Universidade de Brasília
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TESE:

EFEITOS DA PAISAGEM NA MOVIMENTAÇÃO DIÁRIA DAS AVES: UMA ABORDAGEM EMPÍRICA E MODELOS DINÂMICOS DE SIMULAÇÃO

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“Caminho se conhece andando.

Então vez em quando é bom se perder.”

(Deus Me Proteja – Chico César)

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APRESENTAÇÃO GERAL

O presente trabalho é composto por três capítulos em que cada um corresponde a um artigo. Apesar de cada artigo ser destinado para uma revista diferente, para fim de padronização da tese os três capítulos estão com as normas de citação e referência bibliográfica no formato do periódico Ecology (ISSN: 0012-9658). O primeiro capítulo é uma revisão sistemática da literatura em que buscamos descrever as lacunas de conhecimento de demografia e história de vida da família Thraupidae. No segundo capítulo desenvolvemos modelos de simulação para entender os efeitos da perda e fragmentação de hábitat sobre a área de vida, nossos modelos foram parametrizados utilizando dados provenientes do primeiro capítulo. Por fim, o capítulo 3 busca validar os resultados do capítulo 2, para isso realizarmos uma meta-análise sobre o efeito da perda e fragmentação de hábitat sobre a área de vida de aves. Os dados, scripts dos modelos e análises de todos os capítulos estão disponíveis em repositório público do GitHub.

INTRODUÇÃO GERAL

Existe hoje uma grande demanda por alimento e matéria prima para a indústria, reflexo do crescimento da população humana e de crescentes níveis de consumo ao nível mundial. Como consequência, mais de um terço do ambiente terrestre é atualmente ocupado pela agricultura (FAOSTAT 2015). As atividades produtivas demandam mais espaço, gerando um conflito com a conservação da biodiversidade. A perda e fragmentação hábitat tem se destacado como o principal fator responsável pela perda da biodiversidade em todo o mundo (Foley et al. 2005). A perda de hábitat atua reduzindo os recursos e as áreas adequadas para a ocorrência das espécies (Fahrig 2003). Já a fragmentação transforma grandes áreas de habitat em fragmentos menores e isolados entre si, alterando suas condições ambientais por meio do efeito de borda e impedindo o fluxo gênico entre populações (Fahrig 2001, 2013). Desta maneira se torna importante entender como essas alterações na paisagem afetam a movimentação dos indivíduos de diferentes espécies, uma vez que a movimentação é importante para a sobrevivência dos indivíduos e para a persistência das populações.

Os indivíduos podem apresentar diferentes tipos de movimentação (e.g. migração, dispersão e forrageamento), sendo que essas movimentações se diferem pela motivação e escala espaço-temporal em que ocorrem (Clobert et al. 2012, With 2019). Por exemplo, movimentos migratórios ocorrem em grandes escalas espaço-temporais e geralmente estão ligados a sazonalidade climática, onde, o objetivo dos indivíduos é encontrar ambientes com condições e recursos adequados para passar um determinado período do ano (Cumming et al. 2012). Já movimentações dentro da área de vida de um animal ocorrem diariamente, e em escalas espaciais menores, e tem como principais motivos a busca por alimento, fuga de predadores, reconhecimento de novas áreas (Doherty et al. 2019). Durante a sua movimentação diária os indivíduos interagem com os elementos da paisagem podendo mudar o seu comportamento em função de sua estrutura (Hillaert et al. 2018). Por exemplo, indivíduos em paisagens com menor disponibilidade de recursos precisam se movimentar por uma área maior que indivíduos em paisagens com maior disponibilidade de recursos (Kleyheeg et al. 2017). Ao estudar movimentação de coalas (*Phascolarctos cinereus*) Rus et al. 2020 observaram que em paisagens menos conectadas os indivíduos se movimentavam por uma extensão maior que indivíduos em paisagens mais conectadas.

O uso de modelos dinâmicos em ecologia tem se mostrado útil para auxiliar no entendimento dos mecanismos por trás dos padrões e processos ecológicos (Codling and Dumbrell 2012, Bocedi et al. 2014, Zurell et al. 2015). Os modelos são simplificações do mundo real que nos permitem particionar o sistema de estudo e criar cenários nos quais controlamos parâmetros como: tamanho populacional, dispersão e estrutura do hábitat (Epperson et al. 2010, Wallentin 2017). Esse maior controle nos garante que o sistema de estudo não sofrerá interferência de fatores que não são os de interesse, e que podem causar confusão na interpretação dos resultados. Além disso, é possível comparar os padrões de respostas gerados pelo modelo com os padrões apresentados no mundo real, essa abordagem tem sido chamada de “abordagem do ecólogo virtual” (Zurell et al. 2010). Essa abordagem geralmente é composta por quatro etapas: (i) modelo ecológico virtual; (ii) modelo virtual de coleta de dados; (iii) análise estatística dos dados e (iv) avaliação do modelo. A primeira etapa consiste em construir um modelo simulando o processo de interesse incluindo espécies, dinâmica populacional, estrutura espacial. Os passos seguintes consistem em criar um modelo que simule a coleta dos dados de acordo assim como ela é realizada em campo, e então são feitas a analises estatísticas. Por fim é feita a comparação entre o resultado encontrado pela coleta virtual e o conjunto total de dados modelo, isso permite testar se os métodos usados são eficientes em capturar o padrão de interesse e então e feita a comparação dos resultados do modelo com os resultados encontrados a partir de dados empíricos.

O objetivo desta tese é entender como a parda e fragmentação de hábitat afetam a movimentação das aves dentro de sua área de vida, e também, quantificar as lacunas de conhecimento Prestoniana e Raunkiæna. No capítulo 1 iremos avaliar o estado da arte e quantificar as lacunas de conhecimento para dados que são utilizados na parametrização das análises de viabilidade populacionais (AVP) que utilizam abordagem baseada em indivíduo. Além disso, a partir do levantamento de dados do capítulo 1 irei montar um banco de dados com parâmetros necessários para o desenvolvimento da capítulo 2. No capítulo 2 buscaremos entender os mecanismos envolvidos na relação entre a paisagem e movimentação das aves. Para isso iremos desenvolver modelos de simulação baseados em indivíduo para que possamos ter o controle sobre as variáveis que realmente temos interesse. E testaremos as hipóteses de que existe um efeito negativo da perda e fragmentação sobre o tamanho da área de vida, sobreposição da área de vida entre indivíduos e tempo que os indivíduos passam se movimentando na paisagem. Testaremos também se a capacidade de navegação dos indivíduos pode alterar a direção e magnitude dessa relação. Por fim, o capítulo 3 tentará validar parte dos resultados do capítulo 2 por meio de uma meta-análise. E será testado se a perda e fragmentação de hábitat afeta o tamanho da área de vida, o tempo que os indivíduos gastam se movimentando e se o impacto da perda de hábitat é maior do que o da fragmentação.

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Capítulo I

Describing our ignorance about the life history and demography of the Thraupidae family

Abstract

We probably are facing the sixth major mass extinction, and management of interventions for conservation is necessary. However, resources for conserving and managing populations in natural environments are scarce, and tools for assessing population risk extinction for each strategy are essential. The best-known technique for estimating extinction risk is the Populational Viability Analysis (PVA). However, these analyzes need a large amount of information about the biology and ecology of the species. We aimed to evaluate the life history (Raunkiæran) and demography (Prestonian) knowledge shortfall of Thraupidae birds. We reviewed 838 Web of Science and Scopus articles published between 1973 and 2020. Only 57 articles met our selection criteria after review, and were included in the present study. Our results showed that the Prestonian shortfall was more expressive than the Raunkiæran shortfall. The phylogeny and body mass could not explain any pattern in the publication. The ease of collecting life history data compared to demographic data was one of the reasons why the Prestonian shortfall was so much more significant than Raunkiæran. We concluded that publishing data in a public repository is essential for reducing the knowledge shortfall and making data available for PVA.

Keywords: Systematic review, Reproductive Biology, Bird, Non-linear regression, PRISMA Protocol, Biodiversity.

Introduction

We are on the verge of a biodiversity crisis and facing the sixth major mass extinction (Singh 2002, Koh et al. 2004). Even with extinction being part of the earth's history, we can observe anthropic activities like habitat destruction, alien species introduction, and global environmental changes acting together to accelerate this extinction process (Doherty et al. 2015, Bonebrake et al. 2019). Given this scenario, management interventions toward biodiversity conservation are necessary, and species extinction risk species is an essential step in this process, assuring a better resource allocation (McDonald-Madden et al. 2008). These analyses aim to predict populations persistence over time and can therefore estimate the probability of population extinction for each management and conservation strategy (Possingham et al. 1993, Ellner and Fieberg 2003). After this, the extinction risk analysis also helps with population monitoring, guiding which moment to make interventions or changes in the management strategies (Manlik et al. 2018).

The best-known technique for estimating extinction risk is the Populational Viability Analysis (PVA). PVA allows estimates about minimal viable population sizes (MVP) to keep positive growth rates (Reed et al. 2002). PVA techniques encompass a range of different model strategies, such as patch occupation models, matrix projection (Structured population models), and individual-based models (IBM) (Radchuk et al. 2016). These models allow to create different environmental scenarios, like adding catastrophes and disturbances that might affect the individual's survival or reproduction; it also is possible to simulate environmental variations that affect available resources, for example, varying the support capacity (K) (Bradshaw et al. 2018, Machado et al. 2020). This approach to PVA is known as sensitivity analysis, and from there, it is possible to evaluate the importance of life-history parameters to extinction risk and population growth (Mills and Lindberg 2002).

The most significant differences among those models are their population and environmental parameters. The choice among them is usually related to the degree of ecological knowledge about the group under evaluation (Radchuk et al. 2016, DeAngelis and Diaz 2019, García-Díaz et al. 2019). For matrix models like Leslie and Lefkovitch matrices, life table data such as survivor probability for each life stage is necessary. Even for IBM, the individuals are explicitly considered within the populations and may vary in their attributes, such as fecundity, mortality, body size, and movement behavior (Grimm and Railsback 2005). This approach makes the model more realistic and improves the estimation of risk of extinction and MVP (García-Díaz et al. 2019). Moreover, this approach is still effective under data shortage, usually using estimations of life history parameters based on phylogenetically related species data (Hernández-Camacho et al. 2015, Schtickzelle et al. 2019). This general approach became specially relevant for risk assessment and analyzing management options for species conservation or control. An excellent example of the use of PVA to assess the cost-benefit of three management strategies (nests protection, fire management, and recovery of native vegetation) for the conservation of *Neothraupis fasciata* (Passeriformes: Thraupidae) is given by Duca et al. (2009). In the scenarios without considering costs, the nest's protection was the more effective strategy to reduce extinction risk, followed by fire management and natural vegetation recovery. Fire management presented the best cost-benefit in a scenario of limited financial resources, and natural vegetation recovery showed the worst result.

Knowing and describing all biodiversity dimensions (e.g., genetic, interaction, morphology, among others) is virtually impossible due to factors like time, money, and specialized people (Mora et al. 2011). The conscience of our ignorance about biodiversity is an essential step to advancing our knowledge. Seven large types of shortfall knowledge are usually described in Ecology and Evolution areas: Linnean, Wallacean, Darwinian, Hutchinsonian, Eltonian, Prestonian, and Raunkiæran (Hortal et al. 2015). Here we will focus on the last two shortfalls due to their great impact on the analysis of risk extinction through PVA. The Prestonian is defined as the lack of knowledge about species' abundance, demography, and space-time dynamics (Cardoso et al. 2011). The Raunkiæran shortfall represents the lack of knowledge about species traits and life history (Hortal et al. 2015). It is known that biodiversity data collection is geographically and taxonomically skewed, with some regions and taxa receiving greater attention from researchers and funders (Sastre and Lobo 2009, Mora et al. 2011). The taxonomic bias occurs because some species are better known, more conspicuous, or more detectable (Hortal et al. 2015). The species body size can affect this bias in two ways: large body size species are more studied because they are more visibly detectable; populations of small body size species are more abundant, and these species are more studied than less abundant species because they are detectable (Gaston and Blackburn 1996, Felizola Diniz-Filho and Tôrres 2002). The PVA suffers from this bias because good population dynamics and life history studies demand many individuals and a long monitoring period.

In this study, we will work with the Thraupidae family, the second-largest family of Passeriformes, with 377 species (Billerman et al. 2020) being one of the main groups of neotropical birds. The spatial occurrence extends from northern Mexico to South America, passing through high-altitude areas and insular environments like the Andes, Pacific, and South Atlantic islands (Burns et al. 2014, Funk and Burns 2018). This family presents a great diversity of plumage color, vocalization, habitat use, and behavior (Burns et al. 2014). As for habitat use, they use from tropical rain forests to savanna and semiarid environments (Burns et al. 2014). The family also has a diversified use of food resources, having frugivorous, insectivorous, nectarivorous, and granivorous species (Burns et al. 2003, Cestari and Bernardi 2011, Messeder et al. 2020, Sherry et al. 2020). According to the International Union for Conservation of Nature – IUCN, there are 30 Vulnerable species, 13 Endangered, and four classified as Critically Endangered (IUCN 2023). The main threats are habitat loss and illegal trade due to the beautiful vocalization and plumage of the species. The four species classified as Critically Endangered *Nemosia rourei*, *Geospiza heliobates*, *G. pauper*, and *Rowettia goughensis*, share the characteristic of having a small area of occurrence. Besides, the last three are insular species and are threatened by invasive species and diseases (IUCN 2023).

Here we aim to quantify the Prestonian and Raunkiæran shortfalls (life history and demographic data) essential to parameterize the models used in population viability analysis (PVA) in Thraupidae species. We use the number of studies as a surrogate of the knowledge, expecting to find an inverse relation between this variable and body size of the studied species, i.e., the larger is the body size, the fewer the number of publications (hypothesis 1). Furthermore, we test for a phylogenetic bias in the knowledge of life history and demographic data. Phylogenetic bias could result in an uneven distribution of knowledge regarding these parameters across the phylogenetic tree, limiting the use of closely related species in cases where data scarcity prevents a PVA for rare species (hypothesis 2). Finally, we hope our systematic review of such information helps to stimulate further studies on Thraupidae conservation.

Material & Methods

1 Collection and selection of studies

We performed a systematic review following the PRISMA (Moher et al. 2009). We used the Web of Science (WoS) and Scopus databases, where we searched for following terms: Thraupidae OR (Tanagers OR Flowerpiercers OR Tanager finches OR Bananaquit OR Saltators OR Seedeater) OR (Catamblyrhynchinae OR Charitospizinae OR Orchesticinae OR Nemosiinae OR Emberizoidinae OR Porphyrospizinae OR Hemithraupinae OR Dacninae OR Saltatorinae OR Coerebinae OR Tachyphoninae OR Sporophilinae OR Poospizinae OR Diglossinae). We searched these terms in the title, abstract, and keywords-plus and was made from the oldest WoS/Scopus year to 2020. We screened and included articles that presented Prestonian and Raunkiærian primary data.

We collected 27 Prestonian parameters and 35 Raunkiærian parameters, selecting them after a carefull analysis of PVA variables used in Vortex (Lacy 1993). The list of parameters includes body mass, longevity, clutch size, hatch success (Table 1 e 2).

The phylogeny data was obtained in birdsoftheworld.org, and then, we built a consensus tree with 100 random phylogenetic trees using Jetz et al. (2012) topology. The Consensus tree was performed using the "consensus.edges” function of phytools package (Paradis et al. 2004, Paradis and Schliep 2019), and species in the phylogeny that was not resentent in our database were removed with "drop.tip" function of the ape package (Revell 2012).

2. Data analysis

To test the relationship between body size and number of studies, we computed body mean mass and the number of studies for each genus. Then, we adjusted a non-linear regression model, where body mean mass was the predictor and the number of studies was the response variable. We used minpack.lm package (Elzhov et al. 2023) using R 4.0.5 (R Core Team 2022) to adjust the regression model. We tested the correlation between shortfalls parameters and birds’ phylogeny by using a Mantel test with Pearson correlation, where shortfalls parameters and birds’ phylogeny were input as Euclidean and cophenetic distance matrices respectively. We built the similarity matrix with the R software (R Core Team 2022).

We performed descriptive analysis to evaluate Prestonian and Raunkiæran shortfalls. First, we evaluated the temporal publication pattern, calculated the ratio between studies that met the selection criteria and the total of Thraupidae publications for each year, and then performed a graphical analysis. We used graphical analysis to evaluate the number of studies of each parameter for each species. We built a histogram to evaluate the frequency of species that presented a different number of parameters. Also, we assessed the number of species that presented different numbers of studies for the following parameters: body size, body size variation, clutch size, and clutch size variation. We performed all analyses separately for each shortfall using the ggplot2 package (Wickham 2016) in the software R core team.

Table 1. Demographic parameters (Prestonian shortfall), it's unit measurement and description.

Shortfall	**Parameters**	**Unit**	**Description**
Prestonian	Adult Fem. Mortality	%	Mortality rate of adult female.
	Adult Male Mortality	%	Mortality rate of adult male.
	Adult Sex ratio (F)	%	Mean adult female sex ratio.
	Adult Sex ratio (SE)	%	Adult female sex ratio standard error.
	Adult Survival	%	Mean adult survival
	Adult Survival (SE)	%	Adult survival stadard error.
	Age Distribution	n° Ind.	Number of individuals by age group in the population.
	Alle Effect	-	Presence or absence of Alle effect
	Birth Sex ratio (F)	%	Mean birth female sex ratio.
	Birth Sex ratio (SE)	%	Birth female sex ratio standard error.
	Clutch Size	n° Ind.	Mean number of eggs by nest.
	Clutch Size (max)	n° Ind.	Maximum number of eggs by nest.
	Clutch Size (min)	n° Ind.	Minimum number of eggs by nest.
	Clutch Size (SE)	n° Ind.	Standard error number of eggs by nest.
	Eggs Success	%	Percentage of eggs laid and individuals survived until they left the nest
	Hatch Success	%	Percentage of eggs laid that hatched.
	Incubation Period	n° Days	Mean interval from hatching of the first egg until the last juvenile leaves the nest.
	Incubation Period (Max)	n° Days	Maximum interval from hatching of the first egg until the last juvenile leaves the nest.
	Incubation Period (Min)	n° Days	Minimum interval from hatching of the first egg until the last juvenile leaves the nest.
	Incubation Period (SE)	n° Days	Standard error of interval from hatching of the first egg until the last juvenile leaves the nest.
	Mortality Envirmen. Variation	-	Correlation between enviromental variation and mortality.

Continuation of table 1.

Shortfall	**Parameters**	**Unit**	**Description**
Prestonian	Nesttling Period	-	Mean permanence of the chicks from hatching to leaving the nest
	Nesttling Period (SE)	-	Standard error permanence of the chicks from hatching to leaving the nest
	Nesttling Success	%	Percentage of eggs that hatched and individuals survived until they left the nest.
	Reprod. Environ. Var.	%	Correlation between environmental variation and reproduction.
	Reproductive Period	-	Months in which the reproductive period occurs.
	Young Fem. Mortality	%	Mortality rate of young females.
	Young Male Mortality	%	Mortality rate of young males.

Table 2. Life history parameters (Raunkiæran shortfall), its unit measurement and description.

Shortfall	**Parameter**	**Unit**	**Description**
Raunkiæran	Age First Rep.	-	Age of first reproduction.
	Beak	(mm)	Mean beak length from tip to nostril.
	Beak (SE)	(mm)	Beak length from tip to nostril standard error.
	Beak Height	(mm)	Mean beak height.
	Beak Height (SE)	(mm)	Beak height standard error.
	Beak Vol.	(mm^3)	Mean cone volume.
	Beak Vol. (SE)	(mm^3)	Cone volume standard error.
	Beak Width	(mm)	Mean beak width.
	Beak Width (SE)	(mm)	Beak width standard error.
	Body Mass	(g)	Mean body mass.
	Body Mass (max)	(g)	Maximum body mass.
	Body Mass (min)	(g)	Minimum body mass.
	Body Mass (SE)	(g)	Body mass standard error.
	Culmen	(mm)	Mean length of the culmem.
	Culmen (SE)	(mm)	Length standard error of the culmem.
	Eating Habit	-	Type of food observed in the study.
	Habitat Use	-	Type habitat observed and indicated in the study.
	Home Range Size	(m^2)	Mean home range size.
	Home Range Size (SE)	(m^2)	Home range size standard error.
	Longevity	Years	Mean longevity
	Longevity(SE)	Years	Longevity standard error.

Continuation of table 2.

Shortfall	**Parameter**	**Unit**	**Description**
Raunkiæran	Mandible Width	(mm)	Mean mandibule width.
	Mandible Width (SE)	(mm)	Mandibule width standard error.
	Maxilla Width	(mm)	Mean maxila width.
	Maxilla Width (SE)	(mm)	Mandibule maxila standard error.
	Max. Rep. Age	Years	Maximum reproductive age.
	Mixed Flocks	-	If individuals are found foraging in mixed flocks.
	Reproduction System	-	Monogamous or poligamous.
	Resource (Sp)	-	Species used as food resources.
	Tail Size	(mm)	Mean tail size.
	Tail (SE)	(mm)	Tail size standard error.
	Tarsus Size	(mm)	Mean tarsus size.
	Tarsus (SE)	(mm)	Tarsus size standard error.
	Wing Size	(mm)	Mean wing size.
	Wing (SE)	(mm)	Wing size standard error.

Results

A total of 57 studies were included in the shortfall knowledge review (Figure 1). The publication time interval comprised from 2003 to 2020, and we found no temporal pattern in the publication of studies. Publications from 2003 presented proportionately the largest number of articles, followed by 2013 and 2012, respectively (Figure 2). We found 49 parameters with at least one study, 31 Raunkiæran, and 18 Prestonian parameters. Of the total parameters previously determined, 14 and 39% did not record studies for Raunkiæran and Prestonian shortfall respectively.

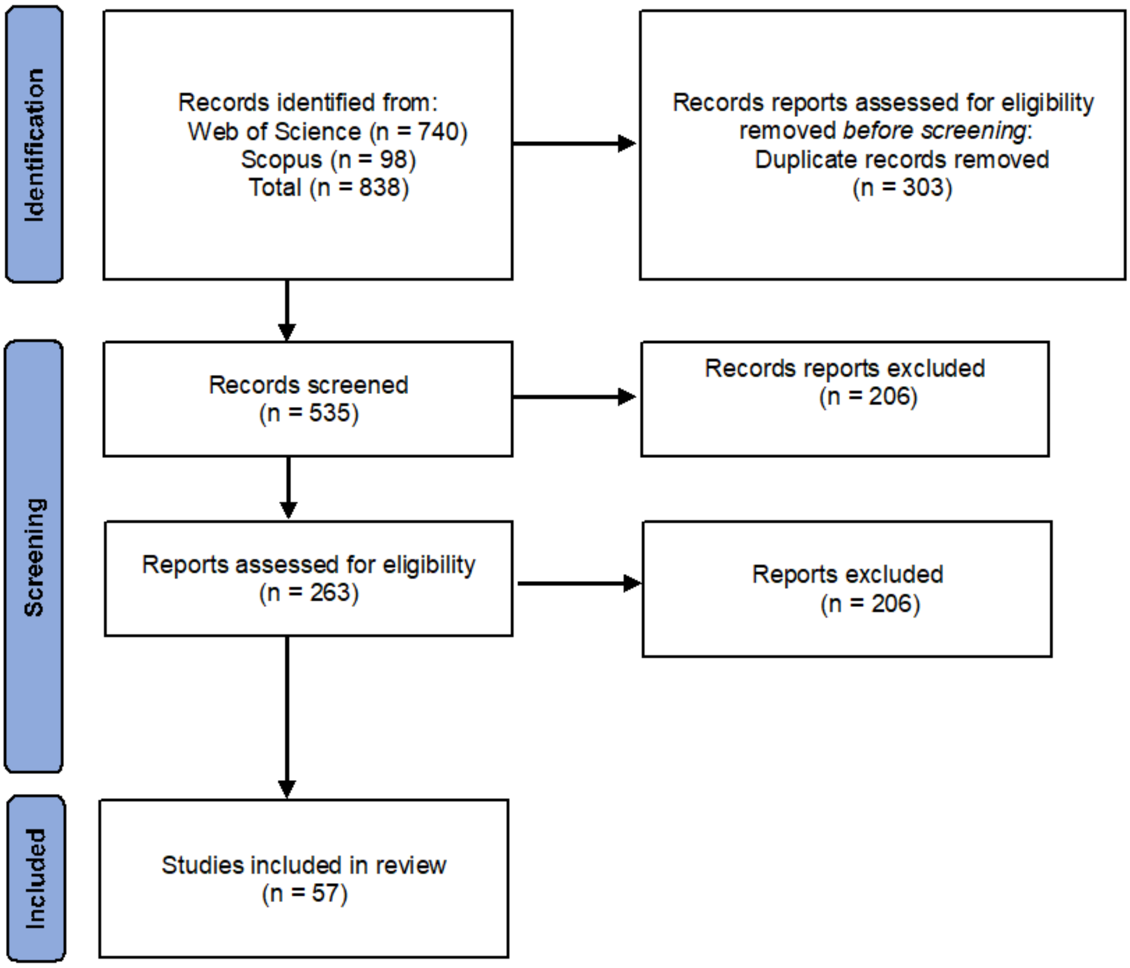


Figure 1: Infograph of PRISMA protocol presenting the number of studies ar each step of review process.

Raunkiæran shortfall presented 85 species and Prestonian 22 species, representing 63 more species, almost triple the number of species. For the Raunkiæran shortfall *Dacnis cayana* presented four studies but just two parameters (Figure 3), already for the Prestonian *S. collaris, S. hypoxantha, and S. lineola* showed two studies (Figure 4). We found many species with few parameters to Raunkiæran shortfall, with 30 species presenting two parameters and 11 species presenting one parameter (Figure 5a). We found only one species with values equal to or greater than 12 parameters (Figure 5a). Species showed a maximum of nine parameters to Prestonian shortfall; the majority (nine species) presented two, and two species presented seven and eigth (Figure 5b).

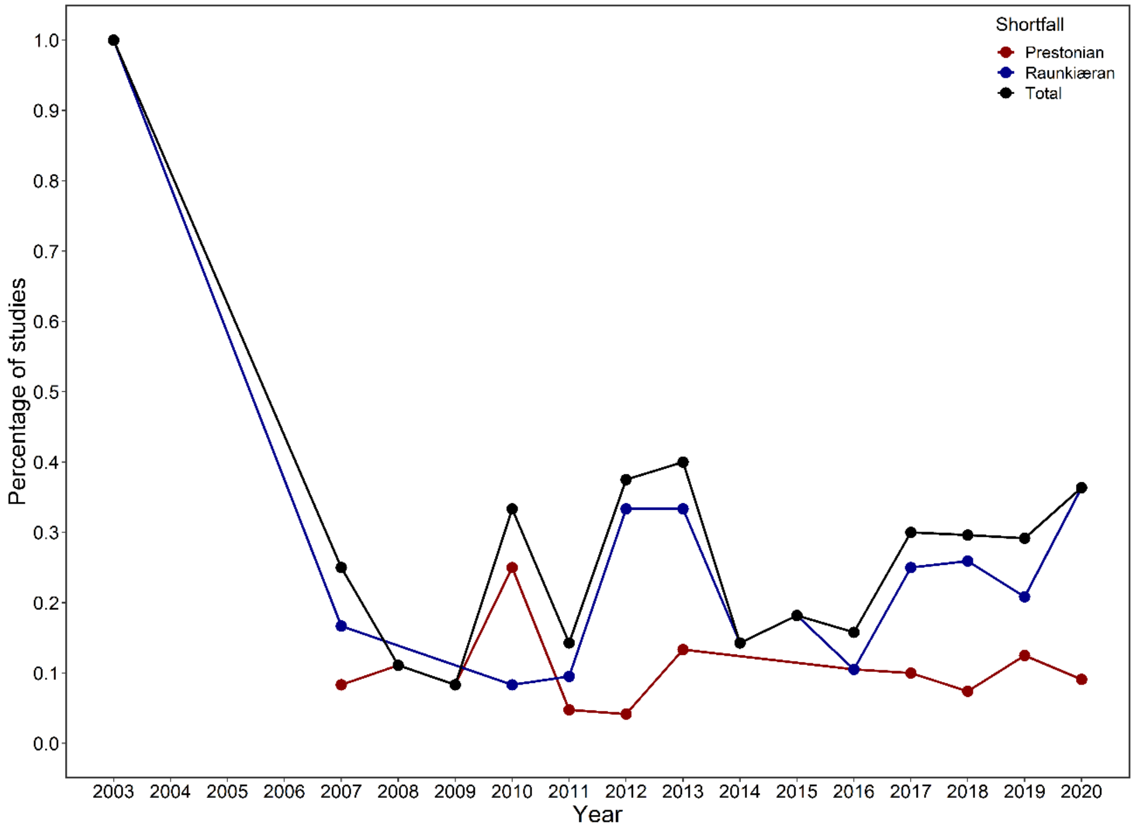
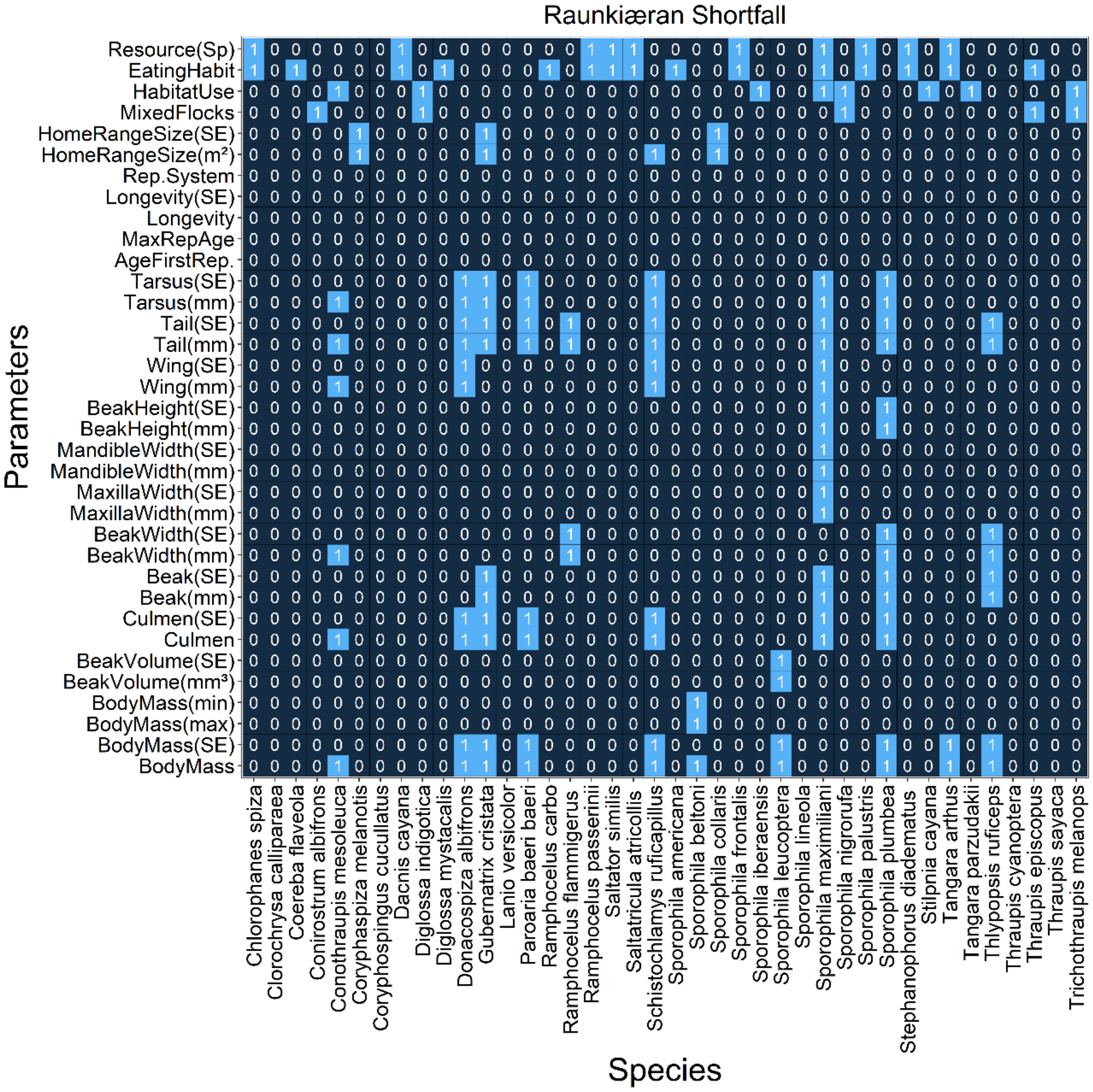


Figure 2. Publication temporal series, the y-axis represents the percentage of studies that passed the selection criteria in relation to the total of studies for each year. The red, blue, and black points and lines represent parameters related to Prestonian, Raunkiæran, and the sum of two shortfalls.

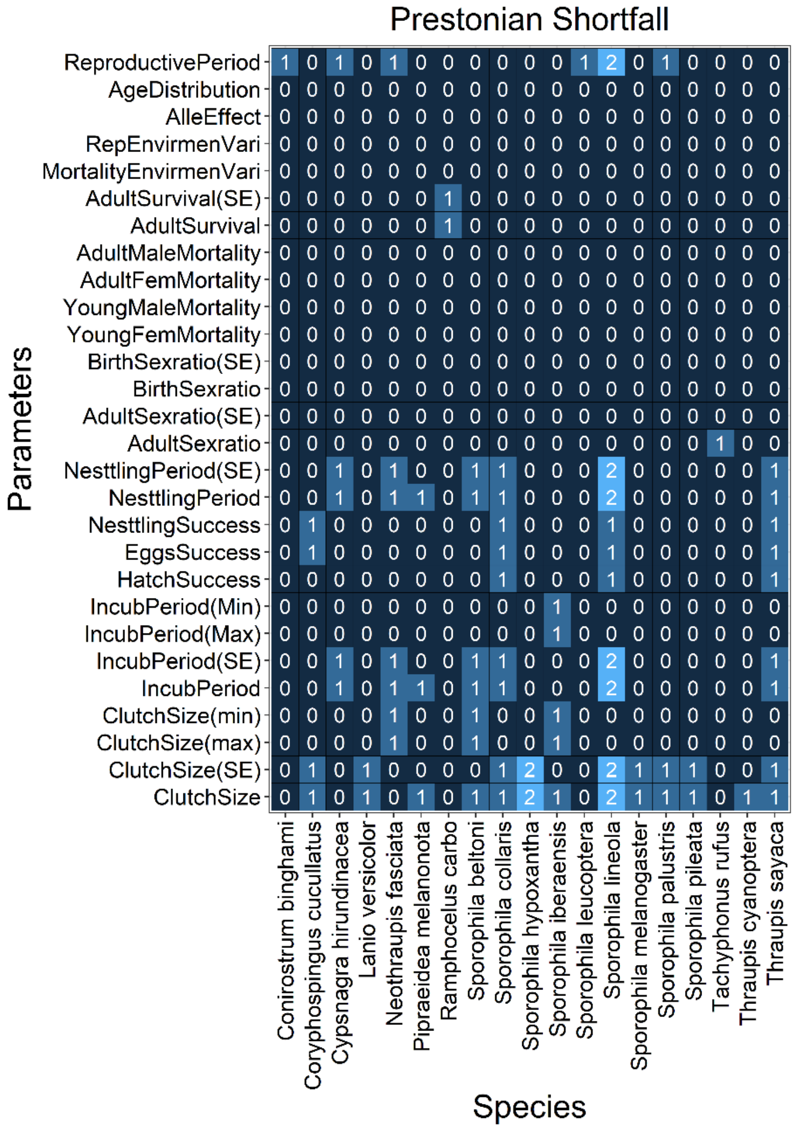
When we evaluate the number of studies each species presented for body size, 31 species presented only one study, three and one species presented two and three studies, respectively (Figure 6a). Although the body mass variation followed the same pattern, three species did not present variation data (Figure 6a). Ten species presented one study related to the clutch size, three showed two, and only one did not present variation data (Figure 6b).

We do not have evidence of a negative relationship between genus body mean mass and the number of studies. Our data presented an outlier due to the *Sporophila* genus having 21 studies (Figure 7). Also, we found no evidence of a correlation between shortfalls parameters and birds' phylogeny in our research (r= 0.005; p= 0.529). Relatively to the Raunkiæran shortfall, eating habits presented the largest data with 15 studies, followed by species resource and body mass with ten studies each. The parameters of Prestonian shortfall with the largest number of studies were Clutch size and Clutch size (SE) with 15 and 11 studies, respectively.



	Chlorophanes spiza	Clorochrysa calliparaea	Coereba flaveola	Conirostrum albifrons	Conothraupis mesoleuca	Coryphaspiza melanotis	Coryphospingus cucullatus	Dacnis cayana	Diglossa indigotica	Diglossa mystacalis	Donacospiza albifrons	Gubernatrix cristata	Lanio versicolor	Paroaria baeri baeri	Ramphocelus carbo	Ramphocelus flammigerus	Ramphocelus passerinii	Saltator similis	Saltatricula atricollis	Schistochlamys ruficapillus	Sporophila americana	Sporophila beltoni	Sporophila collaris	Sporophila frontalis	Sporophila iberaensis	Sporophila leucoptera	Sporophila lineola	Sporophila maximiliani	Sporophila nigrorufa	Sporophila palustris	Sporophila plumbea	Stephanophorus diadematus	Stilpnia cayana	Tangara arthus	Tangara parzudakii	Thlypopsis ruficeps	Thraupis cyanoptera	Thraupis episcopus	Thraupis sayaca	Trichothraupis melanops
Resource(Sp)	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	1	0	0	0	1	0	1	0	1	0	1	0	0	0	0	0	0
EatingHabit	1	0	1	0	0	0	0	1	0	1	0	0	0	0	1	0	1	1	1	0	1	0	0	1	0	0	0	1	0	1	0	1	0	1	0	0	0	1	0	0
HabitatUse	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	0	0	0	1	0	1	0	0	0	0	1
MixedFlocks	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	1
HomeRangeSize(SE)	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
HomeRangeSize(m²)	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Rep.System	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Longevity(SE)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Longevity	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
MaxRepAge	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AgeFirstRep.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Tarsus(SE)	0	0	0	0	0	0	0	0	0	0	1	1	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0
Tarsus(mm)	0	0	0	0	1	0	0	0	0	0	1	1	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0
Tail(SE)	0	0	0	0	0	0	0	0	0	0	1	1	0	1	0	1	0	0	0	1	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	1	0	0	0	0
Tail(mm)	0	0	0	0	1	0	0	0	0	0	1	1	0	1	0	1	0	0	0	1	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	1	0	0	0	0
Wing(SE)	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Wing(mm)	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
BeakHeight(SE)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0
BeakHeight(mm)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0
MandibleWidth(SE)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
MandibleWidth(mm)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
MaxillaWidth(SE)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
MaxillaWidth(mm)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
BeakWidth(SE)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0
BeakWidth(mm)	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0
Beak(SE)	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	1	0	0	0	0
Beak(mm)	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	1	0	0	0	0
Culmen(SE)	0	0	0	0	0	0	0	0	0	0	1	1	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0
Culmen	0	0	0	0	1	0	0	0	0	0	1	1	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0
BeakVolume(SE)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
BeakVolume(mm³)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
BodyMass(min)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
BodyMass(max)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
BodyMass(SE)	0	0	0	0	0	0	0	0	0	0	1	1	0	1	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	1	0	0	1	0	1	0	0	0	0
BodyMass	0	0	0	0	1	0	0	0	0	0	1	1	0	1	0	0	0	0	0	1	0	1	0	0	0	1	0	0	0	0	1	0	0	1	0	1	0	0	0	0

Figure 3. Distribution of the number of published studies that present Raunkiæran parameters among species of Thraupidae. Refer to table 1 and table 2 to the detailed information about parameters.



Parameters	Conirostrum binghami	Coryphospingus cucullatus	Cypsnagra hirundinacea	Lanio versicolor	Neothraupis fasciata	Pipraeidea melanonota	Ramphocelus carbo	Sporophila beltoni	Sporophila collaris	Sporophila hypoxantha	Sporophila iberaensis	Sporophila leucoptera	Sporophila lineola	Sporophila melanogaster	Sporophila palustris	Sporophila pileata	Tachyphonus rufus	Thraupis cyanoptera	Thraupis sayaca
ReproductivePeriod	1	0	1	0	1	0	0	0	0	0	0	1	2	0	1	0	0	0	0
AgeDistribution	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AlleEffect	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RepEnvirmenVari	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
MortalityEnvirmenVari	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AdultSurvival(SE)	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
AdultSurvival	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
AdultMaleMortality	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AdultFemMortality	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
YoungMaleMortality	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
YoungFemMortality	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
BirthSexratio(SE)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
BirthSexratio	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AdultSexratio(SE)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AdultSexratio	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
NesttlingPeriod(SE)	0	0	1	0	1	0	0	1	1	0	0	0	2	0	0	0	0	0	1
NesttlingPeriod	0	0	1	0	1	1	0	1	1	0	0	0	2	0	0	0	0	0	1
NesttlingSuccess	0	1	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	1
EggsSuccess	0	1	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	1
HatchSuccess	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	1
IncubPeriod(Min)	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
IncubPeriod(Max)	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
IncubPeriod(SE)	0	0	1	0	1	0	0	1	1	0	0	0	2	0	0	0	0	0	1
IncubPeriod	0	0	1	0	1	1	0	1	1	0	0	0	2	0	0	0	0	0	1
ClutchSize(min)	0	0	0	0	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0
ClutchSize(max)	0	0	0	0	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0
ClutchSize(SE)	0	1	0	1	0	0	0	0	1	2	0	0	2	1	1	1	0	0	1
ClutchSize	0	1	0	1	0	1	0	1	1	2	1	0	2	1	1	1	0	1	1

Figure 4. The graph presents within cells the number of studies for each species and Prestonian related parameters.

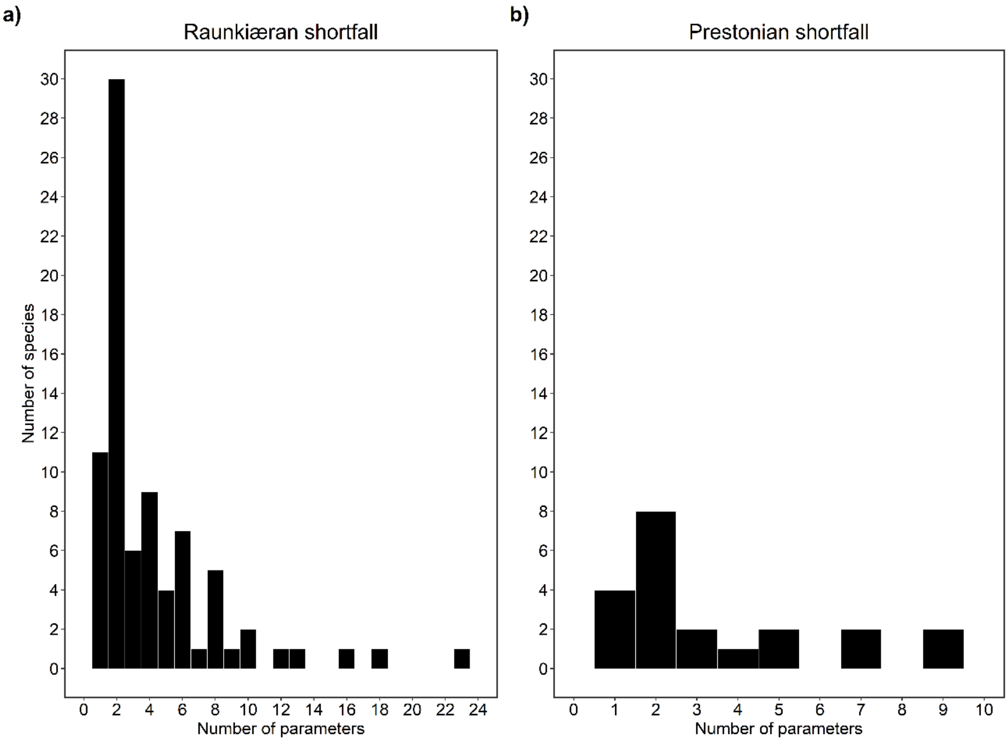


Figure 5. The number of species and number of species for Raunkiæran (a) and Prestonian shortfall (b).

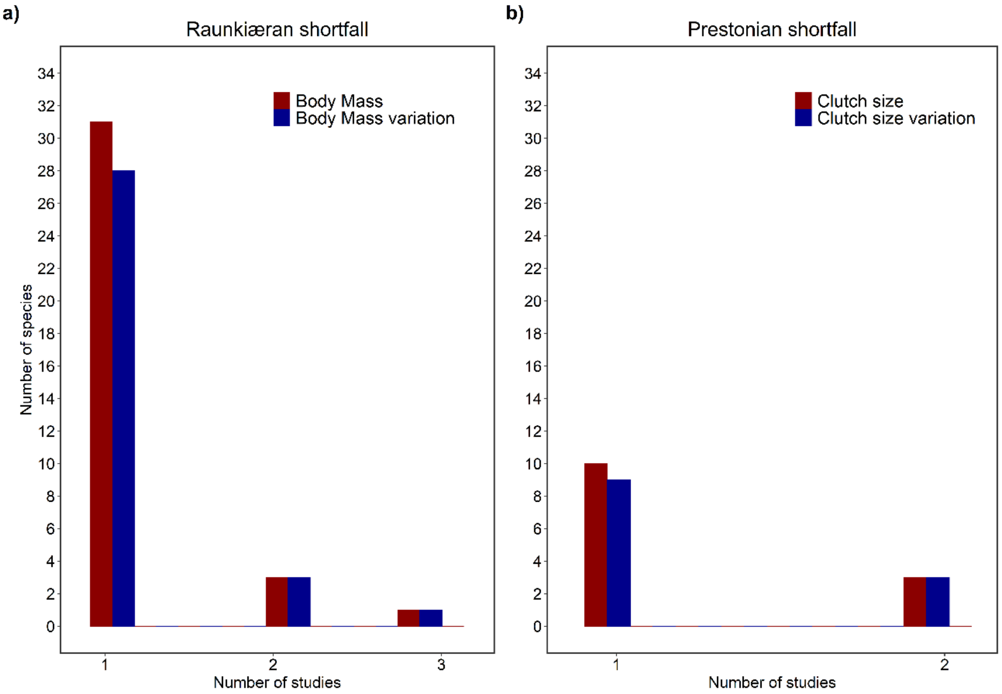


Figure 6. Description of the number of species and studies, red bars represent the body mean mass and mean clutch size, and blue bars represent their variation measure.

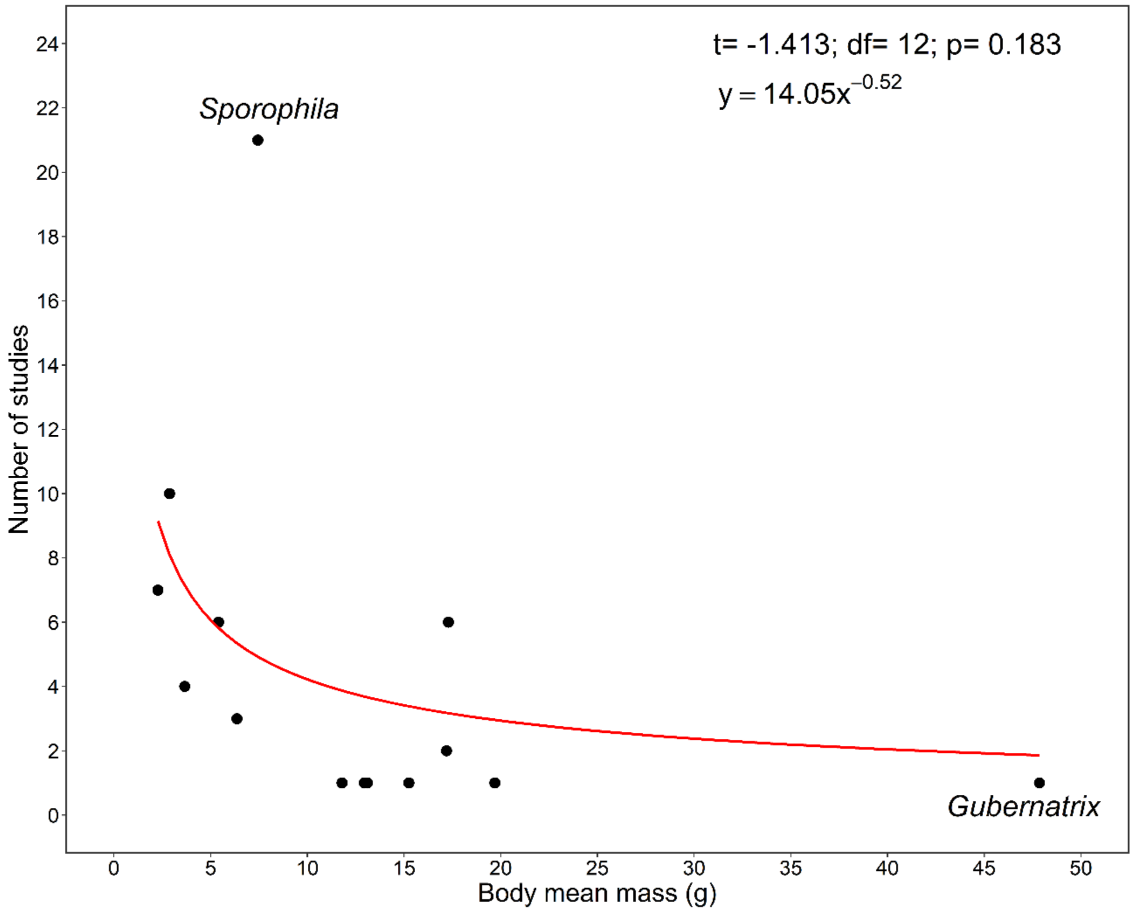


Figure 7. Non-linear regression between the number of studies in function to genus body mean mass. The graph presents the names of the two genera considered outliers, the values of t statistic, degree of freedom, p-value, and curve equation.

Discussion

In the present work, we assessed how much we know about the life story, functional traits, and demography of the Thraupidae family. We show that the Prestonian shortfall was more prevalent than the Raunkiæran shortfall, and there is no phylogeny or body mass effect on our current knowledge about these parameters. We found many studies for the *Sporophila* genus, and we believe it to be related to a sample effect since this is one of the most speciose genera in this family. We also noticed that even those species with data for several parameters do not have more than three studies, and most have only one.

The increase of data on Raunkiæran parameters after 2016 could be related to the growth of functional ecology approach, which has as its primary object of study the functional traits of the species (Blackburn et al. 2005, Etard et al. 2022, Gumede et al. 2022). In functional ecology, the organisms are usually classified acording to food guild, how it obtains, and exploits resources and morphological measures that represent the performance of organisms (McGill et al. 2006, Violle et al. 2007). This biodiversity dimension can contribute to the reduction of Raunkiæran shortfall. The availability of data from these studies and proper presentation of this information, especially variability measures among populations, are important to better appropriation of the results. The increase of data papers on ecological parameters in recent years (e.g., Antunes *et al.* 2022; Beninde *et al.* 2022; Chavan and Penev 2011) is an example of best presentation and availability of information that could be followed here. Data related to the Raunkiæran shortfall, such as food habits, habitat use, and activity time, can be collected for several species simultaneously, often even in an automated way (Iezzi et al. 2018, Jezuíno et al. 2021). Otherwise, the demographic data is hard to sample, especially for birds. Sometimes, it is necessary to find the nests and accompany them at least until the eggs hatch, and eventually monitor them until the chicks leave the nest (Ferreira and Lopes 2017, Turbek et al. 2019). It means higher financial costs due to the need to increase sampling effort, including more time spent on fieldwork. These may discourage researchers from collecting this type of data.

The genus Sporophila, known for its extensive species diversity (n= 41), exhibited the highest number of studies among all genera. This finding demonstrates a simple sampling effect, whereby taxa with a greater number of described species tend to attract more research attention than táxon with fewer described species (Winkler et al. 2020). The lack of knowledge about new species is know as Linnean shotfall, and is correlated with all other shortfalls because we do not collect empirical data for undescribed species (Hortal et al. 2015). The preference for previously described species when selecting a target organism generates a taxonomic bias in data collection (Hortal et al. 2015). Furthermore, species of the *Sporophilla* genus are very common foraging in grasslands, usually in conspecifics or congeners mixed flocks (Severo-Neto et al. 2015).

Knowing the clutch size gives us information on the birth rate and the potential couple fecundity, an essential component of the population growth rate (CASWELL 2000, Rockwood 2015). In the case of structured models and IBMs, the demographic data, at least stage-specific survival and reproduction, is necessary to build PVA models (Radchuk et al. 2016). For example, if we combine clutch size with the number of eggs hatched, we will have the survival rate of eggs to the nestling stage. We can apply the same logic to juvenile and adult survival. Individual data allows a more realistic analysis of population demography by including individual variation in the model (Grimm 1999, Scherer et al. 2016). Nevertheless, stage-specific data may represent a practical compromise where most parameters are unknown for most species. Since survival rates can vary between different life-stages (Oppel and Powell 2010, Kobayashi et al. 2017), a stage-specific approach is still helpful in creating realistic models. On the other hand, body mass (the most common surrogate for body size) is not explicitly used in PVA models. It is usually considered by ecologists to be a super-parameter, as it is a proxy to estimate parameters like life span, generation time, and incubation period (Sæther 1987, Sibly et al. 2012). However, we must be cautious when using generalizations or surrogates in PVA models. For understanding ecological mechanisms acting on populations, using of demography and life history parameters estimated from the allometric relationships may not significantly affect on the model conclusions. For a model whose objective is to assess a local population's extinction risk, an effort should be made to collect primary data to make the best possible management decision (Hernández-Camacho et al. 2015).

The variation within each parameter is very important for more complex PVA models such as IBM. Such models assume that individuals from the same population have morphological, life history, and behavioral differences (Grimm and Railsback 2005, Stillman et al. 2015). Two major sources of variability that need to be considered, especially in models aimed to discuss species distribution at larger scales (De Marco et al. 2008). The first one is the individual variation of those parameters within populations. The second is the geographic variation among populations. In both cases, our study found a lack of appropriate variability measures. Some parameters lack information on variability within the population (e.g. hatch success and nesting success), but usually, this information is provided in the studies. Otherwise, we could estimate geographic variation for measures such as clutch size, incubation period, body mass, and home range size. However, for most of the parameters, we found only a single piece of information due to the small availability of data representing a small portion of all the natural variations of the species and affecting the population viability models.

However, the present results are just a small selection of the literature on the life history and demography of Thraupids. This misrepresentation is because we only searched Scopus and Web of Science, and one of the search terms used was the popular English names of the species. For this reason, although we have had basic biology of species studies in the Neotropics since the 20th century, much of this literature is written in Portuguese or Spanish, and the journals are not part of the above databases (Oniki 1972, Silva 1980, Martínez 2003). In addition, because these studies are often local, they are accepted only in journals from the global south that are not part of the scientific mainstream (Soares et al. 2023). Or they usually end up being published in the so-called gray literature as theses, books, and conference abstracts (Soares et al. 2023). For future systematic reviews of Neotropical species, we recommend including the Scielo database in the literature search and using keywords in Portugues e Espanhol if necessary.

From our results, there exists a relevant knowledge shortfall about the reproductive, life history, and functional traits information of the Thraupidae family. Thinking about improving PVA models, we encourage collecting demographic data on fecundity and mortality rates, which has a major effect on PVA analysis (PVA sensitivity). Considering mortality rates, they are especially relevant because they may also vary largely accordingly to environmental conditions and resources, thus more sensitive to environmental impacts and threat drivers. Prioritizing data for primary data gathering is complex, and we observe that different fieldwork aspects and financial resources determine the scarcity of essential information for PVA analysis. Under resources shortage, specially in biodiversity-richer countries (Meyer et al. 2015, Stephenson 2020), researchers appear to focus on variables more easy to collect, such as presence data for species distribution modeling (Lopes-Lima et al. 2021, Tessarolo et al. 2021) than basic life-history and population abundance data. Unfortunately, despite its relevance to the general use of occurrence data for prioritization schemes (Guisan et al. 2013, Frans et al. 2022), PVA analysis may provide estimations of minimum population sizes, which are most relevant to guarantee long-time persistence of species in fragmented and degraded landscapes (Schippers et al. 2015, Heinrichs et al. 2016). In addition, information gathering is only part of the problem since it is crucial to make them available through publication in articles, data papers, or other public repositories. We must remember that we are in the age of big data and that data is increasingly guiding decisions.

Thus primary data for PVA must be considered essential for bringing ecology and conservation, even more, a status of evidence-based science.

Data availability

The data and scripts of our analysis are available on GitHub: https://github.com/edgar-lima/Thraupidae_Shortfall. DOI: 10.5281/zenodo.8039327.

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Capítulo II

Unraveling the patterns and mechanisms behind the effect of landscape on home range size

Introduction

Since resources are distributed unevenly in space, organisms must move around the landscape to find food, shelter, and reproductive partners (With 2019). Even sedentary organisms, such as plants and corals, have structures or life stages that allow them to move around and explore new environments and resources However, the intense exploitation of natural environments by activities such as agriculture, livestock, and mining alters the availability and distribution pattern of resources in the landscape, a process known as habitat loss and fragmentation (Estavillo et al. 2013, Villard and Metzger 2014). While habitat loss reduces the availability of resources in the landscape, fragmentation alters the quality of resources and makes them even more spatially structured (Crist and With 1995, Fahrig 2013, Lichtenberg et al. 2017). This lower availability of resources and greater spatial isolation affect the movement of individuals in the landscape, who spend more time moving around to meet their energy needs (Mäkeläinen et al. 2015, Poli et al. 2020). Therefore, to develop management and conservation strategies, it is necessary to understand how habitat loss and fragmentation affect the movement patterns of individuals in these landscapes.

An individual's home range is the sum of all the areas it uses to find reproductive partners, food, refuge, and other movements to explore the landscape. (Börger et al. 2008). During movements within their home range, individuals interact with the environment and are affected by the landscape context, such as the type of matrix, the presence of corridors and stepping stones, which may or may not facilitate movement (Doherty et al. 2019, Poli et al. 2020). In addition, during movement, individuals interact with each other, competing directly for resources and being subject to predation (Buchmann et al. 2013). We can, therefore, consider that the larger an individual's home range area, the greater its energy expenditure and the more exposed to predators and inhospitable environments it will be (Charnov 1976, Malishev et al. 2018). Thus, to balance the conflict involved in movement, we expect individuals in landscapes with a greater availability of resources to move less, avoiding large energy expenditures and being less exposed to predation and inhospitable environments (Bautista et al. 2017). In landscapes with lower resource availability, the need to move to meet energy needs will be greater, thus offsetting the risk associated with movement (Vergara et al. 2015, Rus et al. 2020). In this way, we can expect an individual's home range to be larger in landscapes that have suffered habitat loss and fragmentation.

In addition to landscape structure, another factor that can affect the movement of organisms is their navigation capacity (Hillaert et al. 2018). Navigation ability is defined by how individuals gather information and orient themselves to move through space (Nathan et al. 2008). This ability varies between organisms due to differences in their sensory and cognitive systems, affecting the reception of information about the environment and the decision-making process of which direction to move in (Nathan et al. 2008). On this basis, navigation ability can be classified into three main mechanisms: i) non-orientated, ii) orientated, and iii) memory-based (Mueller et al. 2011). For the first mechanism, it is assumed that the individual receives a stimulus to move from their current position; this stimulus could be, for example, the low quality of a resource. However, the decision as to which direction to move is random and does not take into account environmental information or previous experiences of movement (Börger et al.

2008, Doherty and Driscoll 2017). For the oriented mechanism, the individual receives a stimulus from a nearby location and then moves toward it (Doherty and Driscoll 2017). However, this mechanism suffers limitations due to its sensory system (e.g. sight, smell, acoustic) (Nathan et al. 2008). Finally, in the memory-based mechanism, the direction to move takes into account information from sources such as previous experiences of movement and communication with conspecifics (Fagan et al. 2013).

The use of models in ecology is useful for understanding the mechanisms underlying ecological patterns and processes (Codling and Dumbrell 2012). Models are simplifications of the real world, which allow factors of interest, such as landscape structure and movement of individuals, to vary in a controlled manner. In contrast, other factors are constant, avoiding the interference of these factors in the analysis and interpretation of the results (Epperson et al. 2010). One type of simulation model widely used in ecology is the individual-based model (IBM). IBMs take individuals as discrete units within the system and allow morphological and behavioral characteristics to vary between individuals in the same population (Grimm and Railsback 2005).

This study aims to understand how habitat loss and fragmentation alter the movement of individuals in the landscape and whether this effect varies according to the individuals' ability to navigate. To assess how movement is affected by these factors, we will test hypotheses related to the following movement parameters: home range size, home range overlap between individuals, and how much time individuals spend moving. These hypotheses will be evaluated in a controlled computational environment and within a simulation that seeks to represent most of the recognized factors of this system realistically. We tested the following hypothesis: **h_1):** the home range size will be greater in landscapes with less habitat amount and fewer connected landscapes; **h_2):** individuals with memory-based movement ability will use information from the surrounding landscape to move, so they will make better decisions and will move less than non-orientated individuals and have a smaller home range area. **H$_3$):** the impact of habitat loss and fragmentation on home range will be less for individuals with memory-based navigation capacity.

Material & Methods

The model was developed using an adaptation of the ODD protocol (Overview, Design concepts, and Details) for individual-based models (Grimm et al., 2006, 2010). All stages of the model (e.g., dynamics and movement), including the creation of the landscapes, were developed using the Python 3 programming language.

ODD protocol

1. Biological model

We chose the species *Sporophila maximiliani* and *Sporophila cinnamomea* as a biological model. The genus Sporophila, popularly known as the seedeaters are passeriformes of the Traupidae family endemic to the Neotropics (Burns et al. 2014). Individuals of the species *S. maximiliani* weigh approximately 2.5 g, inhabit open and grassy environments near flooded areas, are granivores, and feed mainly on grass seeds (Ubaid et al. 2018, Tobias et al. 2022). The individuals of S. cinnamomea are smaller, weighing approximately 7.5 g. They inhabit grassland environments where they feed on the seeds of grass species (Tobias et al. 2022).

2. Model description

In our model, individuals differ in body size and maximum movement capacity, with maximum capacity being dependent on body size. The model was run separately for each species, and the body size of individuals within the population follows a normal distribution. As we aimed to test only hypotheses relating to movement, we opted to use a simplified model in which there are no population dynamics and the individuals were not classified as male or female.

2.1. Individuals, state variables and scales

The individuals of the two species were created using real body size data (mean and standard deviation) obtained from a previous literature review (Chapter I). For the non-oriented navigation capacity, the individuals have the following state variables: body mass, maximum daily movement capacity, and coordinates of where they are. As for the memory-based model, in addition to the previous characteristics, it also has a memory matrix and a radius of perception of the landscape, representing 50% of the maximum movement capacity. Each iteration (round) of the model will be considered a day, so 365 days will be counted as one year. The landscape used in our model has an area of 200 x 200 cells with a spatial resolution of 10 m^2.

2.3. Overview of processes and stages

The model begins with the colonization of the landscape by the individuals, based on the mean and standard deviation of body size created from a normal distribution. Once the landscape has been colonized, the model begins to run. First, the individual evaluates the cell it is in to see if it needs to move. The general movement logic was applied to both navigation capabilities. The individual receives a stimulus to move from the current position; this can occur because it is not in a suitable cell (matrix) or a habitat cell above half of the carrying capacity (K= 20). To simulate landscape exploration behavior, even if the individual was in a habitat cell below half of K, it had a 10% chance of moving.

2.4. Inicialization

The model starts with 200 individuals arranged randomly in the landscape. After colonization, the model runs for two years (730 iterations), and the coordinates of the individuals are recorded daily.

2.5. Sub-models

2.5.1. Maximum movement capacity

The maximum movement capacity (*D.max*) follows the allometric relationship described by (Eq.1), the equation was parameterized using data on body mass and home range size of herbivorous passerines that use grassland environments as habitat (Appendix).

$$D.max = 3.252M^{1.253} \qquad \text{(Eq.1)}$$

2.5.3. Non-oriented movement

When the individual decides to move, first, a turning angle (*θ*) is chosen at random, indicating the direction in which they will move (Eq. 2). Secondly, the distance that the individual will move (*r*) is randomly drawn from a uniform distribution and the maximum value that r can take is *D.max* (Eq. 3).

$$\theta = Uni(1) * 2 * \pi \qquad \text{(Eq. 2)}$$

$$r = Uni(D.max) \qquad \text{(Eq. 3)}$$

Based on these two parameters, the individual's location coordinates are updated according to Eq. 4 e 5.

$$x_{i+1} = x_i + r * \cos\theta \qquad \text{(Eq.4)}$$

$$y_{i+1} = y_i + r * \text{sen}\,\theta \tag{Eq. 5}$$

In which:

x_i, y_i : coordinates at time *i* represent the coordinates at the current time.

x_{i+1}, y_{i+1}: coordinates at time *i+1* represent the coordinates to which the individual has moved.

2.5.4. Memory-based movement

In memory-based movement, we used reinforcement-based learning to train the individuals; the algorithm we chose was *Q* learning. Firstly, the individual goes through the training stage in which it moves randomly, as described above, for 730 days. During training, it moves around and collects information from the cells it left and went to; its memory is created based on a vector of rewards *R* that updates a *Q* matrix (Figure 1) that will be used to make decisions after the training phase (Sutton and Barto 2018). The cell can assume three states, namely 0: matrix, 1; habitat >= K50%, and 2: habitat < K50%. As a result, our *R* vector has the following values for each state: *R* = (0: -2, 1: 7, 2: 10).

Action (A)

State (S)		0	1	2
	0	s_1, a_1	s_1, a_2	s_1, a_3
	1	s_2, a_1	s_2, a_2	s_2, a_3
	2	s_3, a_1	s_3, a_2	s_3, a_3

Figure 1. *Q* table that represents an individual's memories and is used for decision-making during memory-based movement.

At each learning iteration, the Q table is updated following equation Eq. 6 proposed by Watkins 1989.

$$Q(S_t, A_t) \leftarrow Q(S_t, A_t) + \alpha[R_{t+1} + \gamma \, max_a \, Q(S_{t+1}, a) - Q(S_t, A_t)] \qquad \text{Eq. 6}$$

In which:

max_a: a value of a at which $f(a)$ takes its maximum value.

S_t, A_t: state and action in time t.

R_{t+1}: reward in time $t+1$.

a: an action.

α: learning rate.

γ: discount factor.

After training, individuals use the Q-table to make decisions about movement. First, they evaluate the state of the cell they are in, then they evaluate the state of the cells within their radius of perception, and then, using the Q-table, they consider which is the best course of action for them. The best option may be to stay in the same place or to move; in the case of two or more cells being the best choice, then it chooses the closest cell.

3. Model output

At the end of the model, a table was generated with all the individuals, their navigation capacity, body size, and the coordinates of each iteration.

4. Experimental simulation design

In our experimental design, we simulated a temporal effect of habitat loss, so we generated 20 landscape structures, and for each one, we had 10%, 20%, 30%, 40%, 50%, 60%, 70%, 80%, and 90% of habitat, totaling 180 landscapes. The level of fragmentation was quantified as the average Euclidean distance to the nearest neighbor, and we used the landscapemetrics package (Hesselbarth et al. 2019) from the R Core Team software (2023). Comparisons between navigation capabilities were also made in a nested way; at the end of the simulation of a treatment (e.g., random navigation), we used the same population to run the next treatment.

5. Data analysis

The home range sizes were estimated through a 95% kernel, using the adehabitatHR package, and then the average home range size was calculated for use in our analyses. We used generalized linear mixed models (GLMM) to test our hypotheses. We used the average home range size, the percentage of habitat in the landscape, and the average Euclidean distance to the nearest neighbor as predictor variables. The model was built hierarchically with simulation as a random variable. To compare the home range size between the two navigation capacities, we also used a GLMM in which the simulation and the species were used as random effect variables. The way in which the models were constructed is shown below:

HR mean size ~ Average dist. to nearest neighbor + habitat amount + (1| simulation)

HR mean size ~ Navegation capacity - 1 + (1| simulation/SP)

All the analyses were carried out using Bayesian inference, and the parameters were estimated using the Hamiltonian Monte Carlo algorithm with four Markov chains and 10.000 iterations. We analyzed data using R Core Team (2023) software and the rstanarm and bayestR packages. (Muth et al. 2018, Makowski et al. 2019).

Results

Our results show the home range size is different between navigation capacities; the home range size of non-oriented individuals was greater than that of memory-based individuals (Table 1; Figure 2).

Table 1: Results of the comparison of the size of the living area between the memory-based and non-guided navigation capacity models. CI represents the 95% credibility interval.

Navegation	Median	CI-min	CI-max	Prob. Direction
Memory	75.021	55.267	93.862	1.0
Non-orientated	805.478	786.573	825.548	1.0

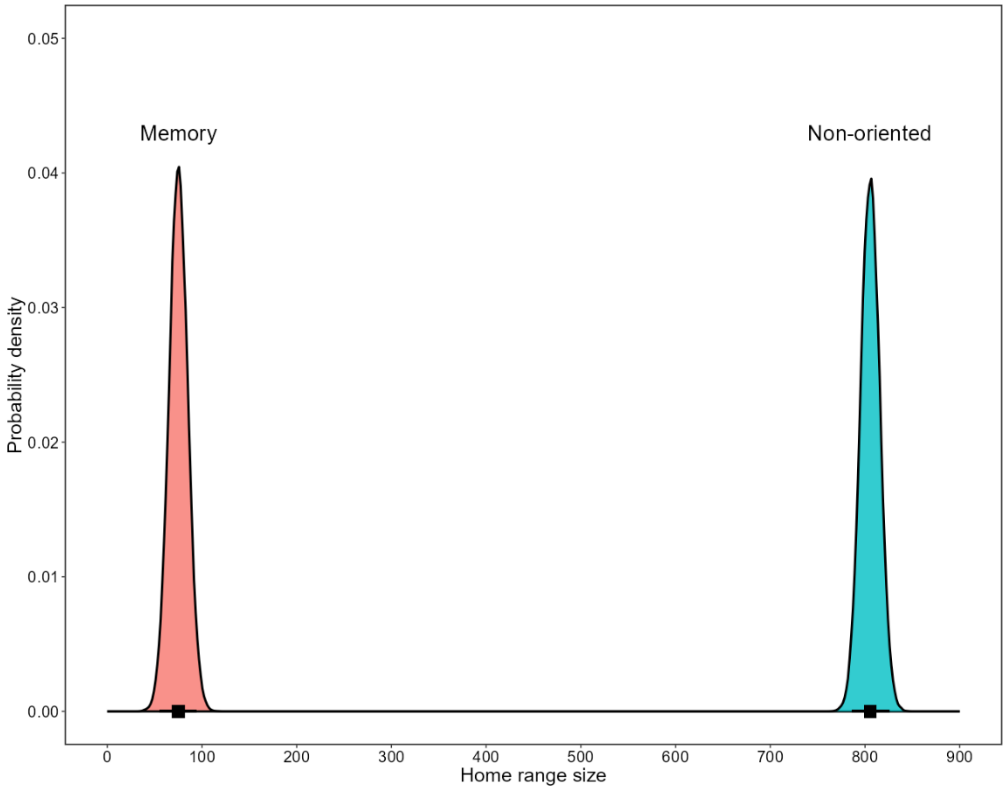

Figure 2: Probability density plot for the home range size of memory-based (red curve) and non-oriented (blue curve) navigation capacity. The squares inside the curves represent the median, and the horizontal bars represent the 95% credibility interval.

In general, we found a negative relationship between the amount of habitat in the landscape and the size of the home range, corroborating our hypothesis that increased habitat loss causes individuals to move over larger areas (Table 2). This relationship was not found only for the memory-based model of the species *S. maximiliani* (Figure 3).

Habitat loss had a greater effect on non-oriented individuals, and for these, the uncertainty associated with this effect was lower than for memory-based individuals (Figure 3; 4). On the other hand, habitat fragmentation, represented by the landscape aggregation index, generally showed no relationship with home range size (Table 2), and the only model that showed any effect was for individuals with unguided navigation ability of the *S. maximiliani* species (Figure 3). Even so, there is a great deal of uncertainty associated with estimating this effect (CI_{min}= -15335.4; CI_{max}= -3183.4).

Table 2: Re Results of the generalized linear mixed models adjusted separately for the two species. CI represents the 95% credibility interval and pd represents the probability of direction of the effect size.

Specie	Navigation	Parameter	Median	IC-min	IC-max	pd
S. cinnamomea	Memory	Intercept	78.93	71.24	86.43	1.0
		Habitat %	**-0.03**	**-0.06**	**-0.01**	**1.0**
		Aggregation index	-58.59	-190.54	71.23	0.8
	non-oriented	Intercept	1339.17	1235.34	1446.35	1.0
		Habitat %	**-9.86**	**-11.05**	**-8.68**	**1.0**
		Aggregation index	-5489.37	-11536.14	772.76	1.0
S. maximiliani	Memory	Intercept	73.17	66.73	79.60	1.0
		Habitat %	-0.01	-0.03	0.02	0.7
		Aggregation index	42.35	-86.64	174.75	0.7
	non-oriented	Intercept	1391.59	1287.92	1496.63	1.0
		Habitat %	**-10.33**	**-11.52**	**-9.16**	**1.0**
		Aggregation index	**-9263.12**	**-15335.4**	**-3183.48**	**1.0**

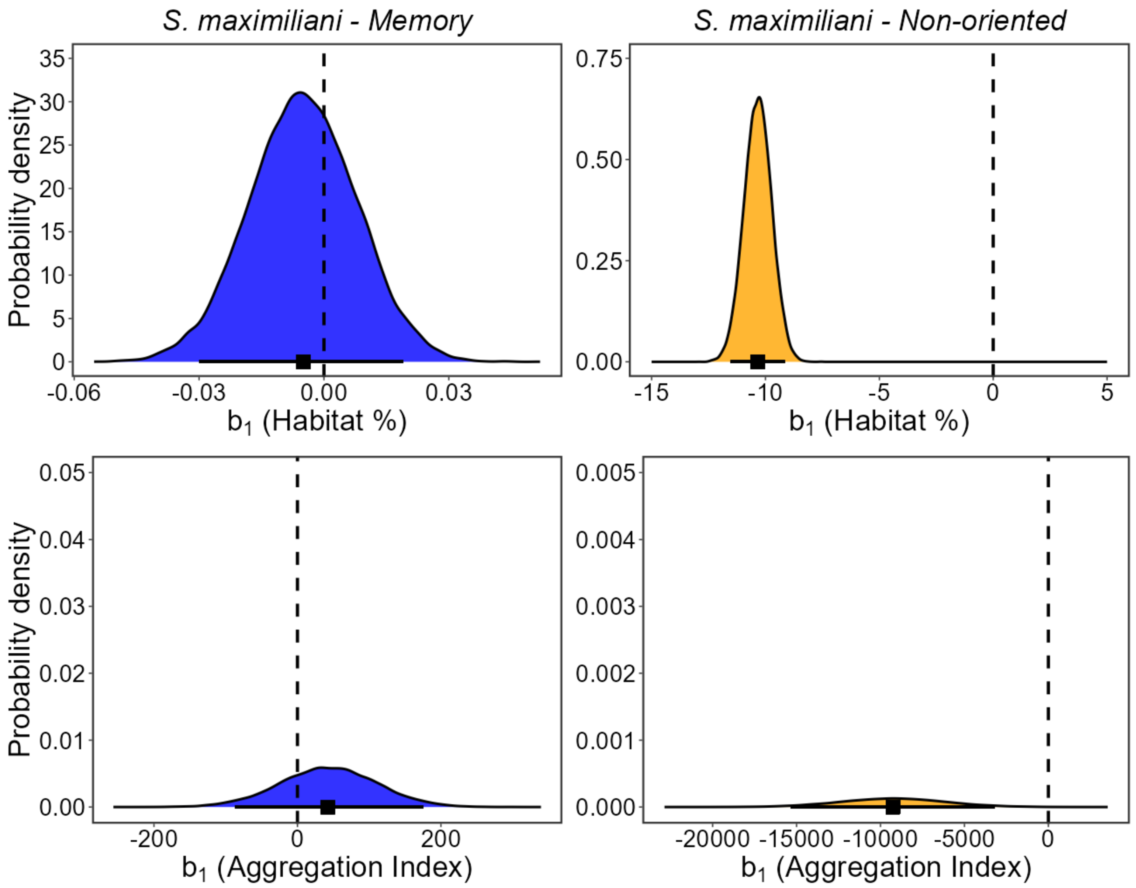

Figure 3: Probability density plot of Bayesian generalized linear mixed model for *S. maximiliani*. The curves represent the probability density of the slope values of the line for the percentage of habitat in the landscape (b_1 Habitat%) and for the average Euclidean distance to the nearest neighbor (b_1 Aggregation index). Yellow and blue curves represent non-oriented and memory-based navigation capacity.

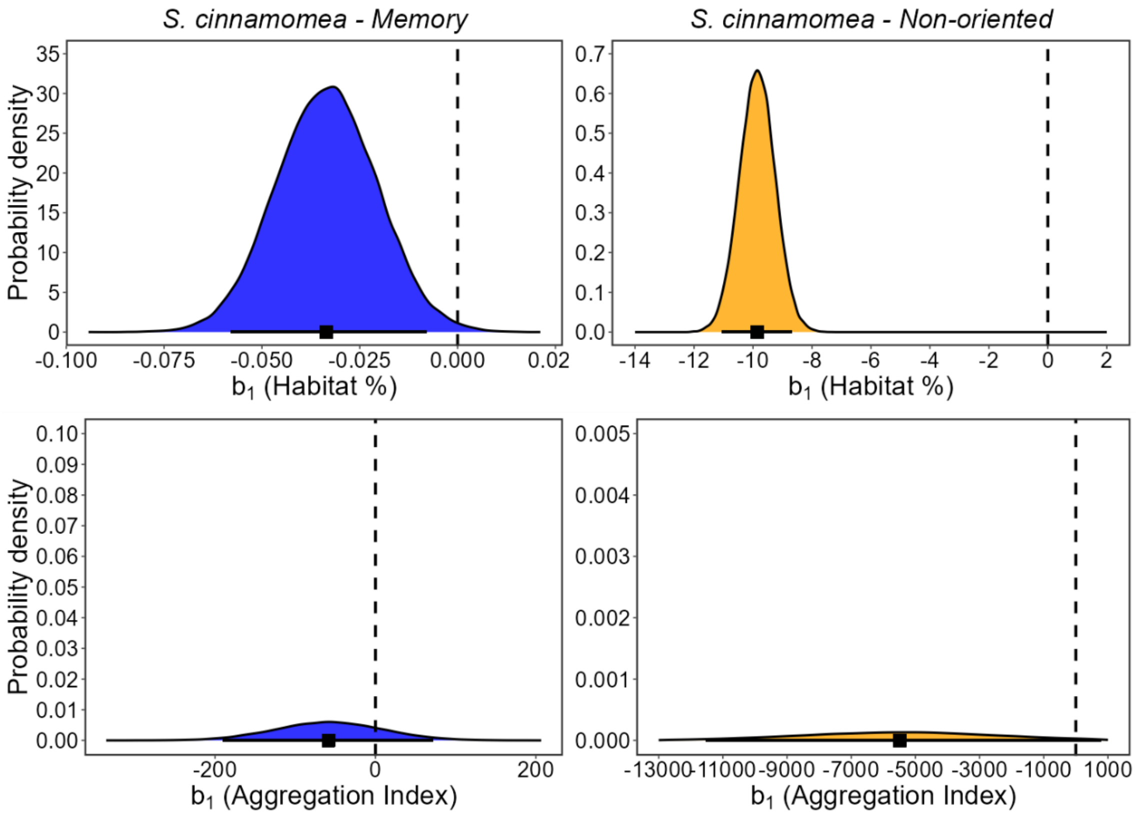

Figure 4: Probability density plot of Bayesian generalized linear mixed model for S. cinnamomea. The curves represent the probability density of the slope values of the line for the percentage of habitat in the landscape (b1 Habitat%) and for the average Euclidean distance to the nearest neighbor (b1 Aggregation index). Yellow and blue curves represent non-oriented and memory-based navigation capacity.

Discussão

Our models' results showed that the home range's size is affected by navigation capacity, non-oriented individuals moving over a much larger area, resulting in a much larger home range than memory-based individuals. The hypothesis that the size of the home range increases as habitat loss progresses was partially corroborated. Our results show that for *S. cinnamomea*, the home range increases as the amount of habitat in the landscape decreases, and this pattern was found for both models of navigational ability.

S. maximiliani showed a relationship between habitat loss and home range size only for non-oriented movement. Habitat fragmentation affected the home range only for *S. maximiliani* non-oriented.

Our results show that individuals with memory-based navigation skills explore the landscape less than non-oriented individuals. In our memory-based model, individuals move around, making the best decision, which causes them to explore the landscape less. Within our model, there are two scenarios in which this individual assumes an exploration behavior; the first is a stochastic factor, in which even if the individual is in an ideal cell, he has a 10% chance of leaving it, but during the choice of where to move it makes an optimal choice. Another scenario is that the individual is in the matrix, and the cell options within the radius of perception are matrix cells, in which case they choose randomly from the available cells. But even with these two exploration scenarios, memory-based choices override exploratory behavior. On the other hand, non-oriented individuals move without using any information about the surrounding landscape and end up moving more simply because they have no control over their direction. This lack of information generates a movement pattern that resembles an individual with an exploratory profile. This difference in the size of the living area between models of memory-based and non-oriented individuals can also be found in other simulation models (Van Moorter et al. 2009, Fagan et al. 2013, Sakiyama and Gunji 2016).

Although we found evidence corroborating our hypothesis that habitat loss increases home range, this effect varied between the navigation capacity models and between the two model species. For memory-based individuals, *S. cinnamomea* showed a positive relationship between the amount of habitat and the home range size. In contrast, *S. maximiliani* showed no evidence of this effect. For non-oriented individuals, both species were affected by habitat loss. When we analyzed the two navigation capacities, we found that habitat loss affects the home ranges of non-oriented individuals much more strongly, regardless of the species, and the uncertainty associated (credibility interval) with this effect is smaller. This gives us a clue that information about the surrounding landscape during movement may affect the relationship between habitat loss and home range size. For non-oriented individuals, as habitat loss progresses, it becomes more difficult for them to move to a habitat cell, which increases the number of times they need to move until they find a habitat cell. This reasoning may also explain why *S. cinnamomea* was affected by habitat loss and *S. maximiliani* was not. During the movement process, the individuals evaluated the cells around them according to the radius of perception, which is half the maximum movement capacity. Because *S. cinnamomea* has a smaller body size, individuals obtain less information from the landscape to move. A model developed by Hillaert et al., (2018), in which the perception radius was also dependent on body size, showed that the increase in habitat loss altered body size distribution within populations. In landscapes with less habitat, the average size of individuals increased, indicating that larger individuals are less affected.

During movement, individuals make decisions based on the experiences they were exposed to during training. Although we had a simple landscape, in which we only had three states and nine possible actions, we can consider that there is a small difference in learning between individuals. This small difference may cause individuals to behave differently, which may explain the greater uncertainty associated with memory-based estimates of individuals' effect sizes.

One challenge encountered in landscape ecology is assessing the effect of habitat fragmentation *per se* (Fahrig 2017), which is not so easy to test with data collected in the field. In our study, it was possible to assess fragmentation independently of habitat loss since, during the landscape creation, we simulated a history of habitat loss, making it possible to generate landscapes with different configurations but with the same amount of habitat. However, in our model, we don't have enough evidence to corroborate that habitat fragmentation affects home range size because the uncertainties associated with estimating the effect are too great. We believe that one of the factors behind this result is the low variability of the aggregation index between landscapes (mean: 0.007, standard deviation: 0.005).

Another component that our model allowed to be controlled was the population. The same individuals were used for the same history of habitat loss, thus preserving the same initial coordinates, maximum movement capacity, radius of perception of the landscape, and Q matrix. This level of control in our study shows how simulation models can be a powerful tool for "experimentation" in ecology. MBIs are highly flexible models that can be developed using different mathematical and statistical techniques and applied to different theoretical and applied ecology problems (Dalleau et al. 2019, Djouda et al. 2021, Vasbinder et al. 2023).

Our model has some limitations. We used a simplified landscape where the cells are binary, so the individuals received information on whether they were in a suitable call or a cell above the carrying capacity. One way of increasing the complexity of the landscape and making it more realistic would be to have cells with continuous values instead of binary values. For habitat cells, the values can represent the availability or quality of the resource. In contrast, for cells expressing the matrix, these values can represent resistance to movement or probability of death (Simpkins and Perry 2017). However, the models presented a trade-off between complexity and generalization. More complex models tend to be more realistic but are more specific and have less generalization power (Evans et al. 2013). The complexity and simplifications present in our model were enough to test our hypotheses; increasing details such as sex differentiation and population dynamics would not add any new insights to our work and would most likely not alter our results.

Despite its limitations, our model provided valuable conclusions, highlighting the importance of navigation capacity for movement in altered landscapes and underscoring the usefulness of IBMs as experimental tools in ecological studies. Our study demonstrated how memory and getting information from the landscape affects home range size, causing individuals to move shorter distances in the landscape. We showed that the home range size of memory-based individuals is less altered than that of non-oriented individuals, thus demonstrating that decisions based on landscape information optimize the movement of individuals. This result is reinforced by the different responses between species, with the smaller species obtaining less information from the landscape and ending up being affected by habitat loss, while the other species' home range is not.

Data availability

All the scripts used to create the model and analyze the data are available in the following Github directory: https://github.com/edgar-lima/IBM_Movement

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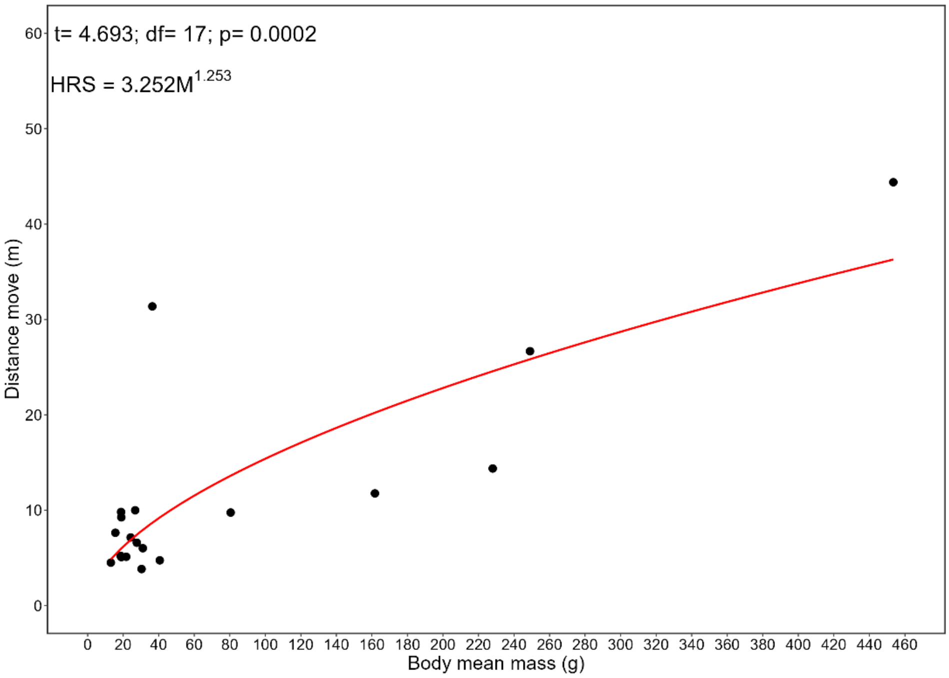
Supporting information

To obtain the parameters of the allometric equations between body size and daily movement capacity, we fitted a non-linear regression model between the body mass of herbivorous passerine species that use grassland as habitats. The data used to adjust the models was obtained from the literature. The regression was fitted using the minpack.lm package in the R software.



S1: Non-linear regression between body mass and daily movement capacity of herbivorous passerines that use grassland habitats.

Capítulo III

The effect of landscape characteristics on bird home range movements: a comprehensive global meta-analysis.

Abstract

The intense expansion of human activities in natural areas is recognized as a major threat to biodiversity. Habitat loss diminishes landscape resources, impacting food availability, nesting sites, and shelters against predators. Habitat loss also leads to fragmentation, altering the distribution of habitats in the landscape, resulting in resource isolation, reduced genetic flow, and compromising individual movement capacity. Individuals adjust their movement behavior to landscape characteristics influenced by habitat loss and fragmentation. In environments with abundant and predictable resources, individuals move within a smaller area, conserving energy by following a sinuous step at a slower speed, reducing mortality risk. Conversely, individuals cover a larger area in resource-scarce environments, moving with less meandering and fast movements. This study assesses the impact of habitat loss and fragmentation on bird movements within their home ranges. Employing a meta-analytic approach, we tested hypotheses about changes in movement within the home range, expecting that individuals will have i) a larger home range size, ii) individuals will move faster and over longer distances in landscapes with less habitat and more fragmented, iii) the effect of habitat loss on individual movement will be greater than the effect of fragmentation. We did not find evidence of landscape effects on bird movement within the home range without considering any moderator. Despite a trend suggesting a positive impact of habitat disturbance, substantial uncertainty implies the outcome could be neutral or negative. Birds were observed to move faster in landscapes with scarce and fragmented habitats, indicating a preference for speed in degraded environments. However, we did not find a significant impact of the landscape context on home range size, core size, and movement distance. The complex interaction of landscape elements and individual decision-making suggests diverse responses in movement distances and home range size, highlighting the intricate nature of this relationship.

Keywords: Movement ecology, Landscape ecology, Marginal Value Theorem, Movement cost, Movement behavior.

Introduction

The strong expansion of human activities towards the natural areas has been considered one of the main threats to biodiversity and ecosystems functioning (Wilcove et al. 1986, Estavillo et al. 2013). In this context, habitat loss reduces resources in the landscape, mainly food availability, nesting sites, and shelters against predators (Fahrig 2001). As a consequence of habitat loss, fragmentation alters the distribution of habitat patches on the landscape, causing the isolation of resources and reducing the genetic flux and compromising the individual movement capacity (With and King 1999, Grande et al. 2020). The population consequences of this involve an increase in local intra- and interspecific competition, an increased risk of local population extinction, and the possibility of losing dispersing individuals crossing a matrix occupied by human activities (Estavillo et al. 2013, Fahrig 2013). Given such impacts, assessing how habitat loss and fragmentation affect individuals during their daily movements within their home range is necessary.

Even those species that do not have their means of locomotion, individuals need to move at least at one stage of their life. However, movement can be a broad term encompassing distinct ecological processes. For example, movement to occupy new areas is generally defined as dispersal and has a different demographic meaning than movement within the home range (Clobert et al. 2012, With 2019). In an approach proposed by Nathan et al. (2008) to study movement in ecology, the authors suggest categorizing explanations for "why individuals move?" into internal state and external factors. The internal state refers to physiological needs that drive movement, such as searching for food to meet their energy requirements or seeking reproductive partners (Nathan et al. 2008). On the other hand, external factors are primarily related to environmental components that cause and affect an individual's movement, such as resource availability in the landscape and climatic seasonality (Nathan et al. 2008).

This study focuses exclusively on movement within an individual’s home range and the processes that can affect it. The home range of an individual is characterized by the sum of areas in which individuals move to feed, reproduce, escape predators, and explore new areas (Börger et al. 2008, With 2019). The external factors related to movement within the home range are typically associated with landscape characteristics because, during their daily movements, individuals interact with the various elements of the environment while exploring it (Kleyheeg et al. 2017, Doherty et al. 2019).

Individuals can alter their movement behavior within the home range in response to landscape characteristics, including changes observed due to habitat loss and fragmentation (Fahrig 2007, Mäkeläinen et al. 2015). For example, individuals in landscapes with abundant and predictable resources tend to move within a smaller area, following a more sinuous path and slower speed (Bautista et al. 2017, Ramos et al. 2020). Therefore, they avoid high energy expenditure and reduce mortality risk (Charnov 1976, Malishev et al. 2018). On the other hand, individuals in landscapes with lower resource availability tend to move over a larger spatial extent in a less meandering manner and at a higher velocity (Vergara et al. 2015). In a study with koalas, Rus et al. (2020) tracked 36 individuals for four months. Their results revealed that individuals in landscapes with lower connectivity walked across an area three times larger than individuals in more connected areas. The authors also found a positive relationship between connectivity and the tortuosity of individuals' movements, indicating that in more fragmented landscapes, individuals use faster movements to access suitable habitats.

Therefore, this study aims to conduct a systematic literature review to assess the effect of habitat loss and fragmentation on movement within birds' home ranges. We chose the group because it is well studied, and several species are habitat specialists, which means habitat loss and fragmentation might affect their movements or dispersal capacity. We employed a meta-analytical approach and tested the following hypotheses: i) habitat loss and fragmentation will reduce and structure the resource on the landscape and affect the daily movement behavior; ii) habitat loss will affect movement more than fragmentation. Therefore, we predict that: i) home range size will be larger in landscapes with lower habitat quantity and higher fragmentation; ii) individuals will exhibit faster movements and move over longer distances in landscapes with lower habitat quantity and higher fragmentation; iii) the effect of habitat loss on individual movement will be greater than the effect of fragmentation.

Material & methods

1. Data sampling and selection criteria

We conducted a systematic review using the PRISMA protocol (Moher et al. 2009), focusing on studies investigating the relationship between landscape effects and movement within the home range of birds. We searched on Web of Science and Scopus databases, by using the following terms: ((Landscape OR "Landscape ecology") AND ("Space use" OR "Home range")) AND (Bird* OR Aves). We conducted the search on November 10, 2022, and the search terms were applied to the title, abstract, keywords, and keywords plus fields of the articles. We removed any duplicated articles, and two reviewers revised the database for abstract screening.

The meta-analysis included studies that met the following criteria: i) the study's purpose should examine the relationship between landscape components and movement within bird home ranges; ii) the study should report effect size, a goodness-of-fit measure (e.g., r^2), a test statistic (e.g., t, F), or provided data that allowed for the calculation of effect size; iii) the study should specify the method used for monitoring movement (e.g., telemetry, GPS); iv) the study should indicate the method used for determining home range (e.g., minimum convex polygon); v) for studies should involve multiple species, reporting measures separated for each species.

2. Landscape variables

To compare the effects of habitat loss and fragmentation, we created a moderator (explanatory variable) based on landscape metrics and treatments employed in the studies. Variables that represented patch distribution patterns, shape index, aggregation index, and amount of edge were classified as indicators of habitat fragmentation (Smith et al. 2009, Didham et al. 2012). On the other hand, variables such as habitat amount, habitat diversity, and total nuclear area were considered as measures of habitat loss (Mcgarigal and Cushman 2002, Cushman et al. 2012).

3. Functional classification of species

We developed two moderators to represent functional groups. The first moderator represents the food resource, while the second represents the primary habitat use. The classification of species was based on the AVONET database (Tobias et al. 2022). We combined information on the trophic level and trophic niche for the food resource moderator. Regarding the habitat use moderator, we utilized the habitat information and grouped woodland and forest types into the forest category. For more detailed information on trophic classifications, please refer to the AVONET metadata (https://figshare.com/s/b990722d72a26b5bfead).

4. Phylogeny data

An essential assumption of statistical analysis is the independence of the residuals, as in our study, there are different species, we used the birds' phylogeny to control the correlation between them (Adams 2008, Koricheva et al. 2013, Gurevitch et al. 2018). We used a consensus phylogeny with 1000 random phylogenetic trees with Hackett constraint from Jetz et al. (2012) topology.

5. Data analysis

To test our hypothesis, we utilized the coefficient of correlation (R) as the standard effect size. We selected this effect size measure because it has a defined range with minimum and maximum values and is easily interpretable by people. In this study, the effect size was estimated for habitat loss and fragmentation, with positive values indicating a positive relationship between movement and the extent of habitat loss and fragmentation (Ellis 2010).

We employed a Multilevel Linear Mixed Models approach, which considers the variation between studies, to estimate the "true" effect size. This method also assigns more weight to studies with larger sample sizes (Borenstein et al. 2009). To account for the phylogenetic correlation between species in our study, we controlled for it by utilizing a phylogenetic variance-covariance matrix. For this purpose, we used the *vcv* function from the *ape* package (Paradis and Schliep 2019).

Initially, we employed a general model with wing length as a moderator. However, the purpose of this moderator was solely to control for the correlation between body size and motion capacity. The study ID, monitoring method, and species were treated as random effects, while the intercept value served as the accumulated effect size. After this, we fitted four models each with one moderator: i) landscape model: habitat loss and habitat fragmentation; ii) movement model: home range size, home range core size, movement distance, movement speed; iii) food resource: Carnivore/Generalist, Carnivore/ Invertivore, Carnivore/Vertivore, Herbivore/Generalist, Herbivore/ Specialist, Omnivore; iv) habitat use: Forest, Grassland, Human modified, and Shrubland. We also controlled the wing length and the same variables for all these models on random effects. The models were fitted using rma.mv from metafor package (Viechtbauer 2010).

We also estimated the T^2 statistics, which reflect the proportion of variation between studies, and I^2 statistics, which indicate the amount of variation that can be attributed to the moderators (Borenstein et al. 2009). We employed the method developed to estimate the mentioned statistics to account for phylogenetic correlation, (Nakagawa and Santos 2012). In models with categorical moderators, we computed the marginal R^2 and utilized the orchaRd package (Shinichi Nakagawa et al 2023).

3. Publication bias

We used the funnel plot associated with Trim and Fill to evaluate the publication bias. The funnel plot was built with effect size on the x-axis and the standard error on y, and each point on the plot represents a study; without publication bias, the plot presents a symmetric distribution of points (Borenstein et al. 2009). In association with the funnel plot, the Trim and Fill method indicates how many studies it would take to generate a symmetric plot (Duval and Tweedie 2000). We also used the Orwin Fail-safe number to evaluate how many studies are needed to reduce the effect size by a predefined percentage by the research (Borenstein et al. 2009). We used an effect size reduction of 50 and 75% in these studies. All analyses were performed on R Core Team (2023) using metafor package (Viechtbauer 2010).

Results

Our search yielded a total of 814 studies, out of which 41 studies met our criteria and were included in the analyses (Fig. 1). These studies were conducted in 23 countries across four continents, including regions such as Scandinavia and Hawaii (Fig. 2). The dataset comprised 58 bird species, including 36 carnivores, 11 herbivores, and omnivorous species. For the general model, movement metrics, and landscape analysis, all 41 studies were utilized. However, guild models were based on 36 studies for home range size and nine studies for home range core size.

In general, without considering any moderator, our study did not find evidence of landscape effects on bird movement within the home range (Fig. 3, Table 1). Although a trend indicated a positive effect of habitat disturbance, the associated uncertainty was substantial, suggesting that the effect could be zero or negative (R = 0.221; CIlw = -0.055; CIup = 0.496). The total heterogeneity (I^2t) observed in our study was 80%, with 43.6% heterogeneity between studies (I^2bs) and less than 5% phylogenetic effects (I^2phy).

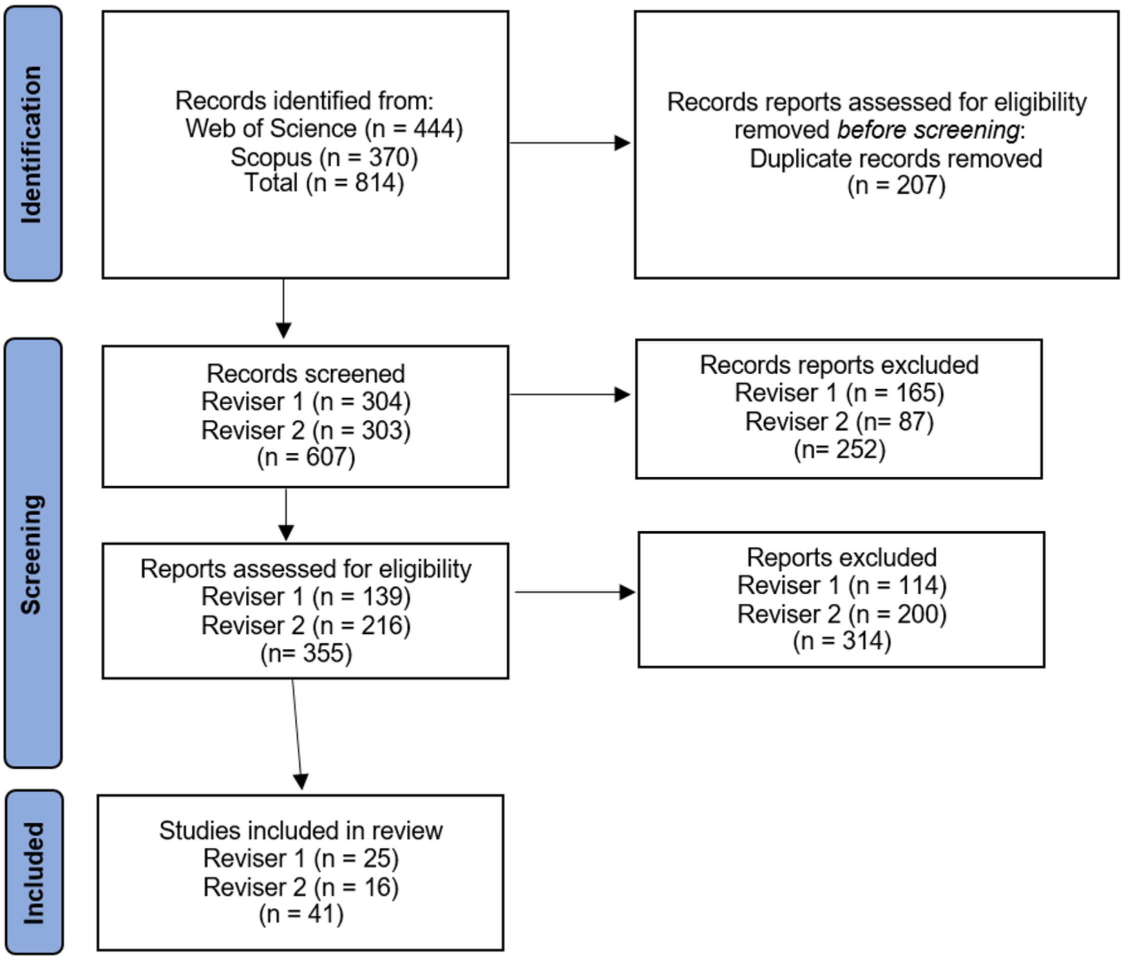


Figure 1: A flowchart illustrating the PRISMA protocol for a systematic review is presented, depicting each stage of study selection, exclusion, and the number of studies included in the meta-analysis.

When we analyzed the effects of habitat loss and fragmentation separately, we found no evidence supporting a positive or negative effect (Fig. 3, Table 1). Therefore, we can conclude that these factors do not explain movement variation within birds' home ranges in response to habitat amount and configuration, as indicated by marginal R^2= 0.055.

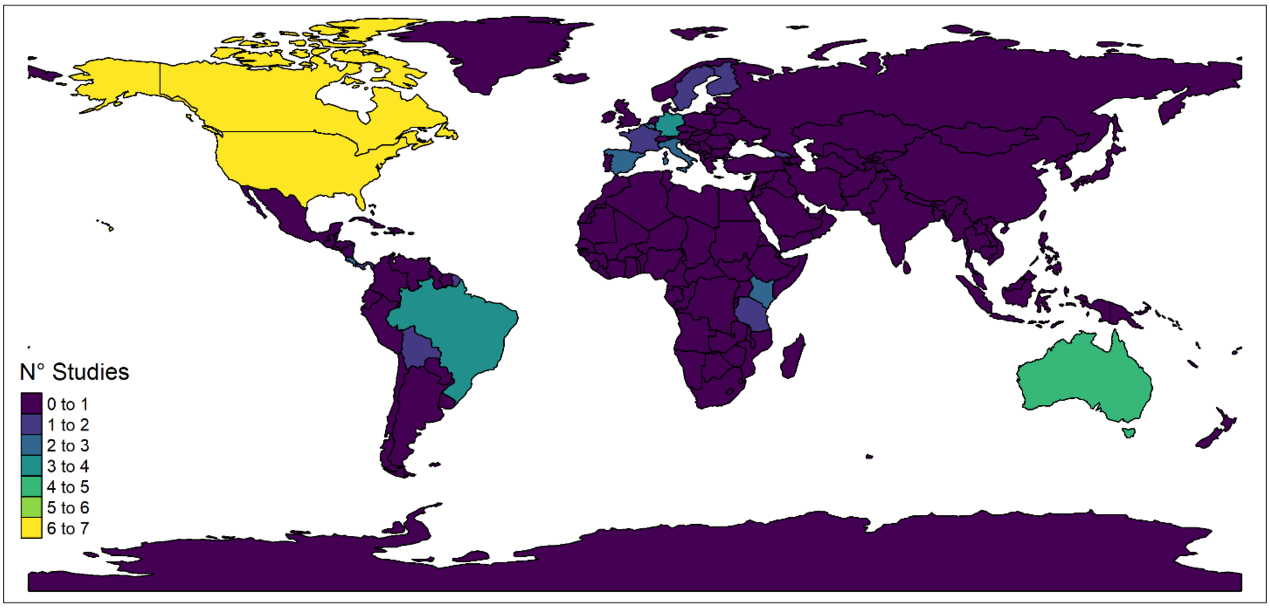


Figure 2: Global distribution and number of studies per country included in the meta-analysis.

We found that birds move faster in landscapes where habitat is less abundant and fragmented (R = 0.504; CIlw = 0.088; CIup = 0.920; Fig. 3). This indicates that birds tend to move faster in more deteriorated landscapes, spending less time on the anthropic matrix. However, we did not find any significant impact of the landscape context on home range size, home range core size, and movement distance. The movement moderator accounted for only 0.19% of the variation in effect sizes (Fig. 3, Table 1).

All functional groups tended to respond positively to the landscape. However, we did not find statistical support for the notion that landscape significantly influences the movement of food resource and habitat use functional groups (Fig. 4 and 5; Table 2).

The funnel plot and trim-and-fill methods indicated that only five studies were required to achieve a symmetrical funnel plot; these findings suggest no substantial publication bias in our dataset (Fig. S1). Additionally, the Orwin fail-safe number revealed that an additional 39 and 139 independent studies would be necessary to reduce our effect size by 50% and 75%, indicating a low test power.

Table 1: Results of general models, landscape processes and movement metrics.

	R	**SE**	**t-val**	**df**	**ci.lb**	**ci.ub**	**R^2m**	**I^2t**	**I^2bs**	**I^2phy**
General model:										
Accumulated size	0.221	0.140	1.582	179	-0.055	0.496	-	80.0	43.6	5.0
Wing lenght	-0.001	0.001	-1.313	179	-0.002	0.000				
Landscape:										
Habitat fragmentation	0.302	0.189	1.602	178	-0.070	0.674	0.055			
Habitat loss	0.213	0.145	1.465	178	-0.074	0.500	-			
Wing lenght	-0.001	0.001	-1.370	178	-0.002	0.000				
Movement metric:										
Home range size	0.094	0.145	0.652	176	-0.192	0.381	0.193			
Home range core size	0.296	0.198	1.497	176	-0.095	0.687	-			
Movement distance	0.279	0.212	1.316	176	-0.139	0.697	-			
Movement speed	0.504	0.211	2.389	176	0.088	0.920	-			
Wing lenght	-0.001	0.001	-1.054	176	-0.002	0.001				

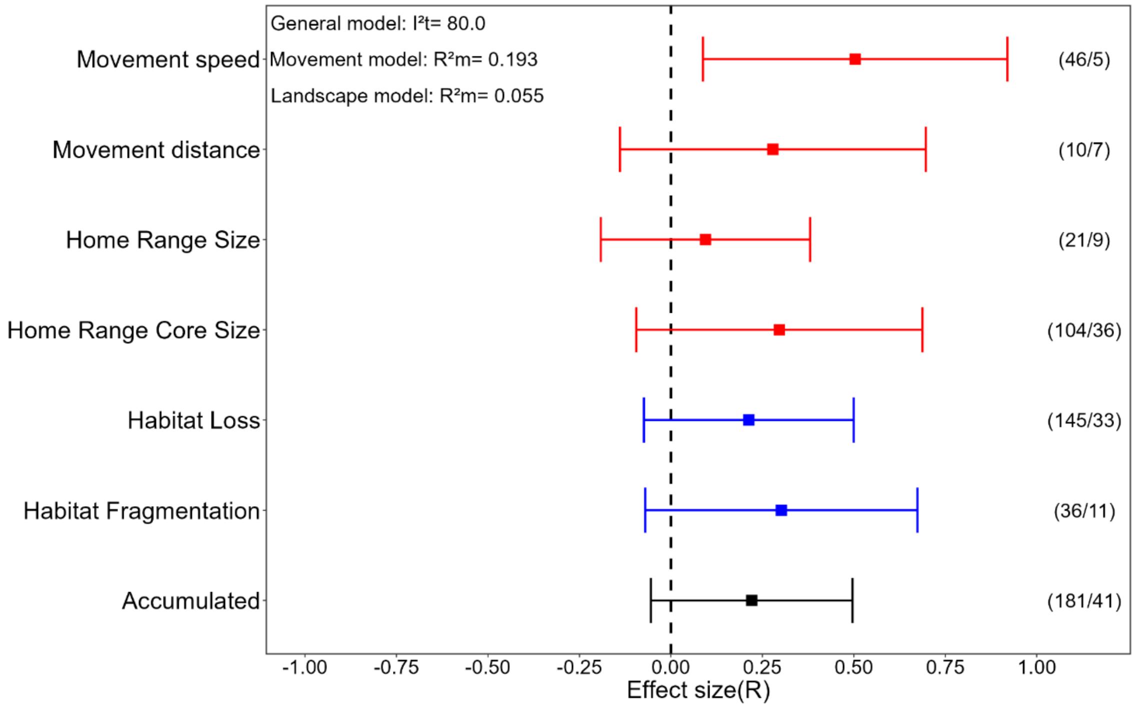


Figure 3: The forest plot presents three models: the movement model is represented by red bars and squares, the landscape model is represented by blue, and the accumulated effect size of the general model is represented by black. The squares represent the effect sizes, and the bars indicate the 95% confidence interval. The numbers on the right side show the number of samples and studies, respectively.

Table 2: Results of meta-analysis models for functional groups of feeding and habitat use.

	R	**SE**	**t-val**	**df**	**ci.lb**	**ci.ub**	**R²m**
Functional feeding:							
Carnivore/Generaslist	0.108	0.406	0.266	174	-0.692	0.908	0.079
Carnivore/Invertivore	0.289	0.192	1.508	174	-0.089	0.668	
Carnivore/Vertivore	0.254	0.332	0.765	174	-0.401	0.909	
Herbivore/Generalist	0.129	0.306	0.421	174	-0.475	0.732	
Herbivore/Specialist	0.046	0.267	0.170	174	-0.482	0.573	
Omnivore	0.297	0.265	1.120	174	-0.227	0.821	
Wing lenght	-0.001	0.001	-0.931	174	-0.002	0.001	

Functional habitat:							
Forest	0.303	0.168	1.807	168	-0.028	0.633	0.080
Grassland	-0.046	0.275	-0.167	168	-0.589	0.497	
Human Modified	0.147	0.230	0.640	168	-0.307	0.602	
Shrubland	0.324	0.232	1.398	168	-0.134	0.783	
Wing lenght	-0.001	0.001	-0.993	168	-0.002	0.001	

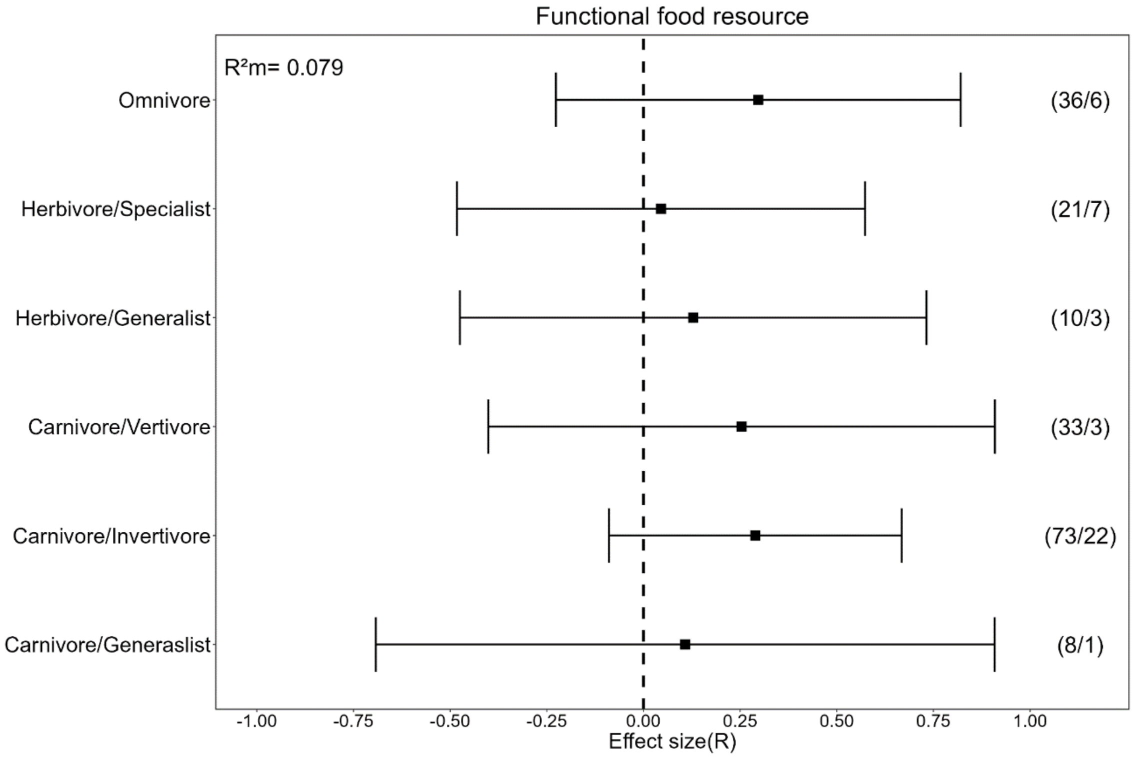


Figure 4: Forest plot reporting the food resource functional group response, square represents effect size, and bar represents confidence interval (95%). The numbers on the right side indicate the number of samples and studies, respectively.

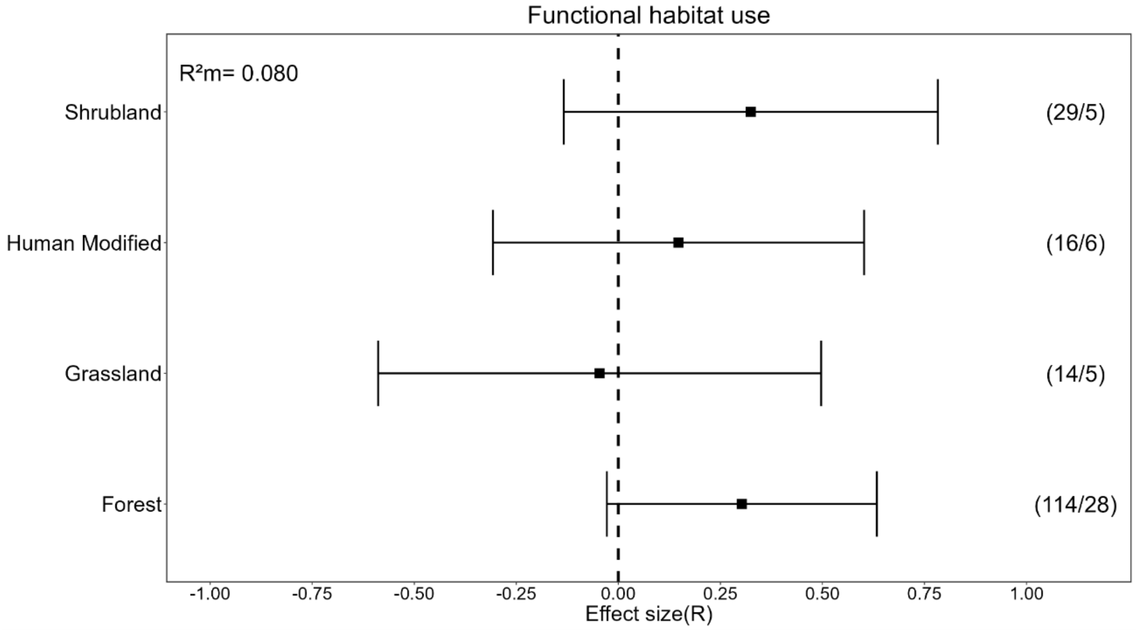


Figure 5: Forest plot reporting the response of habitat use functional group, square represents effect size, and bar represents confidence interval (95%). The numbers on the right side indicate the number of samples and studies, respectively.

Discussion

Here, we present a global overview of the relationship between movement patterns of birds and landscape characteristics (habitat amount and fragmentation). Birds move faster in altered landscapes without increasing their home range sizes and distance traveled. Moreover, home range sizes of birds adopting different resource use strategies (food and habitat use) also remain the same-altered landscapes. We found evidence that bird movement speed increases as landscape degradation increases, revealing that changes in the landscape can alter bird movement behavior (Ramos et al. 2020), even though we cannot assert different responses to habitat loss and habitat fragmentation.

In our study, the birds presented higher movement speed in landscapes with more significant habitat loss and fragmentation (hereafter HLF), agreeing with movement ecology theory, which predicts that individuals alter their behavior due to external factors like land cover (Nathan et al. 2008). In landscapes with reduced and more structured spatial resource arrangement, the individual's movement patterns tend to be more linear, with fewer stops to explore the environment (Doherty and Driscoll 2017). This behavior reduces the exposure to inhospitable environments and predators, counterbalancing the cost of faster movements and death risk. The selection of habitat use within the home range is well documented in ecological literature, and individual preference can vary according to available habitats in the landscape, season, sex, and individual's goal (Weaving et al. 2014, Barbaro et al. 2016). The necessary resources to survive, grow, and reproduce can be distributed in different habitats, and the time an individual stays in a habitat depends on rewards and the risk they are willing to take (Charnov 1976, Kacelnik and Todd 1992). All studies in this meta-analysis that evaluated any movement speed metric found a positive relationship between habitat degradation (habitat loss and fragmentation) and fast movements (Hansbauer et al. 2008, Campioni et al. 2013, Powell et al. 2016, Evens et al. 2018, Habel et al. 2019). This same pattern is also found in mammals and frogs (Vásquez et al. 2002, Gehring and Swihart 2004), reinforcing the evidence that individuals change their movement behavior to adapt to habitat degradation.

However, in addition to high energy costs, fast movements also present a biomechanical price, affecting an individual's maneuverability and reducing perception of the surrounding environment (Chittka *et al.* 2009; Wilson *et al.* 2015). However, these costs can be compensated if fast movements increase survival chances or reproductive success (Hirsch 2010). Assuming that individuals make optimal decisions, we can interpret this increase in movement speed in light of the Marginal Value Theorem (MVT) (Charnov 1976). In the classic MVT, the food is found in patches, and the individual spends time moving between them; the individual must decide which patch to visit and when to leave it. The theorem predicts that individuals will choose to maximize the gain in relation to costs (Charnov 1976). Therefore, the decision to move faster instead of moving more can be interpreted as the best movement strategy in a degraded landscape according to studies presented in our meta-analysis, with the gains compensating the risks.

In landscape and movement ecology literature, we found two hypotheses and examples of the effect of landscape on the movement of organisms. On the one hand, some hypothesis studies predict that the advancement of HLF makes the individual's movement difficult, so individuals will move small distances, resulting in a small home range size (Doherty et al. 2019). Otherwise, individuals must increase their movements in landscape with higher HLF to meet their energy needs (Hillaert et al. 2018, Marcolin et al. 2021). According to the results found here, we do not have evidence for either of the two hypotheses for birds. In our review, we found studies that agree with two hypotheses and do not agree with any one (Bayne and Hobson 2001, Hinam and Clair 2008, Godet et al. 2015). For now, what we can assume for movement distances and home range size is that the relationship between the landscape and bird movement depends on a complex interaction between landscape elements and individual decision-making, which can generate different responses (Fahrig 2007).

However, these results in movement distance and home range size for general model and functional groups should be interpreted cautiously. Our models presented a low-power test, and for any moderator treatments, we found few studies; this increased the uncertainty and generated very large confidence intervals (Ellis 2010). We highlight this caution mainly for omnivores, carnivores/generalists (functional food resource), forest, and shrubland habitat use. Finally, it was not possible to include matrix effects because most studies need to mention or even measure matrix composition. The matrix type can limit or facilitate the movement of individuals, and considering this in the analysis could change our results, especially for the home range size (Cosgrove et al. 2017).

In conclusion, our study reveals a complex dynamic in the relationship between bird movement patterns and landscape characteristics, highlighting the notable acceleration in HLF landscapes. The fast movements interpreted considering the Marginal Value Theorem, suggest a strategic optimization where the benefits outweigh the costs, and individuals prefer this strategy to move long distances. Our study gives a good overview of how bird movement responds to the landscape. Still, more studies on the topic are needed, especially for the tropical region. Also, future studies must consider the impact of the matrix on the movement of individuals in the animal groups. However, we recommend that authors be more careful in presenting results, for performing a meta-analysis, the studies must present some effect size (R, R^2, F, Slope), measure of variation, and number of samples. In addition to allowing meta-analysis study, the adequate presentation of results brings more transparency and facilitates understanding by readers.

Data availability

The data and scripts of our analysis are available on GitHub: https://github.com/edgar-lima/MetaAnalise_HomeRange

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Supporting information

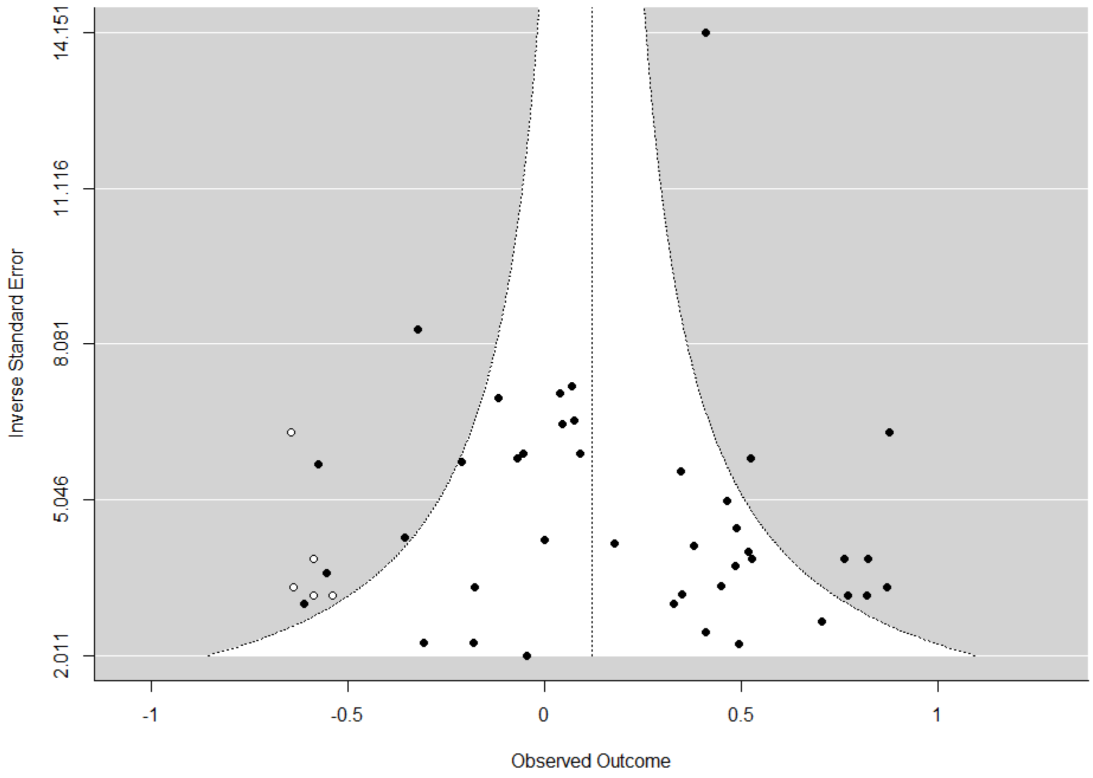

Figure S1: In the funnel plot to publication bias assessment, the x-axis represents effect size values, the y-axis represents inverse standard error values, and the vertical line represents observed effect size. Black points represent observed values, and White points represent the Trim-and-Fill studies that should be added to generate a symmetric funnel plot.