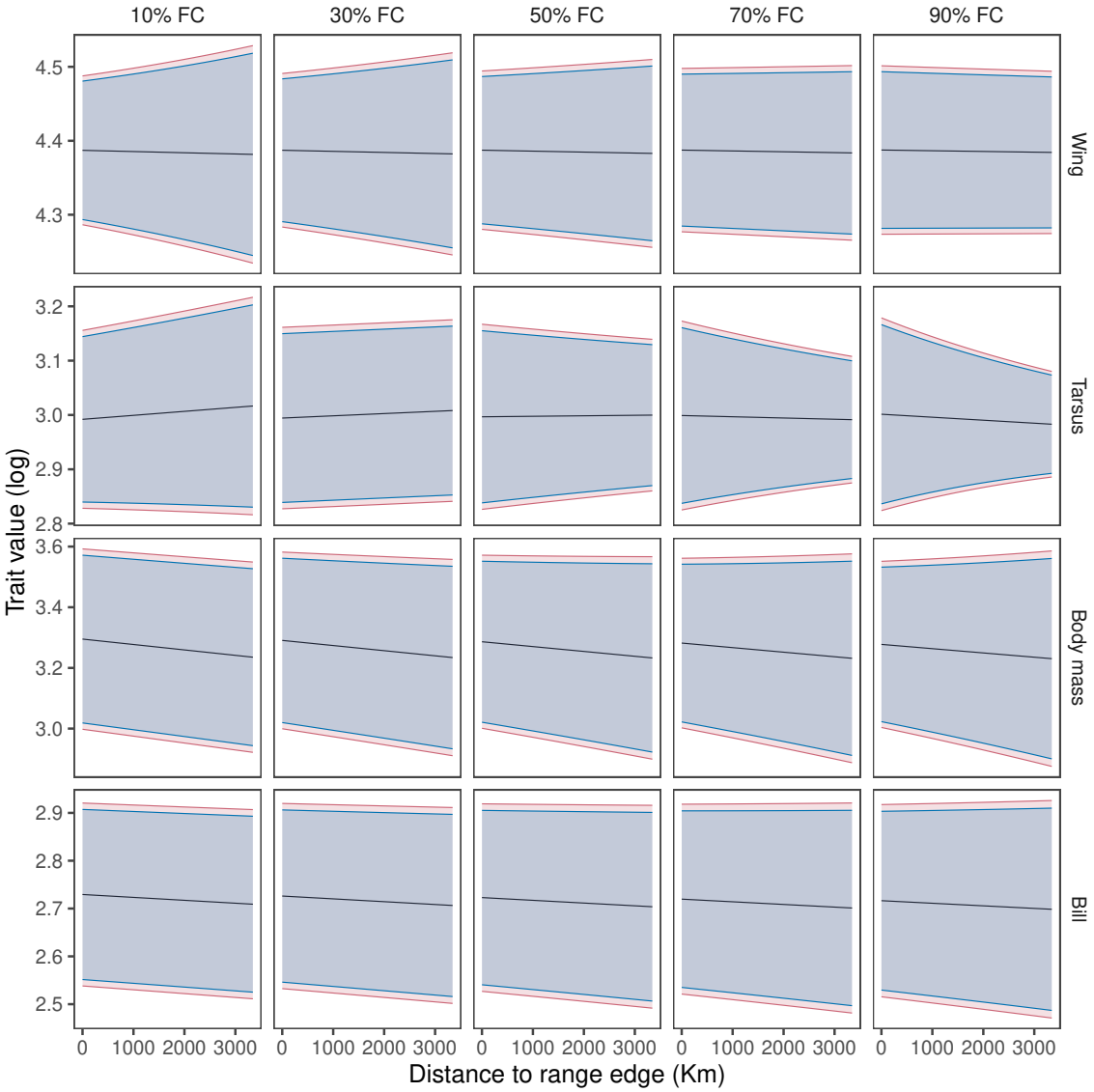


Figure 4.4: Model predictions of mean and variance of trait size (Wing length, Tarsus length, Body mass and Bill length) across different percentages of local forest cover (10% to 90% FC) and distances to the range edge (0 to 3500 Km). The black line represents the predicted mean response in trait size from Equation (4.1), while the shaded area shows the predicted variance in trait size from Equation (4.2), with blue and red representing the 89% and 95% Credible Intervals respectively.

4.4.2 Species-Specific Responses

To assess the relative importance of species-level responses (as opposed to the mean interspecific responses above) I also looked at the variation fitted by the group-level effects for species (i.e. random effects). The variation per species depicted by the group-level effects for the mean model (Table C.3) is high relative to the population-level effects (fixed effects). This indicates that a large degree of the trait variation and its response can be attributed to interspecific differences. The estimated variation in traits showed the same pattern but even stronger (table C.3). This indicates that responses of variation in traits to these drivers is again determined more by species specific responses and that there it no real tendency for traits to respond in the same way across species.

The correlation between these species-specific trait and occurrence responses was very weak with the Mantel Statistic Test showing a small significant effect size (R=0.1, p=0.025) (fig. 4.5). This indicates that species that were similar in the responses of their morphological traits are not necessarily the same to those that are similar in their change in occupancy over forest cover and distance to range edge.

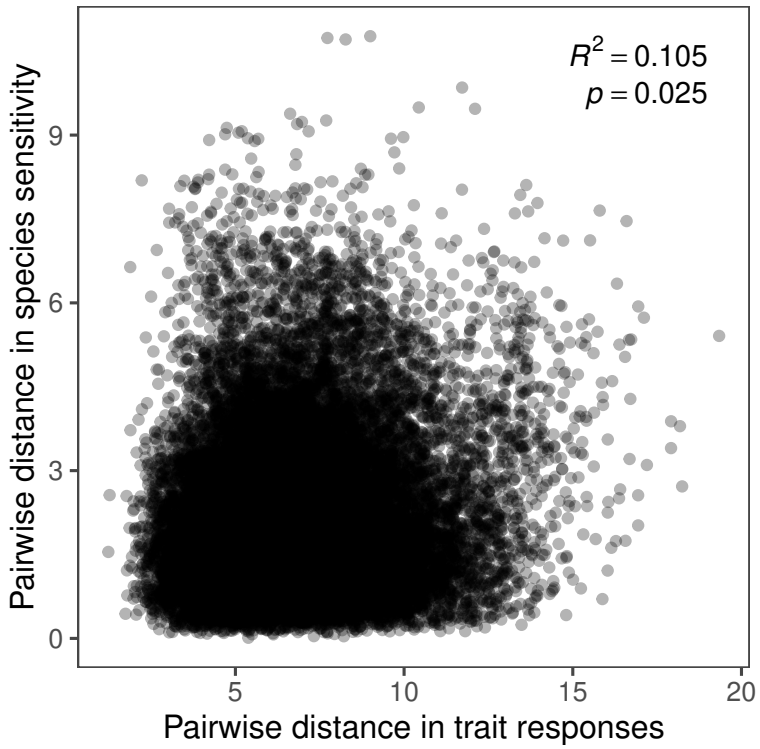


Figure 4.5: Pair-wise distances in species-specific sensitivity to occupancy and trait responses to distance to range edge and habitat change. Each point is a single species pair (n=125,316). There is overall no correlation between the two distances as indicated by a mantel test (R^2 and p-value inset).

4.5 Discussion

My results indicate that species do not show either a consistent change in trait size and variance across the geographic range or a relationship between the sensitivity of occupancy and traits. Though there was an effect of forest habitat amount on trait size in tarsus, bill length, and body mass this was very small and was even smaller for the distance to range edge and their interaction.

Overall species showed no trends in their traits or their variation. This is clearly displayed by the small and non-significant main-effect parameter estimates across most models. The lack of overall trends and the relatively large random effects indicate that patterns of trait change instead are species specific. This result makes sense when considering the varied processes that determine patterns of trait variation across the range including selection and dispersal structure (Moran et al., 2016; Camps et al., 2021). These factors will be unique to each species and make it so any given trait will not change across species in a uniform way.

The lack of general patterns is also possibly due to the variation within species and how it makes identifying patterns across individual ranges difficult. For example Pironon et al. (2015) discussed how species' ranges are not static, as they are always undergoing contraction and expansion at different edges. This means that two points at identical distance from different edges (i.e. north and south) may have very different local conditions and represent different positions within a species niche. The process makes identifying consistent changes difficult as we don't know which edges are "good" and which are "bad". Such effects add significant noise to the effects of distance to edge providing a reason why I am unable to see general patterns here.

Another explanation for the lack of general trends is that in the taxa we consider (birds) traits are mostly not responsive to local conditions. Whilst previous work has successfully identified changes in traits across ranges in plants (Camps et al., 2021) the responses of bird traits are a lot less plastic and may explain why they show no patterns. The inability to significantly change their traits is countered by the mobile nature of birds which (if able) can disperse to

different patches if local conditions are bad.

The interspecific trait responses also showed no correlation with estimates of the same species' sensitivity of occupancy. This result suggests that interspecific variation in responses of occupancy are not affected by differences in traits between populations. It is therefore likely that other mechanisms are responsible for driving species sensitivity. Local ecological conditions (Pironon et al., 2017) may be more important with factors such as the availability of resources and presence of competitors at the range margins driving variation in sensitivity of occupancy across the range as opposed to traits. These additional factors should be the focus of future work to determine the mechanisms behind variation in sensitivity across the habitat range.

Overall trait size was not seen to vary with either habitat amount or distance to range edge. This means that morphological traits do not necessarily change systematically across the range or in response to habitat change and that this variation in morphological traits within species does not correlate with the sensitivity of occurrence in altered landscapes. The results here highlight the complexity in studying species responses at this scale. I suggest future work should expand beyond this and use more targeted approaches to investigate the mechanisms underlying the variation within species responses. In terms of conservation it suggests there is no single golden rule that will work across species at these scales. Specific measures for individual species or specific areas would have to be tailored to particular needs/aims.

Chapter 5

Synthesis

Habitat change stands as one of the largest threats to the survival of the species we know and the many that have not yet been described (MEA et al., 2005). As society faces many challenges at a global scale it is increasingly important that we as scientists make the case for why habitat change is important and action should be taken to prevent it and counteract its negative effects. This is especially true in a global economic system where damage to the environment is considered a secondary concern to the pursuit of economic growth. It is imperative that we keep working on finding how species might be affected and how they will respond so we can try to find ways to mitigate it. We should aim to provide the best science possible so politicians and land managers can do their work better informed.

This is especially important in tropical ecosystems which are estimated to hold 79% of the world's biodiversity and six times more terrestrial endemic birds than temperate regions (Barlow et al., 2018). Despite this, there are many uncertainties surrounding the mechanisms behind sensitivity responses of these bird communities (Henle et al., 2004; Anjos et al., 2010). To a great extent, the uncertainties surrounding the mechanisms behind species sensitivity is due to the complexity of the biotic and abiotic processes affecting them, consisting of many factors linked in space and time (MacArthur, 1972; Brown et al., 1996; Wingfield, 2013). In this thesis, I investigated the effect of distance to range edge on the sensitivity of species in a tropical forest, focusing on three key questions:

1. How does distance to range edge affect inter and intraspecific responses of bird species as a function of habitat amount and fragmentation?

2. How does distance to range edge affect individual levels of stress as a function of habitat amount?

3. Does variation in trait size across geographic ranges and habitat amount provide a mechanism to explain species sensitivity?

5.1 Implications For Our Understanding Of Species Sensitivity

In **chapter 2** I show that habitat fragmentation can affect species positively, negatively or not at all based on populations locations within the distribution range and the amount of forest cover in the local landscape, this corroborates previous work that show inter- and intraspecific variation in responses to habitat amount are also variable within the distribution range Orme et al. (2019). This finding suggests that the responses of individual populations are context dependent and it may be difficult to generalise across species. This finding also provides a potential source of the variation of responses to fragmentation commonly seen in the literature, which caused debate about the relative importance of fragmentation and habitat loss. My results suggest that there is no single answer to this and that both types of habitat change will have differing effects depending on the location of a given population.

I go on then to test in **chapter 3** if species sensitivity near the edges and at low forest cover is reflected in metrics of physiological stress based on individual phenotype. I show that there is a trend for individuals in populations nearer the range edge to show higher variance in asymmetry (indicating higher stress), although they are not statistically significant. This implies that individuals closer to to range edge may be experiencing increased stress, causing lower population performance. This idea will require more investigation though, with larger sample sizes than I was able to collect.

Finally, in **chapter 4** I show that morphological traits do not necessarily change systematically across the range or in response to habitat change and that this variation in morphological traits within species does not correlate with the sensitivity of occurrence in altered landscapes. These results suggest that at least in tropical birds variation in traits between populations are not driving the altered sensitivity at the population level. This would imply that other factors such as changes in the local biotic or abiotic environment (e.g. changes in strength of competition or sub-optimal environmental conditions) are responsible for variation in population responses.

5.1.1 When Does Distance To Range Edge Work?

Overall I found that the position in range was only significant when looking at population-level performance in **chapter 2** not at individual level stress in **chapter 3**. This result is interesting and could indicate that the effects of position in the range don't act equally across ecological scales and are stronger at higher levels of organisation (populations). On one hand this might be due to the relative variation at different scales. At the individual level it is reasonable to expect that there would be more variability (as many complex processes determining phenotype) when compared to the population level where variation across individual responses averages out to determine the population response. On the other hand phenotypic stress might not be effective in predicting population level responses. If increasing stress causes local extinction before strong phenotypic-stress responses appear it might be hard to detect them explaining the disparity in my results.

5.2 Distance To Range Edge

Throughout this thesis I quantified the effects of position within the geographic range using the distance to range edge metric. This is in contrast to some previous work which identifies a range "core" and then classify populations relative to this point. This method has been criticised though, with Pironon et al. (2017) showing that many previous studies using the centre-periphery method identified edge populations incorrectly as those belonging to the center

or vice-versa. Distance to range edge is useful here as it doesn't require us to define a single "core" and gives us a quantitative measure of distance instead. It does however require more data to ensure a good sampling across species' ranges. The results I present here demonstrate that this metric can be useful and I argue that if studies investigating species sensitivity to an array of possible stressors want to account for the location of a population within its range (which for reasons discussed here is important), then distance to range edge is a better choice than classifying centre-periphery populations.

5.3 Understanding Future Deforestation

My results have important implications for understanding the impacts of future deforestation. Even if deforestation slows with time, it is not going to stop at any time soon (Review, 2020; Hoang and Kanemoto, 2021) making it important we understand its effects. The approach I use could in theory be applied to identify areas of forest that are most sensitive to any future habitat change. My results suggest that for birds of the Atlantic Forest, fragmentation or deforestation in patches that are towards the edge of many of local species would result in the greatest negative impacts. Future studies could use similar approaches to predict species occurrence and the effects of deforestation for other locations and taxa by taking into account location within the range.

5.4 Implications For Conservation

To maximise conservation efforts with a limited budget, considering where the populations are in the range is an important factor. If geographic range data is available, calculating distance to the range edge is very straightforward. As I mentioned before, species sensitivity to habitat change is complex by being context dependent. Therefore there is no rule of thumb of what or where conservation initiatives should prioritise efforts. Using distance to range edge in any analysis of sensitivity to habitat change will be able to inform how mitigation strategies should

be implemented based on local context. For example, if the idea is to conserve a specific species, areas where populations of these species are not sensitive should be only monitored to prevent disturbance, while areas that populations are sensitive should actively receive mitigation, via matrix modification (Hatfield et al., 2018b, 2020) or active restoration (Tambosi et al., 2014). While if the aim is to choose an area to conserve with many species, the model in **chapter 2** can be used to determine areas where populations are more sensitive by identifying the threshold where species are negatively affected by fragmentation. The enhancement of habitat cover and connectivity in this areas will increase meta-populations, allowing for unassisted recolonisation (Hatfield et al., 2018b).

5.5 Future Work

Overall, my results highlight the importance in accepting that species sensitivity is context dependent and it can be partly explained by distance to range edge - which can be measured. There are however several features of species ranges that I have not explicitly considered here which may be interesting for future work.

Firstly, the different types of range edges (i.e. historical, ecological, hard and soft). Certainly, there are other aspects of range limits that should be explored so we can estimate if there are significant differences in species responses depending on the type of edge. For example, Pironon et al. (2017) proposes a multifaceted framework to investigate species genetic and demographic performance, which includes using historical and ecological ranges in addition to the geographic range of a species. Historical ranges take into account locations consisting of old populations near a periphery that could be less sensitive to disturbances than locations with younger populations, that also includes areas where the range might be contracting or expanding. Ecological ranges mirror the ecological niche of a species and the authors propose that more than one niche centre exists within the range, and that does not necessarily match the geographic centre (Pironon et al., 2017). Other authors also argue that "hard edges" (i.e. abrupt edge limits, like the ocean or a steep mountain range for terrestrial species) will influence species

sensitivity differently from "soft edges" (i.e. a staggered/fading edge limit, like the transition of one type of forest into another also for terrestrial species) (Banks-Leite et al., 2022; Granville, 2023). All of these aspects of ranges stand as potential avenues for future work.

Secondly, although I found limited effects of distance to range edge on physiological stress, I suggest that when feasible morphological traits are measured for all bilateral traits present in an individual independent of the aim of the research, so more data is available and robust analysis can be conducted in the field. If researchers can have more confidence on the results generated from this area of research, physiological stress could be used as an easy to measure and cheap tool/resource to predict when populations are in danger of local extinction before it is too late. I also suggest that a standardised method of measurement and analysis is used as suggested by Lens et al. (1999) and Dongen (2007), to assure that the different results we see revolving fluctuating asymmetry are not due to methodological biases.

Thirdly, although I found limited signs of morphological variation in trait size explaining species sensitivity. The addition of other species traits, like life-history and functional traits should be explored in the analysis of distance to range edge. The use of recently published datasets like AVONET (Tobias et al., 2022) would allow for a more complete investigation of the mechanisms behind variation in species sensitivity across the range, for example by using the hand-wing index metric (Sheard et al., 2020) to calculate dispersal ability, which can be used to characterise extinction debts after habitat change occurs (Thompson et al., 2019).

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Appendices

Appendix A

Supplementary Information for Chapter 2

A.1 Supplementary Tables

Dataset	Coordinates		Number of species recorded	Number of sites sampled	Year of sampling	Map year used in analysis
PR	23° 3' S	51° 9' W	173	14	1997-2000	1999
BA	15° 2' S	39° 2' W	184	40	2013-2014	2014
SP1	23° 5' S	47° 2' W	152	32	2000-2003	2002
SP2	22° 2' S	52° 2' W	98	28	2002-2004	2003
SP3	23° 1' S	45° 2' W	190	24	2015-2017	2016

Table A.1: Metadata from the five datasets providing bird data. Coordinates are approximates of the centre of the landscape.

Dataset	N	Mean edge density	Ci	Mean number of patches	Ci	Mean distance to range edge	Ci
PR	2,394	20.85	20.09 – 21.62	1.50	1.46-1.53	18.37	17.91 – 18.83
BA	6,552	34.12	33.60 – 34.65	2.19	2.16-2.23	18.69	18.27 – 19.12
SP1	4,928	39.67	38.86 – 40.46	3.34	3.25-3.43	18.07	17.77 – 18.38
SP2	2,744	18.03	17.54 – 18.52	1.25	1.22-1.27	17.42	17.06 – 17.78
SP3	4,560	37.65	36.93 – 38.37	3.04	2.98-3.10	20.57	20.20 – 20.94

Table A.2: Metadata from the five datasets providing bird data. Coordinates are approximates of the centre of the landscape.

Species	BA	PR	SP1	SP2	SP3
TINAMIDAE					
Tinamus solitarius	0	1	4	1	0
Crypturellus soui	9	0	0	0	0
Crypturellus obsoletus	0	14	24	2	7
Crypturellus undulatus	0	2	0	0	0
Crypturellus variegatus	6	0	0	0	0
Crypturellus parvirostris	0	7	0	0	1
Crypturellus tataupa	5	13	6	23	3
CRACIDAE					
Penelope superciliaris	0	14	0	27	0
Penelope obscura	0	4	9	0	14
ODONTOPHORIDAE					
Odontophorus capueira	0	2	5	1	0
CATHARTIDAE					
Coragyps atratus	4	0	0	0	1
Cathartes aura	3	0	0	0	1
Sarcoramphus papa	0	0	0	1	0
ACCIPITRIDAE					
Leptodon cayanensis	2	0	0	0	0
Harpagus diodon	0	1	0	0	0
Ictinia plumbea	0	9	0	0	0
Accipiter striatus	0	2	0	0	0
Geranospiza caerulescens	0	0	0	0	1
Pseudastur polionotus	0	0	0	0	1
Rupornis magnirostris	7	6	4	0	9
Spizaetus tyrannus	2	0	0	0	0
RALLIDAE					
Aramides saracura	0	9	0	0	0
CHARADRIIDAE					
Vanellus chilensis	0	0	0	0	1

COLUMBIDAE					
Patagioenas speciosa	33	3	0	0	0
Patagioenas picazuro	12	14	5	0	14
Patagioenas cayennensis	2	14	12	23	3
Patagioenas plumbea	0	0	9	0	3
Columbina talpacoti	5	0	0	0	1
Claravis pretiosa	2	3	0	9	1
Geotrygon montana	1	12	3	0	3
Leptotila verreauxi	6	14	20	28	14
Leptotila rufaxilla	8	11	17	8	7
CUCULIDAE					
Coccyzus americanus	0	7	0	0	0
Coccyzus euleri	1	0	0	0	0
Coccyzus melacoryphus	0	3	0	5	0
Piaya cayana	26	14	25	27	11
Crotophaga major	0	0	0	6	0
Dromococcyx pavoninus	0	1	0	7	0
STRIGIDAE					
Megascops choliba	0	6	0	15	0
Ciccaba virgata	1	0	0	0	0
Pulsatrix koeniswaldiana	0	1	0	0	0
Glaucidium minutissimum	5	0	0	0	0
Glaucidium brasilianum	6	8	0	0	0
CAPRIMULGIDAE					
Lurocalis semitorquatus	0	0	5	18	0
Nyctidromus albicollis	2	0	0	0	0
Nyctiphrynus ocellatus	0	0	0	6	0
Antrostomus rufus	0	0	0	2	0
TROCHILIDAE					
Glaucis hirsutus	4	0	0	0	0
Phaethornis eurynome	0	12	24	1	5

Phaethornis pretrei	1	1	0	0	6
Phaethornis ruber	32	0	0	0	0
Ramphodon naevius	0	0	4	0	0
Eupetomena macroura	4	0	0	0	0
Florisuga fusca	1	0	2	0	2
Anthracothorax nigricollis	2	4	0	0	0
Chlorostilbon lucidus	4	5	3	0	5
Thalurania glaucopis	8	4	27	1	12
Hylocharis cyanus	0	0	1	0	0
Hylocharis chrysura	0	2	0	0	0
Leucochloris albicollis	0	4	0	0	1
Amazilia versicolor	0	1	2	0	1
Amazilia fimbriata	1	0	0	0	1
Amazilia lactea	0	0	0	0	2
Clytolaema rubricauda	0	0	0	0	3
TROGONIDAE					
Trogon viridis	23	0	4	0	0
Trogon rufus	6	6	15	12	1
Trogon surrucura	0	12	16	15	8
MOMOTIDAE					
Baryphthengus ruficapillus	0	13	2	14	0
Momotus momota	0	0	0	11	0
BUCCONIDAE					
Notharchus swainsoni	0	0	0	4	0
Nystalus chacuru	1	0	0	0	1
Nystalus maculatus	1	0	0	0	0
Malacoptila striata	3	0	0	4	1
Nonnula rubecula	0	1	0	0	0
Monasa morphoeus	2	0	0	0	0
Chelidoptera tenebrosa	1	0	0	0	0
GALBULIDAE					

Galbula ruficauda	12	0	0	18	0
RAMPHASTIDAE					
Pteroglossus castanotis	0	0	0	20	0
Pteroglossus aracari	11	1	0	0	0
Pteroglossus bailloni	0	2	0	0	0
Selenidera maculirostris	0	13	3	0	1
Ramphastos ariel	10	0	4	0	0
Ramphastos dicolorus	0	7	5	0	5
Ramphastos toco	0	0	0	0	3
PICIDAE					
Picumnus exilis	9	0	0	0	0
Picumnus temminckii	0	14	0	0	0
Picumnus albosquamatus	2	0	0	0	0
Picumnus cirratus	0	0	22	0	12
Melanerpes flavifrons	6	11	2	6	0
Veniliornis spilogaster	0	12	21	0	14
Veniliornis affinis	11	0	0	0	0
Piculus flavigula	6	0	0	0	0
Piculus aurulentus	0	3	9	0	2
Colaptes melanochloros	5	13	0	0	2
Colaptes campestris	0	0	0	0	2
Celeus flavescens	1	11	21	17	9
Celeus tinnunculus	1	0	0	0	0
Hylatomus lineatus	7	8	11	20	3
Campephilus robustus	0	6	0	0	2
FALCONIDAE					
Herpetotheres cachinnans	2	8	0	0	0
Micrastur ruficollis	0	6	8	1	1
Micrastur semitorquatus	0	3	1	11	0
Caracara plancus	5	0	0	0	1
Milvago chimachima	8	0	0	0	5

PSITTACIDAE					
Ara chloropterus	0	0	0	15	0
Primolius maracana	0	4	0	0	0
Diopsittaca cumanensis	1	0	0	0	0
Psittacara leucophthalmus	2	7	0	0	5
Aratinga auricapillus	4	5	0	0	0
Eupsittula aurea	14	0	0	0	0
Pyrrhura cruentata	4	0	0	0	0
Pyrrhura frontalis	0	13	6	17	3
Forpus xanthopterygius	10	10	1	0	3
Brotogeris tirica	8	3	18	0	1
Pionopsitta pileata	0	6	7	0	1
Pionus maximiliani	1	13	10	25	16
Pionus reichenowi	1	0	0	0	0
Amazona rhodocorytha	5	0	0	0	0
Amazona aestiva	0	6	0	0	0
Amazona amazonica	2	0	0	0	0
Triclaria malachitacea	0	3	6	0	0
THAMNOPHILIDAE					
Hypoedaleus guttatus	0	14	6	0	3
Batara cinerea	0	0	21	0	3
Mackenziaena severa	0	14	0	0	0
Mackenziaena leachii	0	1	5	0	5
Taraba major	6	0	0	0	0
Thamnophilus doliatus	0	7	0	0	0
Thamnophilus palliatus	4	0	0	0	0
Thamnophilus caerulescens	0	14	26	15	21
Thamnophilus torquatus	1	0	0	0	0
Thamnophilus pelzelni	0	0	0	28	0
Thamnophilus ambiguus	24	0	0	0	0
Dysithamnus stictothorax	0	0	4	0	0

Dysithamnus mentalis	0	13	32	17	19
Dysithamnus xanthopterus	0	0	3	0	0
Thamnomanes caesius	5	0	0	0	0
Rhopias gularis	0	0	7	0	3
Myrmotherula minor	1	0	0	0	0
Myrmotherula luctuosa	20	0	0	0	0
Myrmotherula unicolor	0	0	1	0	0
Myrmotherula urosticta	17	0	0	0	0
Herpsilochmus atricapillus	0	0	0	17	0
Herpsilochmus pileatus	21	0	0	0	0
Herpsilochmus rufimarginatus	0	6	19	12	1
Herpsilochmus scapularis	1	0	0	0	0
Formicivora grisea	7	0	0	0	0
Drymophila ferruginea	1	0	0	0	2
Drymophila rubricollis	0	4	0	0	3
Drymophila ochropyga	0	0	0	0	3
Drymophila malura	0	2	3	0	3
Drymophila squamata	20	0	4	0	0
Terenura maculata	3	3	3	0	0
Pyriglena leucoptera	13	13	26	11	9
Myrmoderus squamosus	0	0	16	0	2
CONOPOPHAGIDAE					
Conopophaga lineata	0	13	27	26	19
Conopophaga melanops	3	0	3	0	0
RHINOCRYPTIDAE					
Psilorhamphus guttatus	0	9	0	0	0
Merulaxis ater	0	0	1	0	0
Scytalopus speluncae	0	0	0	0	1
Eleoscytalopus psychopompus	1	0	0	0	0
Eleoscytalopus indigoticus	0	8	5	0	0
FORMICARIIDAE					

Formicarius colma	2	0	6	0	0
Chamaeza campanisona	0	4	8	9	2
Chamaeza meruloides	0	0	5	0	1
Grallaria varia	0	5	26	0	1
Hylopezus nattereri	0	4	4	0	4
FURNARIIDAE					
Lepidocolaptes falcinellus	0	0	1	0	1
Furnarius figulus	2	0	0	0	0
Furnarius rufus	1	0	0	0	0
Cranioleuca pallida	0	0	4	0	4
Cranioleuca obsoleta	0	4	0	0	0
Synallaxis ruficapilla	0	14	18	1	20
Synallaxis frontalis	5	1	0	2	0
Synallaxis spixi	0	6	0	0	3
Synallaxis cinerascens	0	4	0	0	2
Phacellodomus erythrophthalmus	0	0	0	0	2
Lochmias nematura	0	0	13	0	1
Cichlocolaptes holti	0	0	7	0	1
Syndactyla rufosuperciliata	0	3	20	0	9
Anabacerthia amaurotis	0	0	4	0	1
Anabacerthia lichtensteini	1	10	0	6	0
Philydor rufum	0	10	8	0	2
Philydor atricapillus	2	0	8	0	2
Anabazenops fuscus	0	0	3	0	8
Automolus leucophthalmus	4	7	20	5	3
Sclerurus mexicanus	1	0	0	0	0
Sclerurus scansor	0	0	24	7	5
Heliobletus contaminatus	0	9	4	0	4
Xenops minutus	15	0	18	0	0
Xenops rutilus	9	10	4	3	12
Dendrocincla turdina	15	4	5	0	1

DENDROCOLAPTIDAE					
Sittasomus griseicapillus	21	12	23	14	15
Glyphorynchus spirurus	23	0	0	0	0
Xiphocolaptes albicollis	0	8	9	18	1
Dendrocolaptes platyrostris	0	13	17	22	3
Dendroplex picus	4	0	0	0	0
Xiphorhynchus guttatus	8	0	0	0	0
Lepidocolaptes angustirostris	0	9	0	0	2
Xiphorhynchus fuscus	16	10	28	3	17
Campylorhamphus falcularius	0	3	1	0	6
TYRANNIDAE					
Mionectes oleagineus	3	0	0	0	0
Mionectes rufiventris	0	6	12	0	1
Leptopogon amaurocephalus	23	14	28	7	8
Hemitriccus diops	0	6	16	0	5
Hemitriccus obsoletus	0	0	0	0	1
Hemitriccus orbitatus	0	0	3	4	2
Hemitriccus nidipendulus	0	0	0	0	4
Poecilotriccus plumbeiceps	0	6	2	10	13
Todirostrum poliocephalum	0	0	0	0	8
Todirostrum cinereum	14	5	0	0	0
Corythopis delalandi	0	4	0	6	2
Phyllomyias fasciatus	0	0	4	0	12
Phyllomyias burmeisteri	0	1	2	0	0
Phyllomyias virescens	0	0	0	0	2
Phyllomyias griseocapilla	0	0	0	0	1
Camptostoma obsoletum	10	8	17	0	10
Capsiempis flaveola	6	12	0	0	0
Myiopagis caniceps	6	13	0	13	3
Myiopagis viridicata	0	0	0	1	0
Elaenia flavogaster	15	1	0	0	1

Elaenia mesoleuca	0	2	11	0	0
Serpophaga subcristata	0	1	0	0	0
Phylloscartes paulista	0	1	3	0	0
Phylloscartes oustaleti	0	0	1	0	4
Phylloscartes ventralis	0	12	1	0	1
Myiornis auricularis	23	13	6	25	4
Rhynchocyclus olivaceus	2	0	0	0	0
Tolmomyias sulphurescens	3	11	31	0	22
Tolmomyias poliocephalus	12	0	0	0	0
Tolmomyias flaviventris	29	0	0	0	0
Platyrinchus mystaceus	0	1	27	14	18
Platyrinchus leucoryphus	0	0	2	0	0
Myiophobus fasciatus	0	3	0	0	1
Myiobius barbatus	11	0	0	0	0
Myiobius atricaudus	0	0	0	0	1
Cnemotriccus fuscatus	4	4	0	27	1
Lathrotriccus euleri	5	11	28	22	17
Colonia colonus	0	6	0	7	2
Attila phoenicurus	0	0	12	0	4
Attila rufus	0	0	23	0	2
Attila spadiceus	6	0	0	0	0
Casiornis rufus	0	0	0	15	0
Rhytipterna simplex	27	0	0	0	0
Sirystes sibilator	0	10	0	9	0
Myiarchus tuberculifer	14	0	0	0	0
Myiarchus swainsoni	2	12	18	12	13
Myiarchus ferox	17	0	0	8	2
Myiarchus tyrannulus	1	0	0	0	0
Tyrannus melancholicus	25	6	0	0	2
Empidonomus varius	2	8	0	0	0
Megarynchus pitangua	32	14	8	0	10

Myiodynastes solitarius	1	14	0	10	12
Myiozetetes similis	28	1	0	0	2
Legatus leucophaius	4	0	0	7	1
Pitangus sulphuratus	30	13	17	0	8
OXYRUNCIDAE					
Oxyruncus cristatus	0	1	2	0	1
COTINGIDAE					
Carpornis cucullata	0	0	7	0	4
Carpornis melanocephala	1	0	4	0	0
Lipaugus vociferans	10	0	0	0	0
Xipholena atropurpurea	2	0	0	0	0
Pyroderus scutatus	0	0	18	0	1
Procnias nudicollis	3	0	14	11	1
PIPRIDAE					
Pipra fasciicauda	0	0	0	1	0
Ceratopipra rubrocapilla	20	0	0	0	0
Pseudopipra pipra	16	0	0	0	0
Chiroxiphia pareola	5	0	0	0	0
Chiroxiphia caudata	0	8	32	6	15
Ilicura militaris	0	0	3	0	2
Manacus manacus	22	0	0	3	2
Machaeropterus regulus	22	0	0	0	0
Neopelma chrysolophum	0	0	3	0	3
Piprites chloris	0	6	2	1	0
TITYRIDAE					
Tityra braziliensis	2	12	9	21	0
Tityra inquisitor	0	4	0	14	0
Schiffornis turdina	7	0	0	0	0
Schiffornis virescens	0	3	24	8	11
Laniisoma elegans	0	0	0	1	0
Pachyramphus viridis	0	5	0	0	0

Pachyramphus castaneus	0	8	2	0	3
Pachyramphus polychopterus	0	6	20	13	8
Pachyramphus marginatus	23	0	3	0	2
Pachyramphus validus	0	13	3	0	6
VIREONIDAE					
Cyclarhis gujanensis	10	14	31	0	21
Vireo olivaceus	6	3	30	4	17
Hylophilus poicilotis	0	1	26	0	5
CORVIDAE					
Cyanocorax cristatellus	0	0	0	0	3
Cyanocorax chrysops	0	11	0	26	0
HIRUNDINIDAE					
Pygochelidon cyanoleuca	0	0	0	0	1
Stelgidopteryx ruficollis	0	0	0	0	2
TROGLODYTIDAE					
Campylorhynchus turdinus	5	0	0	0	0
Pheugopedius genibarbis	15	0	0	0	0
Troglodytes aedon	3	4	0	0	1
POLIOPTILIDAE					
Ramphocaenus melanurus	15	0	3	0	0
TURDIDAE					
Turdus flavipes	1	0	17	0	6
Turdus subalaris	0	9	0	0	0
Turdus rufiventris	27	13	28	0	9
Turdus leucomelas	22	14	0	14	16
Turdus amaurochalinus	5	14	0	8	2
Turdus albicollis	1	9	32	1	13
MIMIDAE					
Mimus saturninus	1	0	0	0	0
PARULIDAE					
Setophaga pitiayumi	14	11	19	9	4

Basileuterus auricapilla	0	14	32	14	24
Myiothlypis flaveola	0	0	0	11	0
Myiothlypis leucoblephara	0	11	27	1	12
Myiothlypis rivularis	1	0	2	0	2
THRAUPIDAE					
Coereba flaveola	25	0	11	0	8
Conirostrum speciosum	5	14	1	11	5
Cissopis leverianus	0	13	0	3	0
Thlypopsis pyrrhocoma	0	7	0	0	0
Hemithraupis guira	0	14	0	14	0
Hemithraupis ruficapilla	0	0	2	0	2
Hemithraupis flavicollis	7	0	0	0	0
Nemosia pileata	11	0	0	0	0
Orthogonys chloricterus	0	0	4	0	0
Islerothraupis cristata	0	0	1	0	0
Tachyphonus coronatus	0	13	13	0	16
Tachyphonus rufus	2	0	0	0	0
Trichothraupis melanops	0	14	22	0	18
Ramphocelus bresilius	2	0	0	0	0
Tangara sayaca	12	14	10	0	9
Tangara cyanoptera	0	0	10	0	2
Tangara ornata	0	0	0	0	2
Tangara palmarum	31	0	0	0	1
Pipraeidea bonariensis	0	1	0	0	0
Pipraeidea melanonota	0	8	0	0	2
Tangara brasiliensis	12	0	0	0	0
Tangara seledon	2	0	5	0	0
Tangara cyanocephala	0	0	3	0	0
Tangara desmaresti	0	0	1	0	3
Tangara cyanoventris	0	0	0	0	4
Tangara flava	14	0	0	0	13

Tangara cyanomelas	15	0	0	0	0
Dacnis cayana	20	8	2	0	6
Chlorophanes spiza	3	0	0	0	0
Cyanerpes cyaneus	1	0	0	0	0
Tersina viridis	6	1	0	0	4
Haplospiza unicolor	0	0	0	0	2
Sicalis flaveola	2	0	0	0	0
Sporophila frontalis	0	0	0	0	3
Sporophila falcirostris	3	0	0	0	0
Asemospiza fuliginosa	3	0	0	0	2
Saltator fuliginosus	0	11	3	0	2
Saltator maximus	29	0	0	0	0
Saltator similis	0	13	17	0	19
PASSERELLIDAE					
Arremon semitorquatus	0	0	0	0	4
Arremon flavirostris	0	3	0	22	0
Zonotrichia capensis	0	0	0	0	1
CARDINALIDAE					
Habia rubica	0	13	13	6	3
Caryothraustes canadensis	15	0	0	0	0
ICTERIDAE					
Psarocolius decumanus	4	0	0	0	1
Cacicus cela	22	0	0	0	0
Cacicus haemorrhous	17	8	0	13	0
Cacicus chrysopterus	0	0	6	0	3
Icterus jamacaii	14	0	0	0	0
Icterus pyrrhopterus	0	0	0	7	0
Gnorimopsar chopi	2	0	0	0	0
FRINGILLIDAE					
Euphonia chlorotica	12	5	3	24	5
Euphonia violacea	31	7	0	0	2

Euphonia chalybea	0	0	0	0	2
Euphonia cyanocephala	1	0	0	0	0
Euphonia xanthogaster	9	0	0	0	0
Euphonia pectoralis	5	4	7	0	4
Spinus magellanicus	0	0	0	0	1

Table A.3: Species included in the analysis and and number of sites in which the species was detected.

A. Fixed effects	**Estimate**	**Std. Error**	**z value**	**Pr(>|z|)**
Intercept	-2.152	0.384	-5.594	0.001
Distance to range edge (DE)	0.052	0.009	5.783	0.001
Forest edge density (ED)	-0.891	0.417	-2.136	0.05
Forest cover (FC)	1.171	0.541	2.16	0.05
DE:ED	0.027	0.005	5.438	0.001
DE:FC	-0.032	0.012	-2.638	0.01
ED:FC	0.667	0.580	1.150	0.250
DE:ED:FC	-0.022	0.008	-2.706	0.01

B. Random effects		**Variance**	**Std. Dev**
Species	Intercept	5.376	2.318
	Distance to range edge (DE)	0.010	0.103
	Forest edge density (ED)	0.857	0.925
	Forest cover (FC)	2.231	1.493
	DE:ED	0.0005	0.022
	DE:FC	0.011	0.106
	ED:FC	0.958	0.979
	DE:ED:FC	0.001	0.042
Datasets	Intercept	0.534	0.731
	Forest edge density (ED)	0.723	0.850
	Forest cover (FC)	1.133	1.064
	ED:FC	1.446	1.202

Table A.4: Mixed effects model coefficients for edge density (ED). Number of observations: 21,142; species: 362; datasets: 5.

A. Fixed effects		**Estimate**	**Std. Error**	**z value**	**Pr(>|z|)**
Intercept		-2.474	0.468	-5.277	0.001
Distance to range edge (DE)		0.064	0.009	7.075	0.001
Forest number of patches (NP)		-0.307	0.402	-2.136	0.445
Forest cover (FC)		1.704	0.594	2.16	0.005
DE:NP		0.017	0.004	5.438	0.001
DE:FC		-0.052	0.013	-2.638	0.001
NP:FC		0.182	0.561	1.150	0.745
DE:NP:FC		-0.017	0.011	-2.706	0.138
B. Random effects		**Variance**		**Std. Dev.**	
Species	Intercept	6.184		2.486	
	Distance to range edge (DE)	0.010		0.104	
	Forest number of patches (NP)	0.497		0.705	
	Forest cover (FC)	4.269		2.066	
	DE:NP	0.0005		0.024	
	DE:FC	0.015		0.124	
	NP:FC	1.46		1.208	
	DE:NP:FC	0.002		0.050	
Datasets	Intercept	0.876		0.935	
	Forest number of patches (ED)	0.656		0.809	
	Forest cover (FC)	1.329		1.152	
	ED:FC	0.982		0.991	

Table A.5: Mixed effects model coefficients for number of patches (NP). Number of observations: 21,142; species: 362; datasets: 5.

Term	VIF	Increased SE	Tolerance
Distance to range edge (DE)	**1.14**	**1.07**	**0.87**
Forest edge density (ED)	**1.38**	**1.17**	**0.72**
Forest cover (FC)	**1.36**	**1.17**	**0.73**
DE:ED	**3.79**	**1.95**	**0.26**
DE:FC	**1.90**	**1.38**	**0.53**
ED:FC	**1.15**	**1.07**	**0.87**
DE:ED:FC	**4.10**	**2.02**	**0.24**

Table A.6: Multicollinearity between explanatory variables in the mixed effects model of species probability of occurrence for edge density. Number of observations: 21,142; species: 362; studies: 5

Term	VIF	Increased SE	Tolerance
Distance to range edge	**1.38**	**1.17**	**0.73**
Number of patches	**1.28**	**1.13**	**0.78**
Forest cover	**1.36**	**1.17**	**0.73**
DE:NP	**3.92**	**1.98**	**0.26**
DE:FC	**2.47**	**1.57**	**0.40**
NP:FC	**1.26**	**1.12**	**0.80**
DE:NP:FC	**5.28**	**2.30**	**0.19**

Table A.7: Multicollinearity between explanatory variables in the mixed effects model of species probability of occurrence for number of patches. Number of observations: 21,142; species: 362; studies: 5

A.2 Supplementary Figures

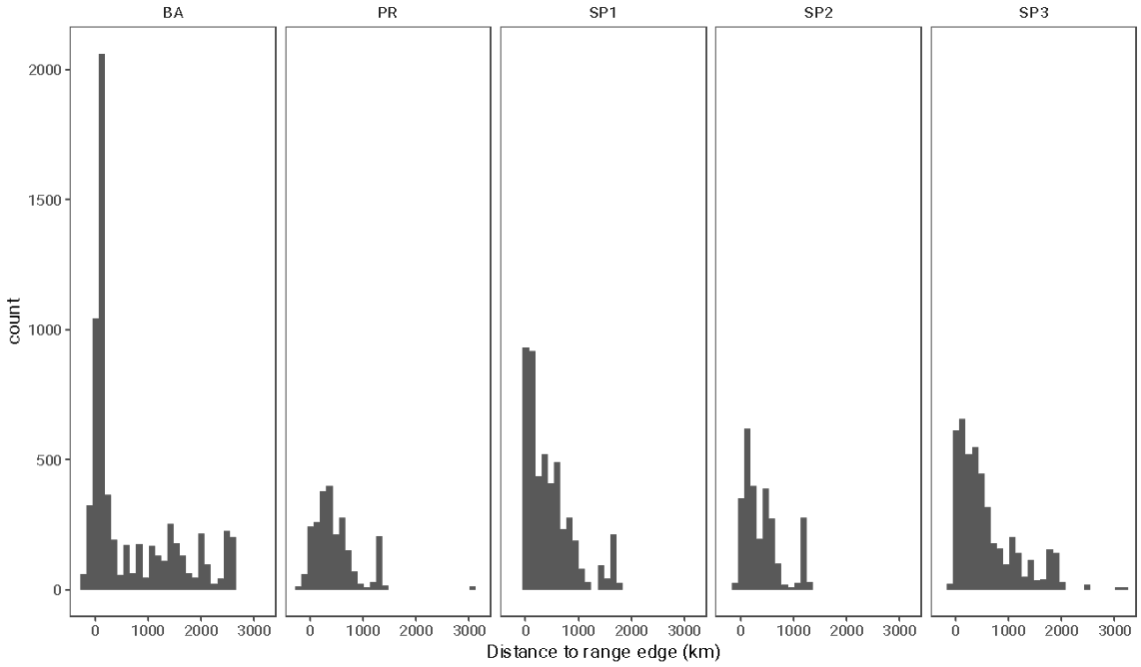


Figure A.1: Frequency of distance to range edge in kilometres per study (sample sizes per study = BA:6,552; PR:2,394; SP1:4,928; SP2:2,744; SP3:4,560; figure extracted from Bellotto-Trigo et al. (2023)).

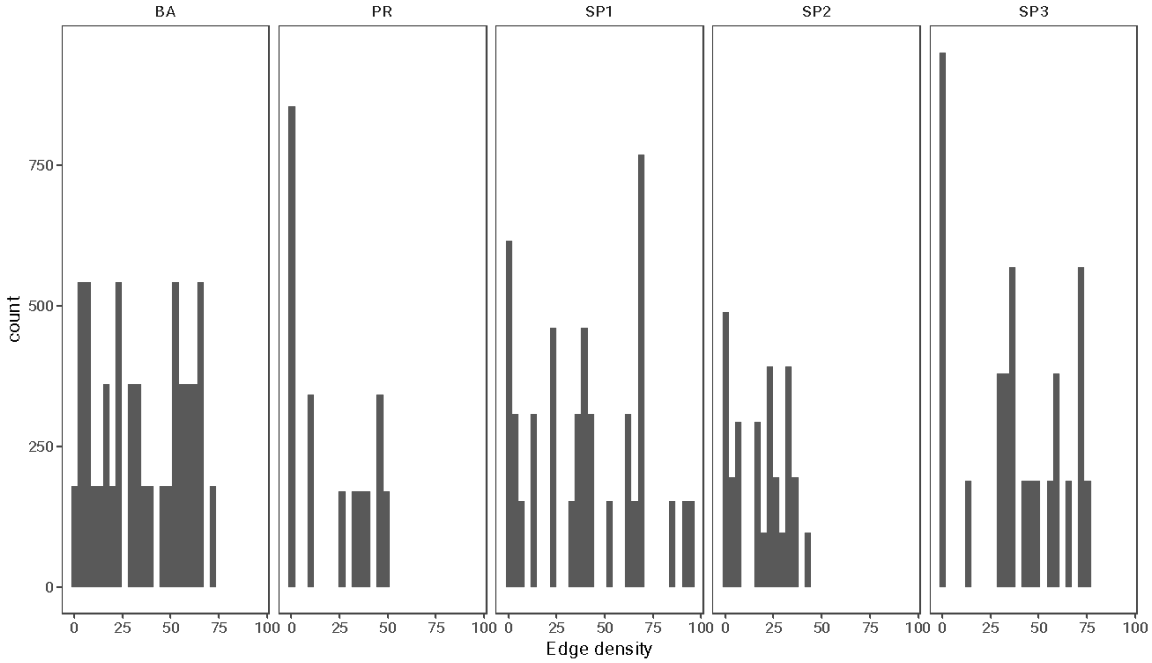


Figure A.2: Frequency of edge density per study (sample sizes per study = BA:6,552; PR:2,394; SP1:4,928; SP2:2,744; SP3:4,560; figure extracted from Bellotto-Trigo et al. (2023)).

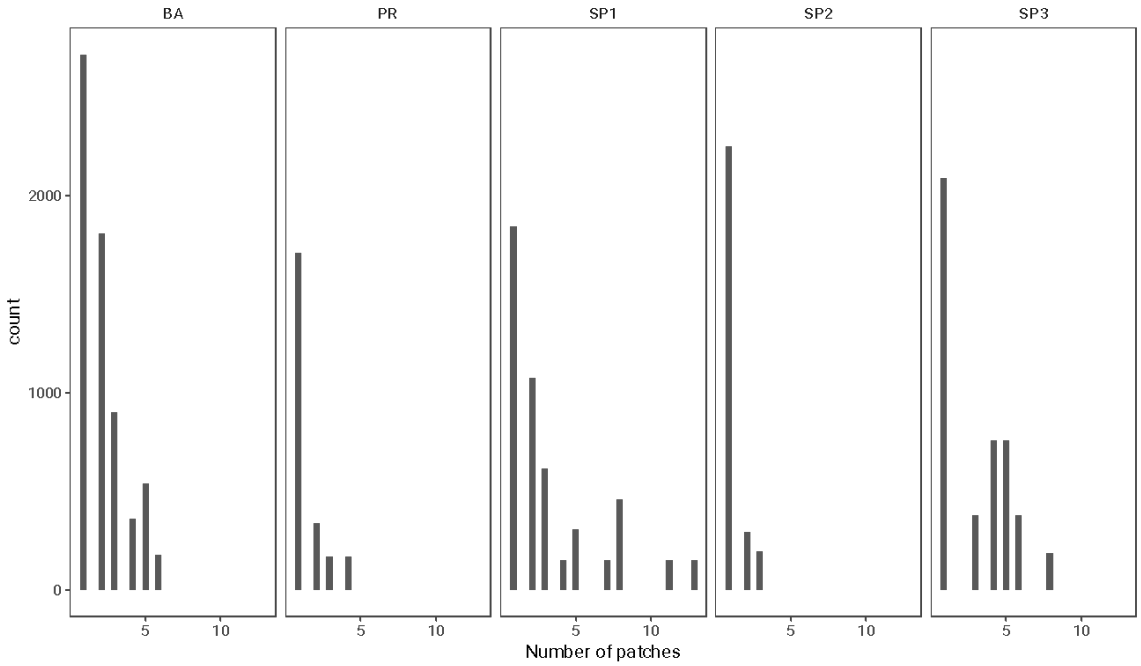


Figure A.3: Frequency of number of patches per study (sample sizes per study = BA:6,552; PR:2,394; SP1:4,928; SP2:2,744; SP3:4,560; figure extracted from Bellotto-Trigo et al. (2023)).

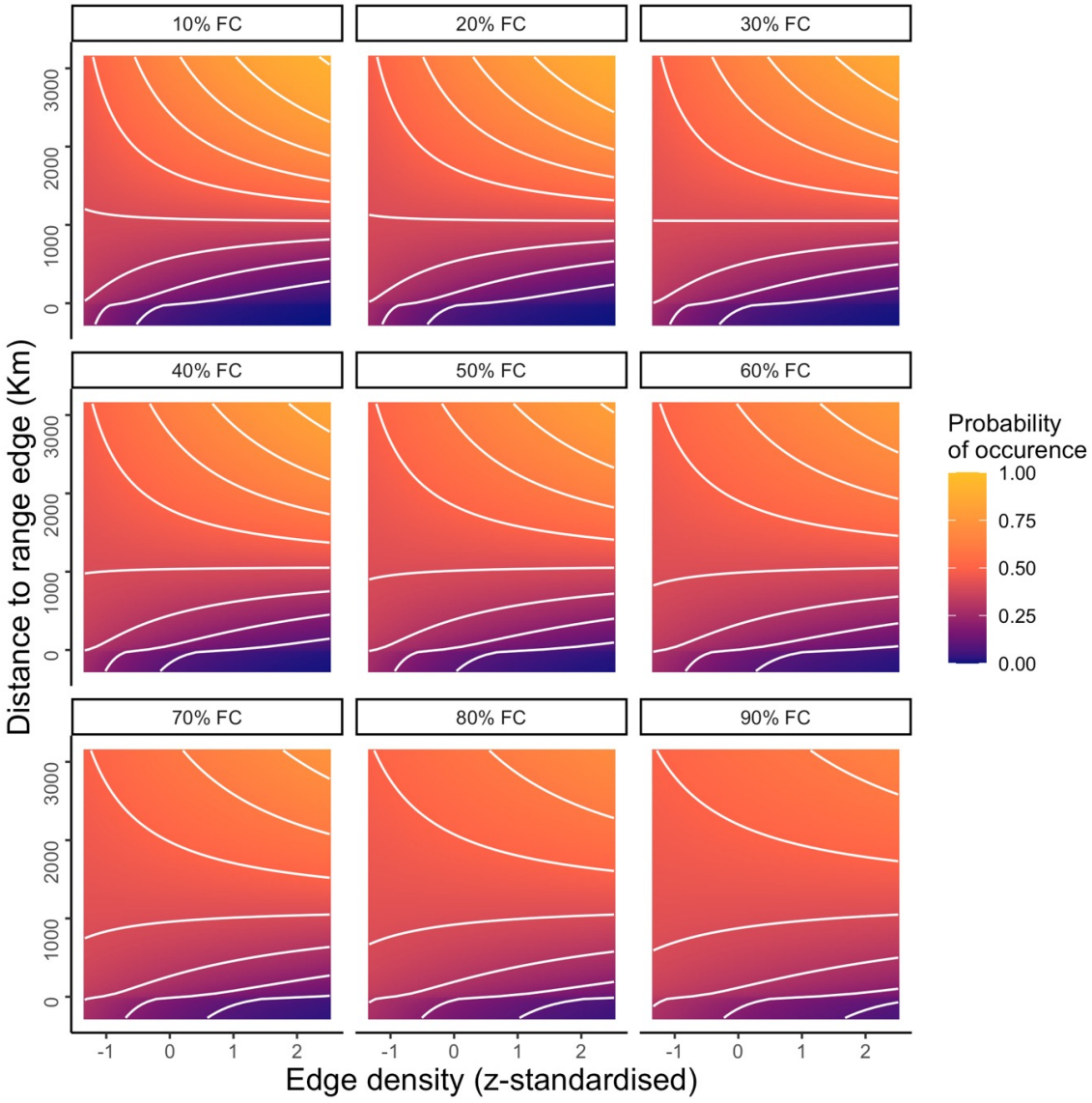


Figure A.4: Probability of incidence as a function of distance to range edge, forest cover and forest edge density. The x axis shows the distance to the range edge in km, data located below of the 0 represent incidence outside the range. The y axis shows responses to distance to range edge. The x axis shows the standardised forest edge density. Each panel shows each level of forest cover. Colour changes from navy blue for low probability of incidence to yellow for high probability of incidence along the three-way interaction amongst distance to range edge, forest cover and forest edge density. The white contour lines show where probability of occurrence changes (figure extracted from Bellotto-Trigo et al. (2023)).

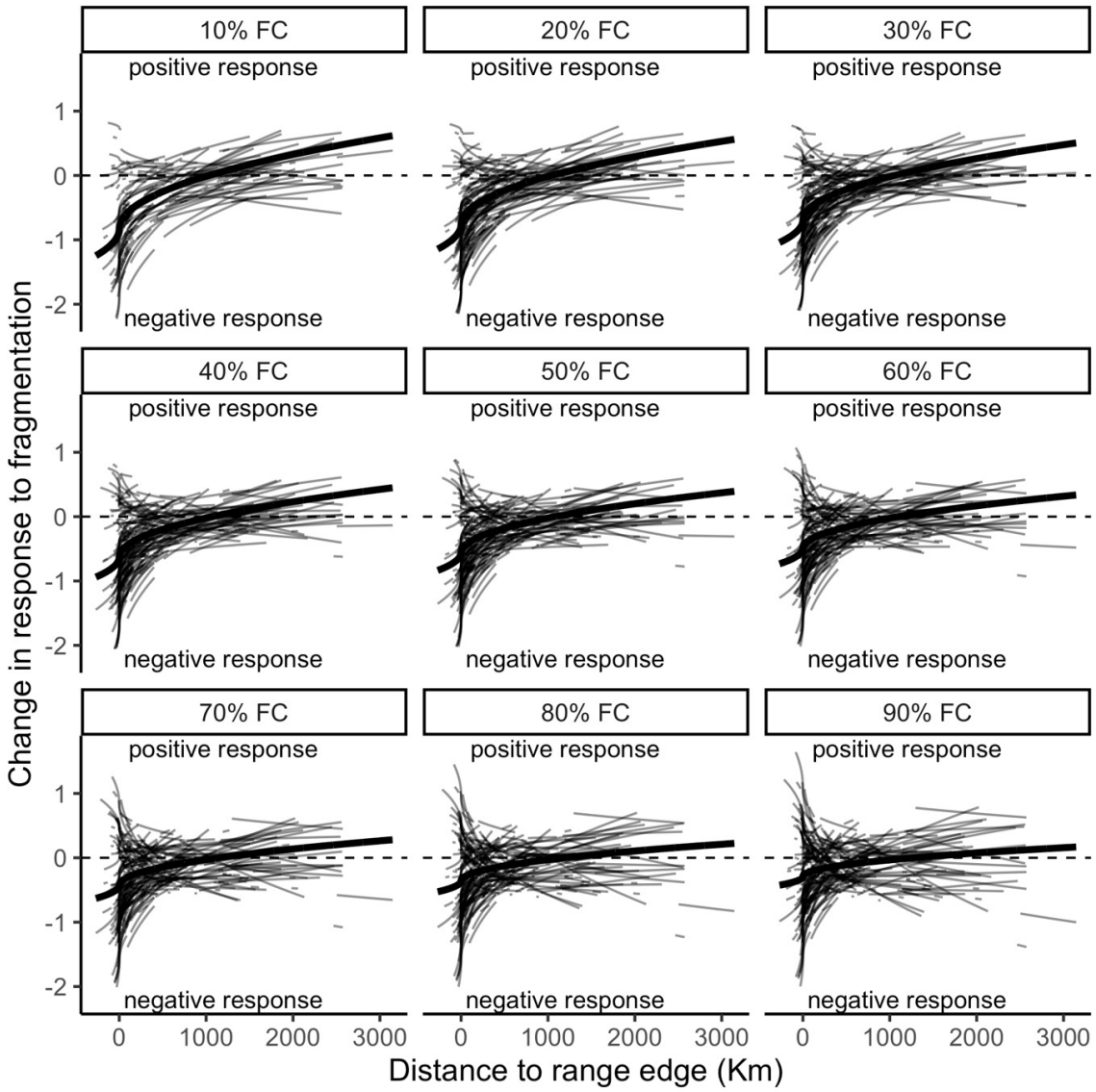


Figure A.5: Change in species' responses to fragmentation is modulated by distance to range edge and forest cover. Dark bold lines show how the average community response to fragmentation (y axis) changes with distance to the range edge (x axis) at each forest cover (panels 10% to 90% FC). The thinner lines represent the trajectory for individual species (n=362) (i.e., intraspecific variation), while the variation between lines shows the interspecific variation. The dotted line shows the point where responses to fragmentation change from positive (above) to negative (below). This figure was plotted by taking the derivative of the mixed effects model parameters with respect to fragmentation (figure extracted from Bellotto-Trigo et al. (2023)).

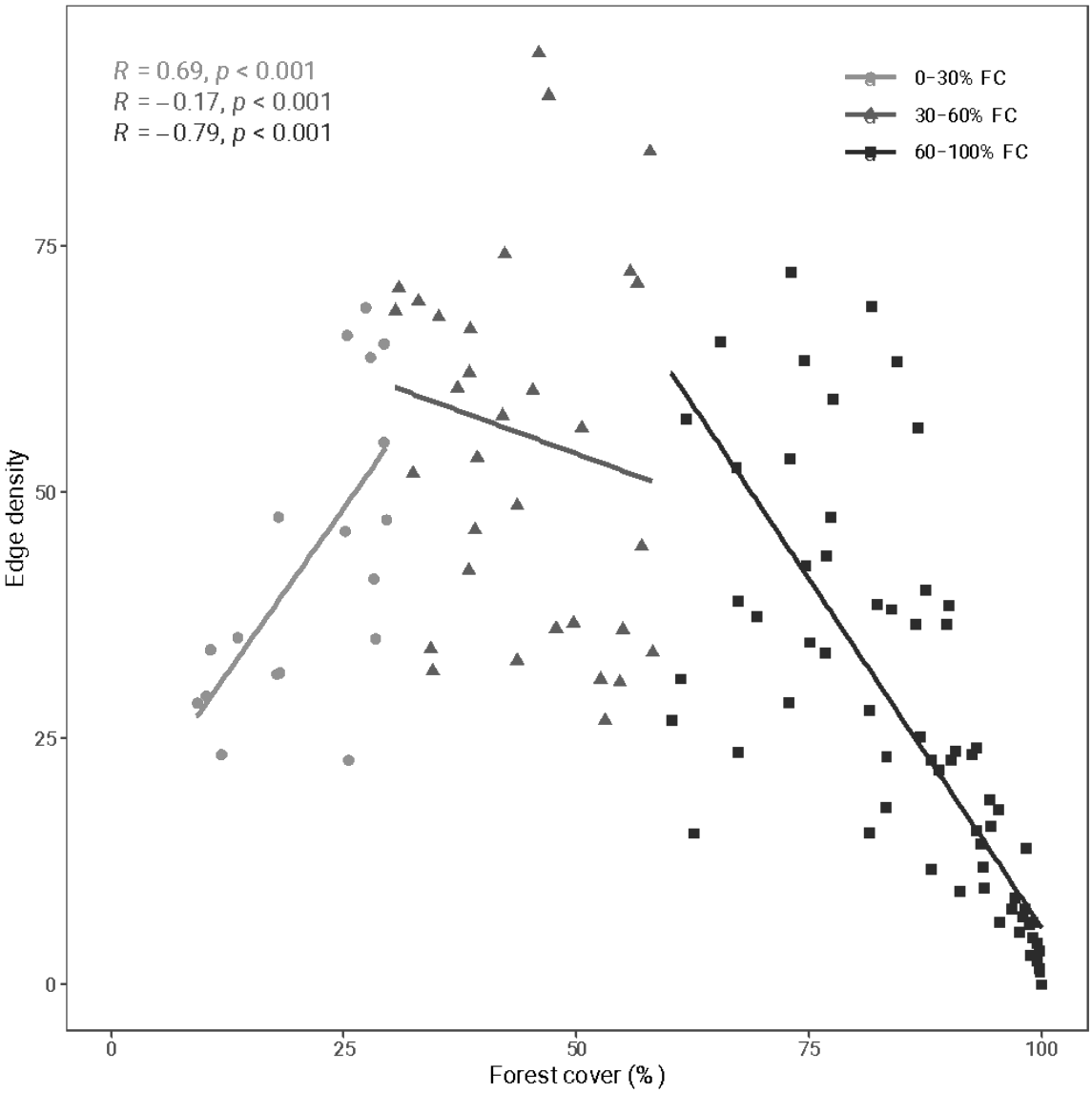


Figure A.6: Pearson's correlation between forest cover (FC) and edge density (ED). Each line (colour hue/shape) represents one category of forest cover (n=134); (figure extracted from Bellotto-Trigo et al. (2023)).

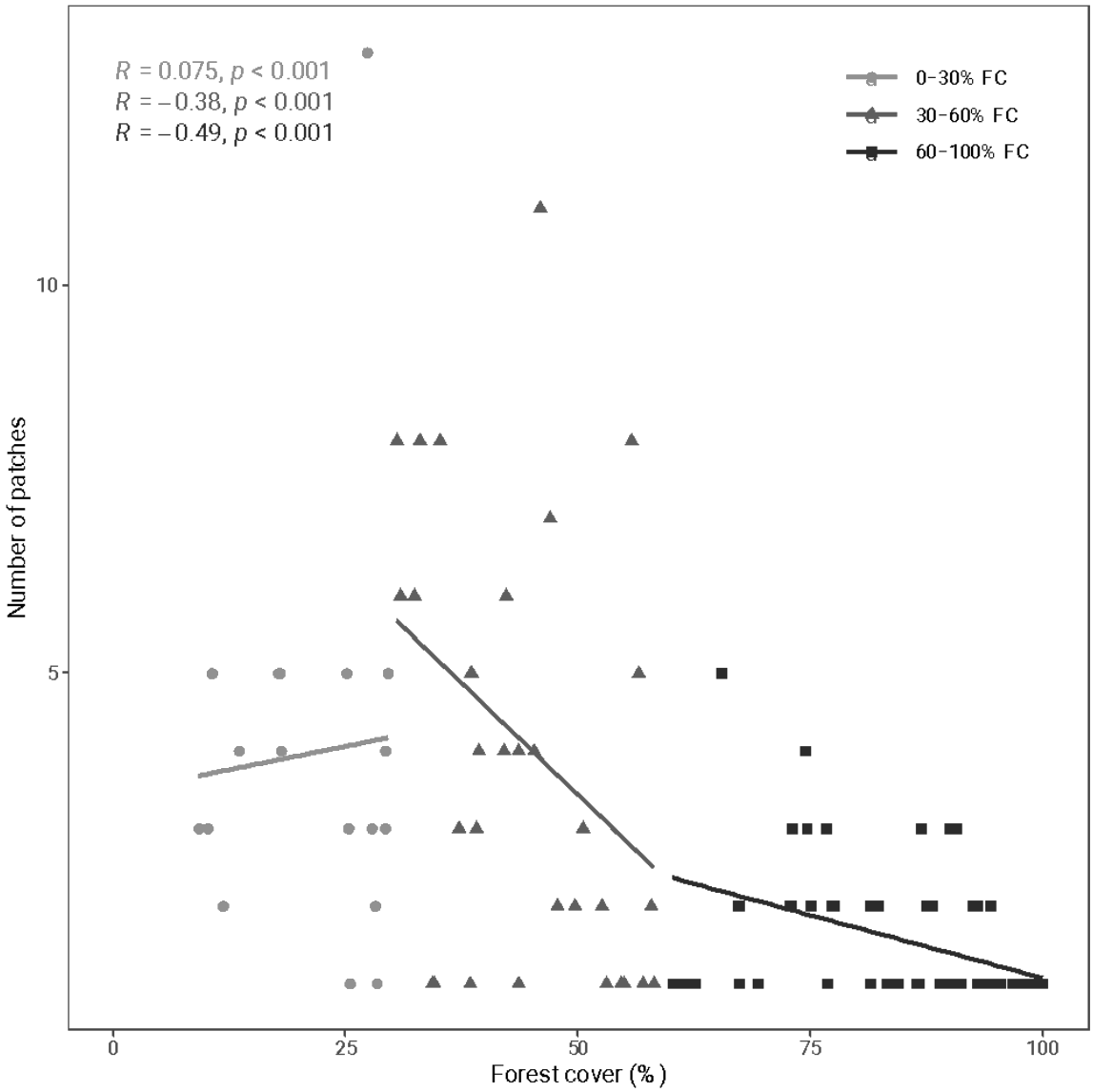


Figure A.7: Pearson's correlation between forest cover (FC) and number of patches (NP). Each line (colour hue/shape) represents one category of forest cover (n=134); (figure extracted from Bellotto-Trigo et al. (2023)).

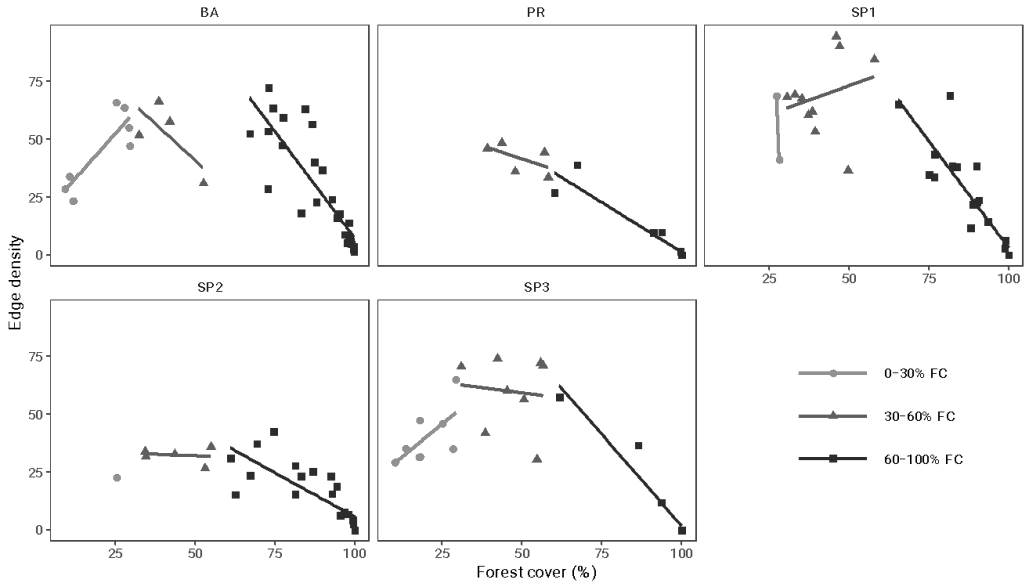


Figure A.8: Pearson's correlation between forest cover (FC) and edge density (ED) per study. Each line (colour hue/shape) represents one category of forest cover (BA=40; PR=14; SP1=32; SP2=28; SP3=24); (figure extracted from Bellotto-Trigo et al. (2023)).

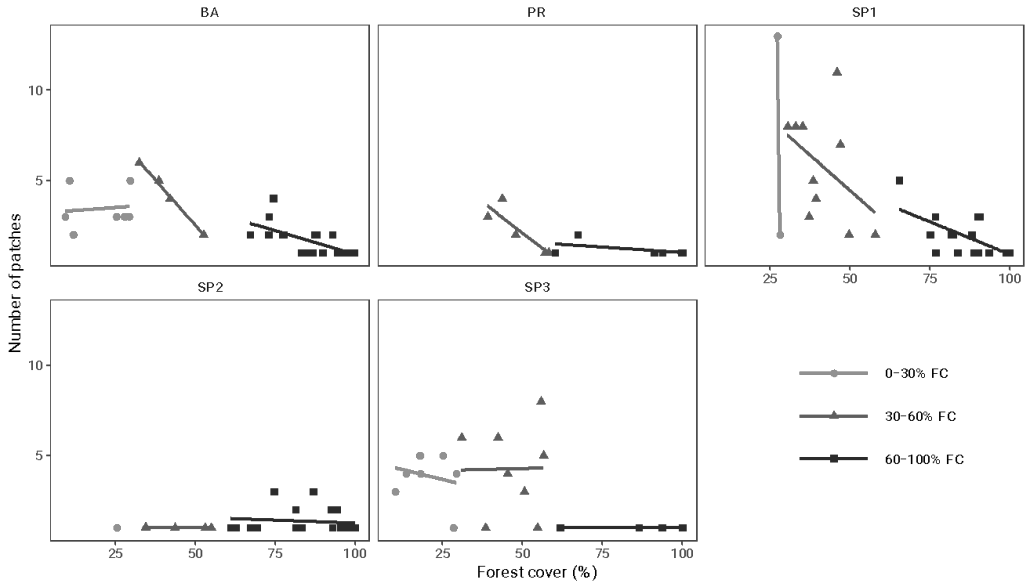


Figure A.9: Pearson's correlation between forest cover (FC) and number of patches (NP) per study. Each line (colour hue/shape) represents one category of forest cover (BA=40; PR=14; SP1=32; SP2=28; SP3=24); (figure extracted from Bellotto-Trigo et al. (2023)).

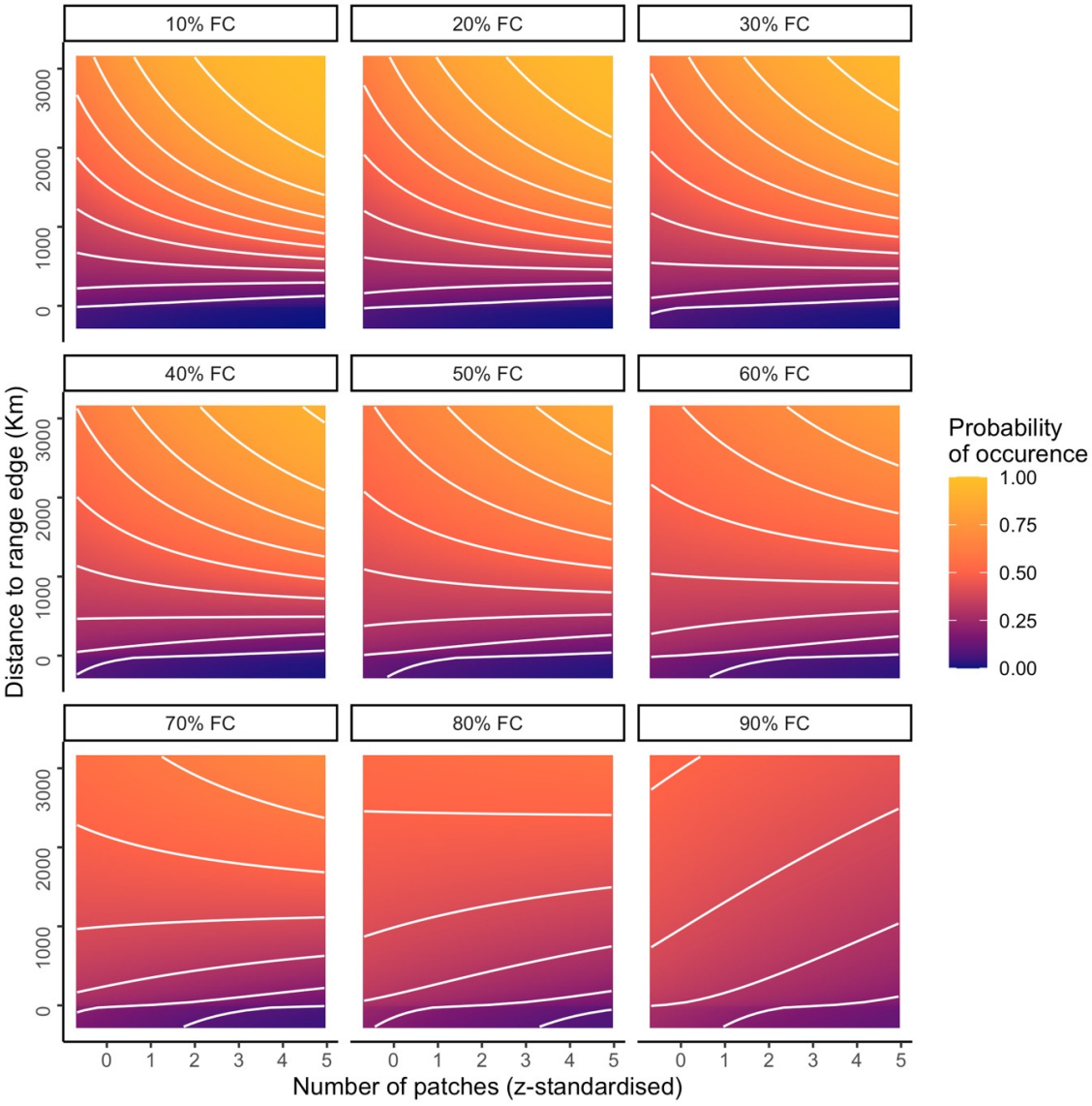


Figure A.10: Probability of incidence as a function of distance to range edge, forest cover and forest number of patches. The x axis shows the distance to the range edge in km, data located below of the 0 represent incidence outside the range. The y axis shows responses to distance to range edge. The x axis shows the standardised forest edge density. Each panel shows each level of forest cover. Colour changes from navy blue for low probability of incidence to yellow for high probability of incidence along the three-way interaction amongst distance to range edge, forest cover and forest edge density. The white contour lines show where probability of occurrence changes; (figure extracted from Bellotto-Trigo et al. (2023)).

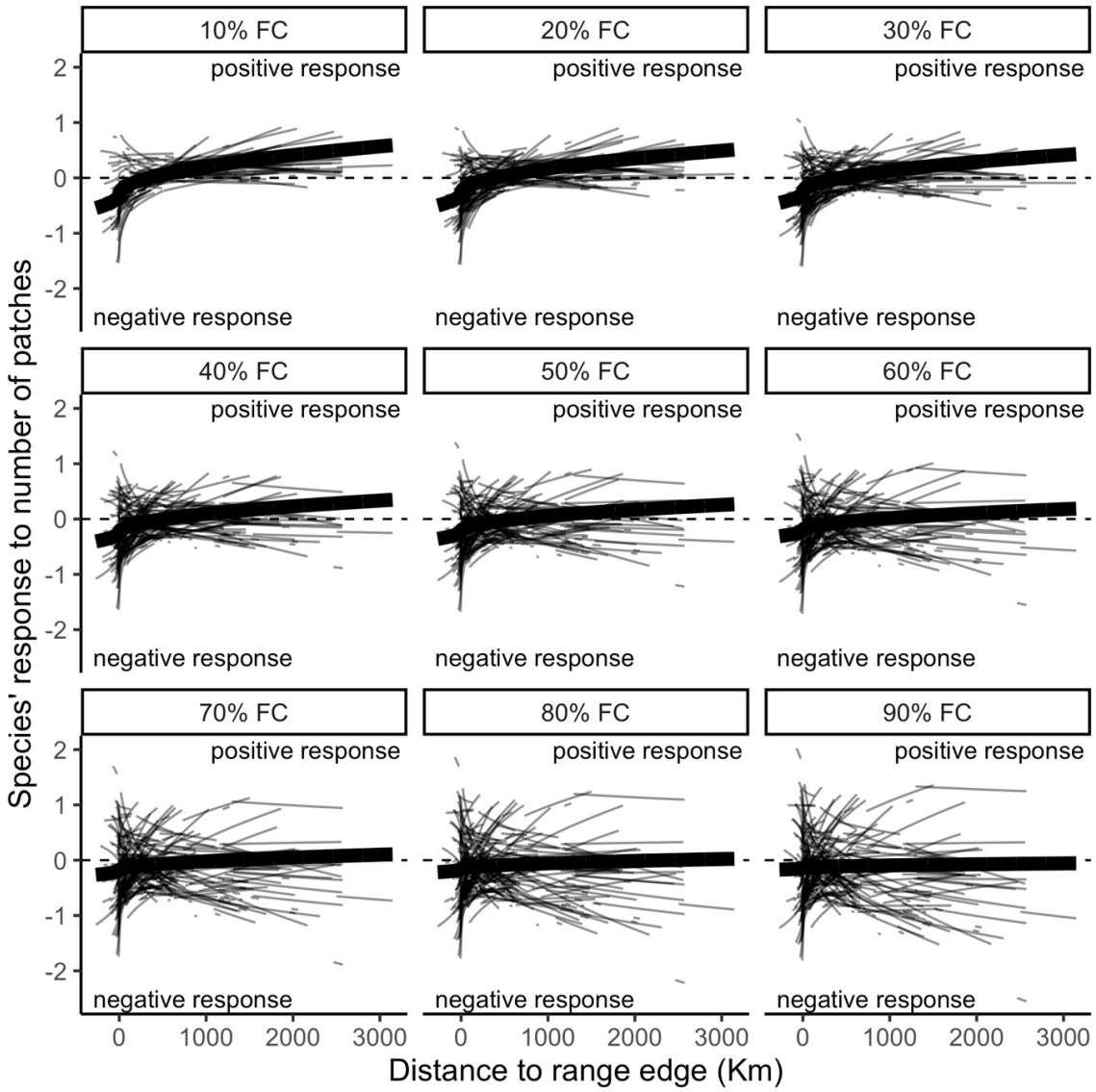


Figure A.11: Change in species' responses to fragmentation is modulated by distance to range edge and forest cover. Dark bold lines show how the average community response to fragmentation (y axis) changes with distance to the range edge (x axis) at each forest cover (panels 10% to 90% FC). The thinner lines represent the trajectory for individual species (n=362) (i.e., intraspecific variation), while the variation between lines shows the interspecific variation. The dotted line shows the point where responses to fragmentation change from positive (above) to negative (below). This figure was plotted by taking the derivative of the mixed effects model parameters with respect to fragmentation ; (figure extracted from Bellotto-Trigo et al. (2023)).

A.3 Derivative

Taking the occurrence model with all variables and their interactions:

$$\begin{aligned} I = &\beta_{Intercept} + \beta_{DE}X_{DE} + \beta_{FR}X_{FR} + \beta_{FC}X_{FC} + \\ &\beta_{DE:FR}X_{DE}X_{FR} + \beta_{DE:FC}X_{DE}X_{FC} + \beta_{FC:FR}X_{FC}X_{FR} + \\ &\beta_{DE:FR:FC}X_{DE}X_{FC} \end{aligned} \tag{A.1}$$

We take the derivative with respect to fragmentation (FR). This gives us the expression:

$$\Delta_{FR} = \frac{dI}{dX_{FR}} = \beta_{FR} + \beta_{DE:FR}X_{DE} + \beta_{FC:FR}X_{FC} + \beta_{DE:FR:FC}X_{DE}X_{FC} \tag{A.2}$$

Which is the same expression presented in the main text.

Appendix B

Supplementary Information for Chapter 3

B.1 Supplementary Tables

Species	N sampled	Measured		Model	
		FA	FGB	FA	FGB
TINAMIDAE					
Crypturellus tataupa	20	Yes	No	No	No
COLUMBIDAE					
Patagioenas cayennensis	20	Yes	Yes	No	No
Leptotila verreauxi	20	Yes	Yes	Yes	Yes
Leptotila rufaxilla	20	Yes	Yes	Yes	Yes
CUCULIDAE					
Piaya cayana	20	Yes	Yes	No	No
TROCHILIDAE					
Thalurania glaucopis	20	Yes	No	Yes	No
TROGONIDAE					
Trogon rufus	20	Yes	Yes	Yes	Yes
PICIDAE					
Celeus flavescens	20	Yes	No	Yes	No
Hylatomus lineatus	20	Yes	Yes	Yes	Yes
PSITTACIDAE					
Pionus maximiliani	20	Yes	Yes	No	No
THAMNOPHILIDAE					
Pyriglena leucoptera	20	Yes	Yes	Yes	Yes
FURNARIIDAE					
Automolus leucophthalmus	20	Yes	Yes	Yes	Yes
Xenops rutilus	20	Yes	Yes	Yes	Yes
DENDROCOLAPTIDAE					
Sittasomus griseicapillus	20	Yes	Yes	Yes	Yes
Xiphorhynchus fuscus	20	Yes	No	Yes	No
TYRANNIDAE					

Leptopogon amaurocephalus	20	Yes	Yes	Yes	Yes
Myiornis auricularis	20	Yes	Yes	Yes	Yes
Lathrotriccus euleri	20	Yes	Yes	Yes	Yes
Myiarchus swainsoni	20	Yes	Yes	Yes	Yes
VIREONIDAE					
Vireo olivaceus	20	Yes	Yes	Yes	Yes
TURDIDAE					
Turdus albicollis	20	Yes	Yes	Yes	Yes
PARULIDAE					
Setophaga pitiayumi	20	Yes	Yes	Yes	Yes
THRAUPIDAE					
Conirostrum speciosum	20	Yes	Yes	Yes	Yes
FRINGILLIDAE					
Euphonia chlorotica	20	Yes	Yes	Yes	Yes
TOTAL	480	24	20	19	17

Table B.1: Species used in the fluctuating asymmetry (FA) and ptilochronology (FGB) analyses. Columns show the number of individuals measured, and specify the species that were measured in the museum and the ones that were used to fit the models. Some species were not included in the analysis after data cleaning.

Trait	Parameter	Est	Error	Credible Intervals				Pd
				lower 89%	upper 89%	lower 95%	upper 95%	
Wing FA	FC	0.41	0.54	-0.44	1.28	-0.63	1.48	77.76%
	DE	-0.0001	0.01	-0.02	0.02	-0.02	0.02	51.97%
	FC:DE	-0.01	0.02	-0.04	0.02	-0.04	0.03	65.39%
	FC Sigma	0.27	0.66	-0.77	1.35	-1.01	1.62	65.14%
	DE Sigma	-0.02	0.02	-0.05	0.0001	-0.06	0.01	92.13%
	FC:DE Sigma	-0.0001	0.02	-0.04	0.03	-0.05	0.04	54.60%
Tarsus FA	FC	0.31	0.39	-0.29	0.93	-0.43	1.08	79.38%
	DE	0.01	0.01	-0.0001	0.02	-0.01	0.03	90.24%
	FC:DE	-0.01	0.01	-0.03	0.02	-0.03	0.02	69.08%
	FC Sigma	-0.18	0.62	-1.15	0.82	-1.37	1.05	62.32%
	DE Sigma	-0.0001	0.01	-0.03	0.02	-0.03	0.03	65.39%
	FC:DE Sigma	0.0001	0.02	-0.03	0.03	-0.04	0.04	52.70%
Feather GB	FC	0.09	1.20	-1.84	2.02	-2.26	2.44	53.26%
	DE	0.16	0.40	-0.48	0.81	-0.62	0.97	64.92%
	FC:DE	-0.21	0.21	-0.54	0.13	-0.62	0.22	84.77%
	FC Sigma	-0.25	0.77	-1.48	0.98	-1.75	1.27	62.92%
	DE Sigma	0.0001	0.02	-0.02	0.03	-0.03	0.03	56.77%
	FC:DE Sigma	-0.0001	0.02	-0.04	0.03	-0.05	0.04	54.84%

Table B.2: Coefficients for both mean and sigma models population-level effects (i.e. fixed effects) for all metrics. Est stands for Estimate, Pd refers to the probability of direction. Credible intervals (CI) are shown both at the 89% and 95% thresholds.

Trait	Parameter	Est	Error	Credible Intervals			
				lower 89%	upper 89%	lower 95%	upper 95%
Wing FA	sd(Intercept)	0.30	0.20	0.03	0.65	0.01	0.74
	sd(FC)	0.32	0.23	0.03	0.72	0.02	0.84
	sd(DE)	0.01	0.01	0.0001	0.02	0.0001	0.03
	sd(FC:DE)	0.01	0.01	0.0001	0.03	0.0001	0.03
	sd(Intercept Sigma)	0.79	0.32	0.35	1.34	0.25	1.51
	sd(FC Sigma)	0.38	0.30	0.03	0.92	0.01	1.13
	sd(DE Sigma)	0.02	0.01	0.92	0.05	0.0001	0.06
	sd(FC:DE Sigma)	0.02	0.01	0.0001	0.04	0.0001	0.05
Tarsus FA	sd(Intercept)	0.11	0.08	0.01	0.26	0.0001	0.31
	sd(FC)	0.12	0.11	0.01	0.32	0.0001	0.40
	sd(DE)	0.0001	0.0001	0.0001	0.01	0.0001	0.01
	sd(FC:DE)	0.0001	0.0001	0.0001	0.01	0.0001	0.01
	sd(Intercept Sigma)	0.74	0.36	0.26	1.38	0.19	1.57
	sd(FC Sigma)	0.32	0.25	0.03	0.78	0.01	0.93
	DE Sigma	0.02	0.01	0.0001	0.04	0.0001	0.05
	FC:DE Sigma	0.01	0.01	0.0001	0.03	0.0001	0.03
Feather GB	sd(Intercept)	19.99	8.45	6.12	33.52	3.38	37.25
	sd(FC)	10.11	7.26	0.95	23.05	0.44	27.34
	sd(DE)	0.47	0.31	0.05	1.01	0.02	1.16
	sd(FC:DE)	0.31	0.25	0.03	0.78	0.01	0.95
	sd(Intercept Sigma)	0.42	0.24	0.07	0.84	0.03	0.97
	sd(FC Sigma)	0.31	0.25	0.03	0.78	0.01	0.94
	sd(DE Sigma)	0.01	0.01	0.0001	0.02	0.0001	0.03
	sd(FC:DE Sigma)	0.01	0.01	0.0001	0.02	0.0001	0.03

Table B.3: Coefficients for both mean and sigma models group-level effects (i.e. random effects) for all metrics. Est stands for Estimate, Pd refers to the probability of direction. Credible intervals (CI) are shown both at the 89% and 95% thresholds.

B.2 Supplementary Figures



Figure B.1: Feather growth bars (alternating light and dark bands) on tail feather of Lineated Woodpecker (Dryocopus lineatus). Picture taken by Flavia C. B. Trigo at MZUSP, Brazil.

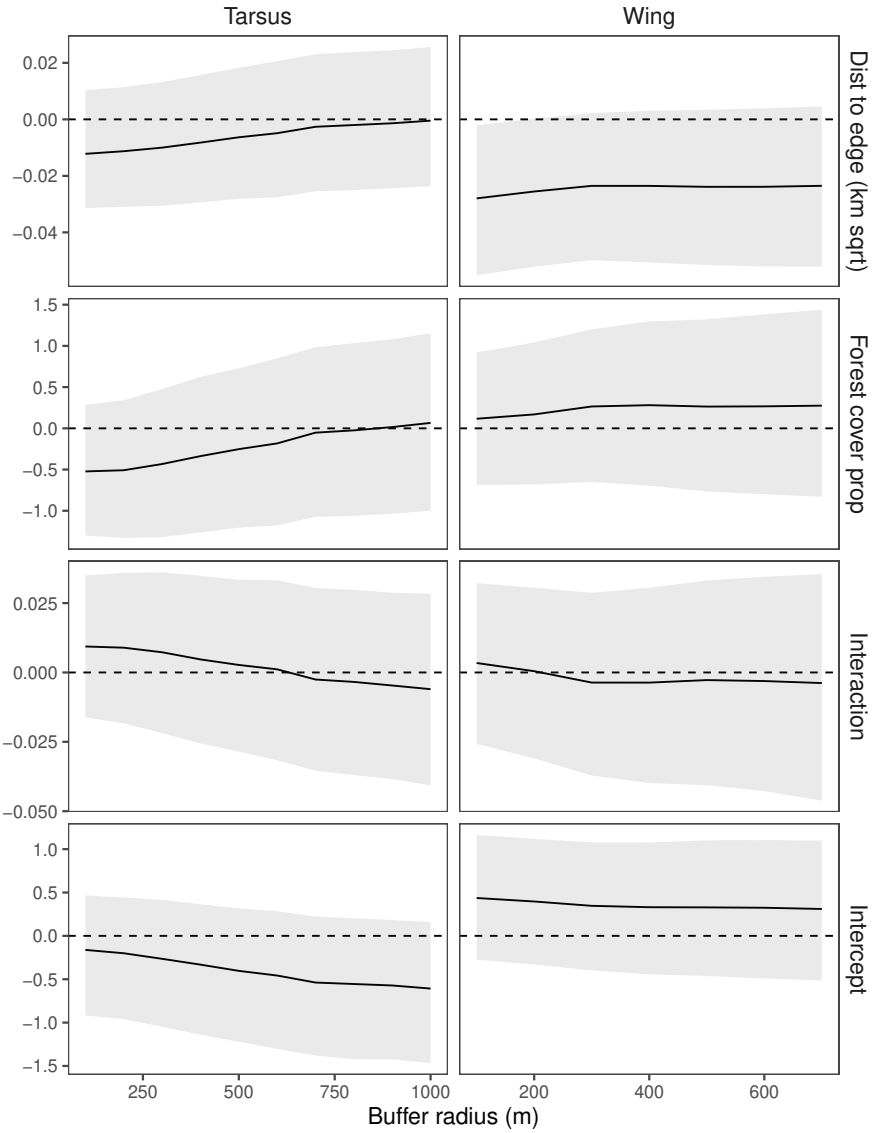


Figure B.2: Model coefficients for each fluctuating asymmetry model fitted with forest cover buffers from 100 to 1000 metres at 50 metres increments.

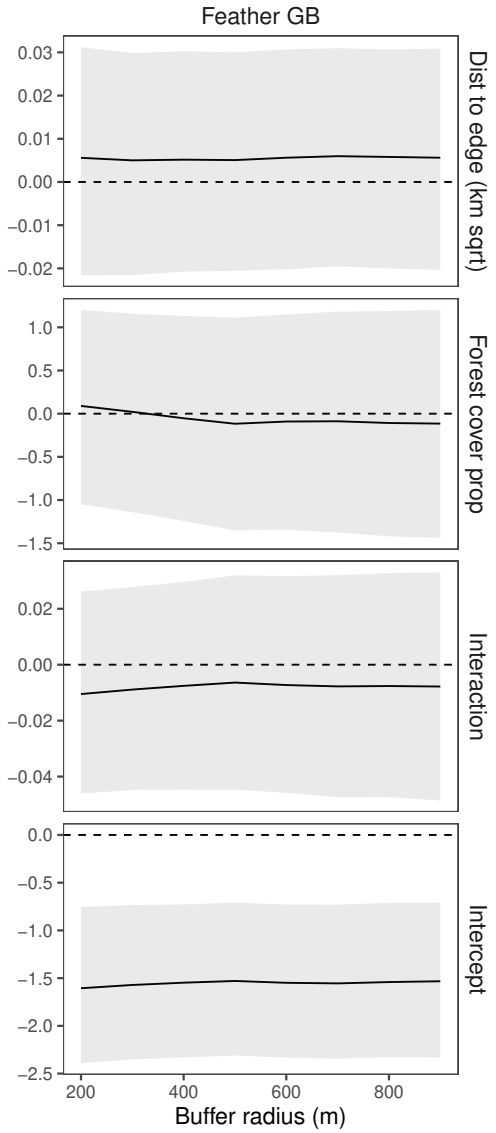


Figure B.3: Model coefficients for each ptilochronology model fitted with forest cover buffers from 100 to 1000 metres at 50 metres increments.

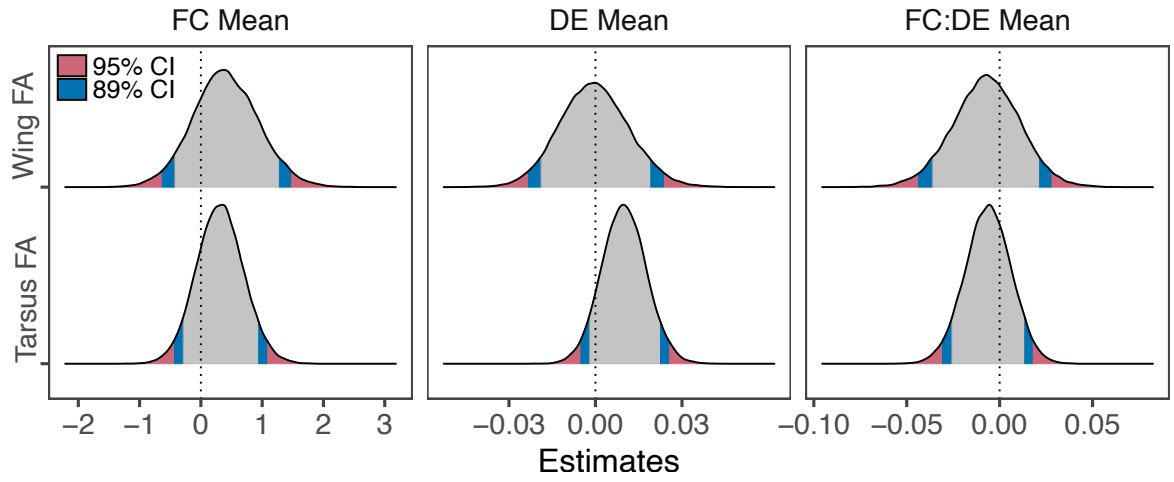


Figure B.4: Distribution of model estimates for the mean fluctuating asymmetry (wing and tarsus) values. The distributions represents the 2500 posterior draws, which show no responses with respect to forest cover, distance to range edge and the interaction between forest cover and distance to range edge. The dotted line at zero overlapping the grey area shows the theoretical area of no effect. If the line overlaps the blue area, then the estimated effect falls within the 89% Credible Interval (CI), similarly, if the line overlaps the red area the estimated effect falls within the 95% CI. The first panel shows the coefficient distribution for forest cover proportion (FC), the second panel shows the distribution for distance to range edge (DE), the third panel shows the distribution of coefficients for the interaction of forest cover proportion and distance to range edge (FC:DE), for the mean model (Mean)

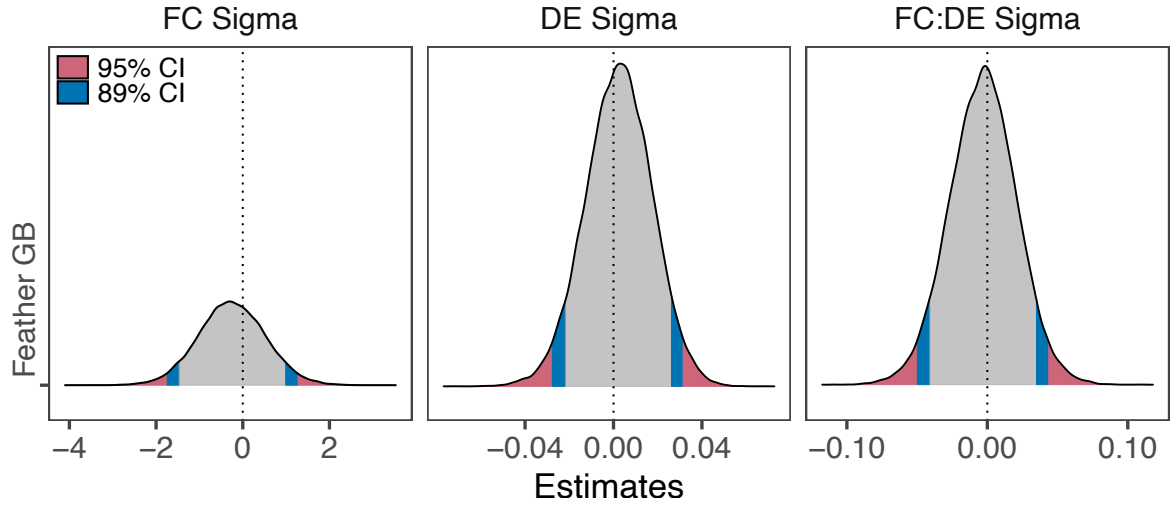


Figure B.5: Distribution of model estimates for the feather growth bar values. The distributions represents the 2500 posterior draws, which show no responses with respect to forest cover, distance to range edge and the interaction between forest cover and distance to range edge. The dotted line at zero overlapping the grey area shows the theoretical area of no effect. If the line overlaps the blue area, then the estimated effect falls within the 89% Credible Interval (CI), similarly, if the line overlaps the red area the estimated effect falls within the 95% CI. The first panel shows the coefficient distribution for forest cover proportion (FC), the second panel shows the distribution for distance to range edge (DE), the third panel shows the distribution of coefficients for the interaction of forest cover proportion and distance to range edge (FC:DE), for the variance model (Sigma)

Appendix C

Supplementary Information for Chapter 4

C.1 Supplementary Tables

Trait	N Observations	N Species	DE Median [range] (km)
Body Mass (g)	39,655	354	537.34 [0.25 - 3343.13]
Wing Length (mm)	28,620	330	516.58 [0.31 - 3343.13]
Tarsus Length (mm)	28,247	327	506.01 [0.29 - 3343.13]
Bill Length (mm)	26,321	308	485.41 [0.29 - 3343.13]

Table C.1: Total number of observations, species, and the median, minimum and maximum values of distance to range edge (DE) per trait.

Trait	Parameter	Est	Error	Credible Intervals				Pd
				lower 89%	upper 89%	lower 95%	upper 95%	
Wing	FC	0.001	0.001	-0.0001	0.01	-0.01	0.01	64.24%
	DE	0.001	0.001	-0.02	0.01	-0.02	0.02	60.85%
	FC:DE	0.001	0.001	-0.01	0.01	-0.01	0.01	54.84%
	FC Sigma	0.02	0.03	-0.02	0.06	-0.03	0.07	74.41%
	DE Sigma	0.04	0.03	-0.01	0.09	-0.02	0.10	88.60%
	FC:DE Sigma	-0.03	0.03	-0.08	0.01	-0.09	0.02	87.13%
Tarsus	FC	0.001	0.001	-0.01	0.01	-0.01	0.01	54.77%
	DE	-0.001	0.01	-0.01	0.02	-0.01	0.02	64.45%
	FC:DE	**-0.01**	**0.001**	**-0.02**	**-0.0001**	**-0.02**	**-0.0001**	97.67%
	FC Sigma	-0.04	0.03	-0.09	0.01	-0.1	0.02	91.55%
	DE Sigma	-0.02	0.04	-0.08	0.03	-0.09	0.05	74.76%
	FC:DE Sigma	**-0.06**	**0.04**	**-0.12**	**-0.01**	-0.14	0.01	96.24%
Body	FC	**-0.01**	**0.001**	**-0.01**	**-0.0001**	**-0.01**	**-0.0001**	99.64%
	DE	-0.01	0.01	-0.02	0.00	-0.03	0.0001	94.12%
	FC:DE	0.001	0.001	-0.01	0.01	-0.01	0.01	62.51%
	FC Sigma	-0.02	0.03	-0.06	0.02	-0.07	0.03	76.12%
	DE Sigma	0.02	0.03	-0.02	0.07	-0.03	0.08	81.00%
	FC:DE Sigma	0.02	0.03	-0.03	0.06	-0.04	0.07	71.17%
Bill	FC	**-0.01**	**0.01**	**-0.02**	**-0.01**	**-0.03**	**-0.0001**	99.83%
	DE	-0.01	0.01	-0.03	0.01	-0.03	0.02	77.33%
	FC:DE	0.00	0.01	-0.01	0.01	-0.01	0.01	53.35%
	FC Sigma	0.03	0.02	-0.01	0.07	-0.01	0.08	90.83%
	DE Sigma	0.01	0.03	-0.04	0.07	-0.05	0.08	64.69%
	FC:DE Sigma	0.01	0.03	-0.03	0.05	-0.04	0.06	60.64%

Table C.2: Coefficients for both mean and sigma models population-level effects (i.e. fixed effects) for all traits. Est stands for Estimate, Pd refers to the probability of direction. Credible intervals (CI) are shown both at the 89% and 95% thresholds. Estimates in bold show parameters that are significant at least at the 89% CI.

Trait	Parameter	Est	Error	Credible Intervals			
				lower 89%	upper 89%	lower 95%	upper 95%
Wing	sd(Intercept)	1.37	0.06	1.29	1.46	1.27	1.49
	sd(FC)	0.02	< 0.001	0.02	0.03	0.02	0.03
	sd(DE)	0.11	0.01	0.09	0.13	0.09	0.13
	sd(FC:DE)	0.04	0.01	0.03	0.05	0.03	0.05
	sd(Sigma Intercept)	0.36	0.03	0.31	0.40	0.31	0.41
	sd(FC Sigma)	0.27	0.03	0.23	0.32	0.22	0.33
	sd(DE Sigma)	0.35	0.04	0.29	0.41	0.28	0.42
	sd(FC:DE Sigma)	0.31	0.03	0.26	0.37	0.25	0.38
Tarsus	sd(Intercept)	1.37	0.06	1.28	1.46	1.26	1.48
	sd(FC)	0.03	0.01	0.02	0.04	0.02	0.04
	sd(DE)	0.08	0.01	0.06	0.09	0.06	0.09
	sd(FC:DE)	0.04	0.01	0.03	0.05	0.02	0.05
	sd(Sigma Intercept)	0.47	0.03	0.42	0.53	0.41	0.54
	sd(FC Sigma)	0.30	0.03	0.25	0.35	0.24	0.36
	sd(DE Sigma)	0.39	0.04	0.32	0.46	0.31	0.47
	sd(FC:DE Sigma)	0.43	0.04	0.37	0.49	0.35	0.51
Body	sd(Intercept)	1.35	0.05	1.27	1.44	1.26	1.46
	sd(FC)	0.02	0.00	0.02	0.03	0.02	0.03
	sd(DE)	0.09	0.01	0.08	0.10	0.07	0.11
	sd(FC:DE)	0.04	0.00	0.04	0.05	0.04	0.05
	sd(Sigma Intercept)	0.30	0.02	0.26	0.34	0.26	0.35
	sd(FC Sigma)	0.31	0.03	0.27	0.36	0.26	0.37
	sd(DE Sigma)	0.33	0.03	0.28	0.39	0.27	0.40
	sd(FC:DE Sigma)	0.29	0.04	0.24	0.35	0.23	0.37
Bill	sd(Intercept)	1.14	0.05	1.07	1.22	1.05	1.24
	sd(FC)	0.04	0.01	0.03	0.05	0.03	0.06
	sd(DE)	0.12	0.01	0.10	0.15	0.10	0.15
	sd(FC:DE)	0.05	0.01	0.03	0.06	0.03	0.07
	sd(Sigma Intercept)	0.31	0.02	0.28	0.35	0.27	0.36
	sd(FC Sigma)	0.22	0.02	0.19	0.26	0.18	0.27
	sd(DE Sigma)	0.39	0.03	0.34	0.44	0.33	0.45
	sd(FC:DE Sigma)	0.23	0.03	0.18	0.27	0.18	0.28

Table C.3: Coefficients for both mean and sigma models group-level effects (i.e. random effects) for all traits. "Est" stands for Estimate. Credible intervals (CI) are shown both at the 89% and 95% thresholds.