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EFEITOS DA ESTRUTURA DA PAISAGEM E DE ATRIBUTOS FUNCIONAIS SOBRE O MOVIMENTO DE AVES EM PAISAGENS FRAGMENTADAS

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Março 2018

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Orientador: Marco Aurélio Pizo

Coorientador: Milton Cezar Ribeiro

Tese apresentada ao Instituto de Biociências do Câmpus de Rio Claro, Universidade Estadual Paulista, como parte dos requisitos para obtenção do título de Doutora em Ecologia e Biodiversidade.

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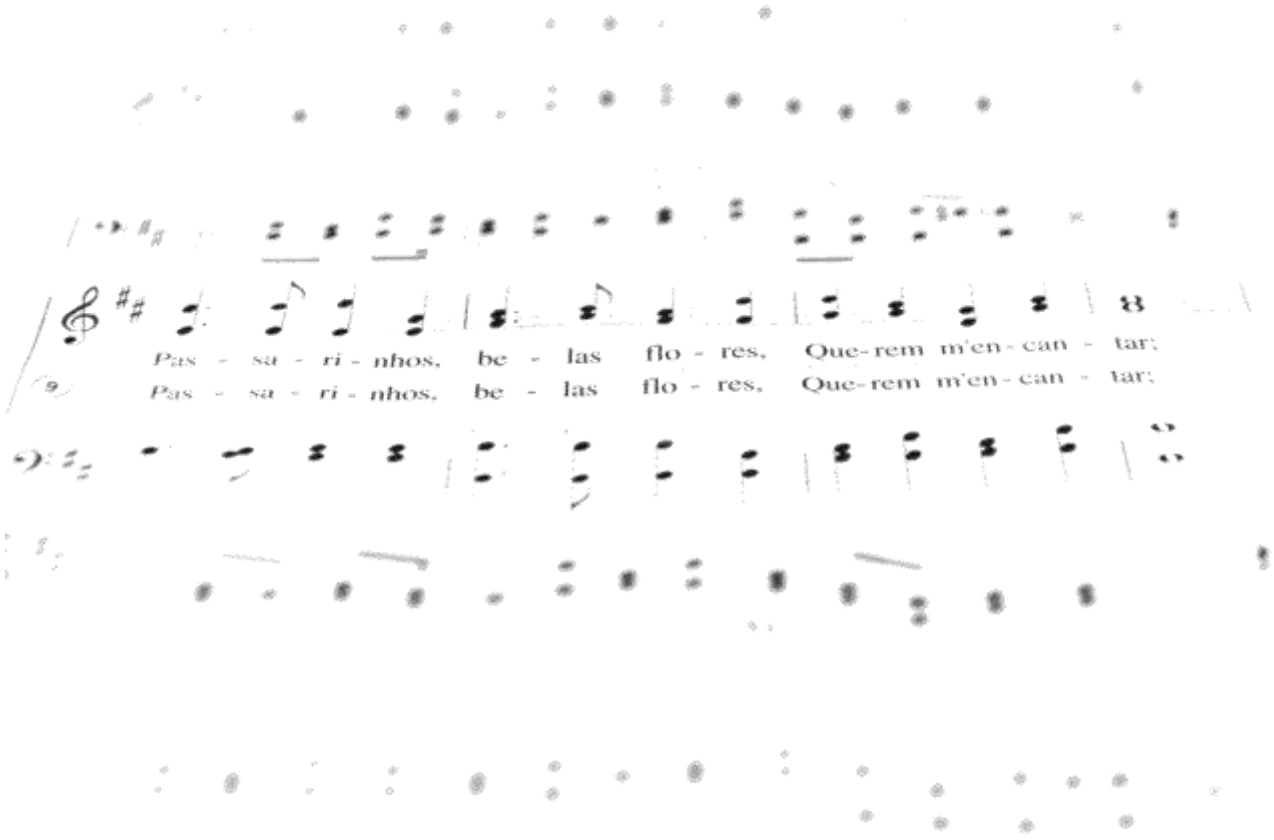
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(Justus H. Nelson)

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RESUMO

O movimento determina o conjunto de indivíduos, recursos e ambientes com os quais os organismos vivos interagem e, assim, tem um papel chave na manutenção da biodiversidade. Dadas as atuais mudanças ambientais promovidas pela atividade humana, faz-se necessário preencher lacunas no estudo do movimento das espécies para melhor compreensão das mudanças ecossistêmicas e aprimoramento da ciência da conservação. Nesta tese, exploramos o efeito da estrutura de paisagens rurais, modificadas pelo homem, sobre o movimento de aves, e suas possíveis implicações para o funcionamento de ecossistemas. Para isso, coletamos dados de movimento de aves na região do Corredor Cantareira-Matiqueira, no estado de São Paulo . Durante duas estações chuvosas (outubro de 2014 a janeiro de 2015 e setembro a dezembro de 2015), monitoramos o movimento de aves por observação direta com auxílio de binóculos, a partir de pontos que permitiam uma ampla visão do ambiente . Coletamos os dados em cinco paisagens de 600 x 600 m, compostas por mosaicos de fragmentos florestais imersos em uma matriz de pasto com diversas estruturas arbóreas remanescentes, como cercas vivas, corredores de mata ripária, árvores isoladas e pequenos capões. Após cerca de 360 horas de observação, compilamos dados de movimento de 80 espécies de aves, abordando componentes espaciais – posições e tipos de poleiros usados, distâncias de voo – e componentes temporais – tempo de repouso e velocidade de voo. Para permitir a análise eficiente desse conjunto de dados, desenvolvemos um modelo de movimento conjunto para espécies (*joint-species movement model*, JSMM) (Capítulo 1). O JSMM estima parâmetros de movimento espécie-específicos em função de atributos funcionais e correlações filogenéticas das espécies. Assim, ele permite o entendimento

de como atributos funcionais influenciam o movimento, e sobre o quanto espécies filogeneticamente mais próximas compartilham movimentos similares. Somado a isso, mostramos que esse método aumenta a precisão das estimativas dos parâmetros espécie-específicos por modelar respostas compartilhadas entre espécies, especialmente para aquelas com dados limitados. Posteriormente, expandimos esse modelo para análises multipaisagem (Capítulo 2) para entender como a cobertura florestal e o isolamento da paisagem modificam o movimento de aves florestais. Nós mostramos que o aumento da cobertura florestal reduz as distâncias de voo das aves e a preferência por poleiros arbóreos, enquanto que o aumento do isolamento aumenta a preferência por poleiros em fragmentos florestais e o tempo em repouso. Nós resumimos as consequências dessas alterações para o fluxo de serviços ecossistêmicos das paisagens com um quadro conceitual. Por fim, buscamos entender a contribuição da disponibilidade de frutos, da abundancia de dispersores e da estrutura da matriz sobre os padrões de dispersão de sementes (Capítulo 3). Para isso, usando dados das aves dispersoras mais abundantes coletados em campo e experimentalmente, nós parametrizamos um modelo mecanístico de dispersão de sementes em paisagens virtuais. Nós mostramos que a presença de poleiros na matriz é o único fator que aumentou a distância de dispersão na matriz, enquanto que a densidade de sementes aumentou principalmente devido ao aumento da abundância de aves na paisagem. Essa tese contribui para uma mudança de escala em estudos de movimento – de abordagens baseadas em espécie para as baseadas em comunidades – e para o entendimento dos mecanismos de variação dos fluxos de serviços ecossistêmicos em resposta às alterações humanas nos ambientes naturais.

ABSTRACT

EFFECTS OF LANDSCAPE STRUCTURE AND FUNCTIONAL TRAITS ON BIRD MOVEMENT IN FRAGMENTED AREAS. The movement of organisms is key to shape biodiversity, since it determines the resources, habitats and individuals with which the organisms will interact. Given the rapid environmental changes caused by human activities, it is fundamental to fulfill knowledge gaps in the movement ecology framework and properly understand the ecosystem changes to improve biodiversity conservation. In this thesis, we studied the effects of agricultural landscape structure on bird movement, and its consequences for ecosystem functions and services. We collected bird movement data in the Cantareira-Mantiqueira Corridor region, in southeastern Brazil. From October 2014 to January 2015 and September to December 2015, we used binoculars to track birds by direct observations from vantage points. We recorded data in five square plots (600 x 600 m), all of them composed by a mosaic of forest patches, live fences, small groups of trees and remnant trees within cattle pasture. We collected movement data from 80 bird species after 360 field working hours. The movement data were composed by a spatial component – sequences, spatial positions and types of perches used– and a temporal component – perching time and flight speed. To enable the analysis of this multi-species dataset, we developed joint species movement models (JSMM) (Chapter 1). The species-level movement parameters are modelled as a function of species traits and phylogenetic relationships, allowing one to ask how species traits influence movements, and whether phylogenetically related species are similar in their movement behaviour. We show that the precision of species-specific parameter estimates increases by modelling shared responses among species to the environment, especially for those

species with limited data. We extended this framework from single-landscape to a multiple-landscape model to allow understanding how forest cover and landscape isolation shape the movement of forest birds (Chapter 2). We show that increasing forest cover reduces the flight distances of birds and the movement bias to forest patches and remnant trees, while increasing landscape isolation increases the movement bias to forest patches and perching time. We summarized the main consequences of these changes on habitat connectivity and ecosystem services provision in a conceptual framework. Finally, we aimed to disentangle the effects of fruit availability, bird abundance, and matrix structure on seed rain density and seed dispersal distance into the open matrix of landscapes (Chapter 3). We used observed movement data and gut passage times from three common seed-dispersing birds to fit a mechanistic model to simulate seed dispersal in virtual landscapes. The presence of perches within matrix was the only factor increasing seed dispersal distances from forest edge into matrix, and the abundance of birds was the main factor influencing seed density in the landscape. This thesis contributes to a change in scale in movement ecology studies – from single-species to community-based studies – and to the understanding of the mechanisms behind ecosystem responses to human-caused environmental changes.

INTRODUÇÃO GERAL

Ecologia do Movimento

Todos os organismos vivos se movem em alguma fase de suas vidas, seja ativamente, pelas suas próprias capacidades locomotoras, ou por agentes de transporte, como fatores abióticos (vento e água, por exemplo) e outros organismos. Como o movimento determina o contexto ambiental e o conjunto de outros indivíduos com os quais os organismos irão interagir, estudá-lo em seus aspectos causais e mecanísticos é promissor para o entendimento de processos ecológicos e evolutivos (Jeltsch et al. 2013). De fato, o interesse do homem pelo estudo do movimento é histórico e remete-se à Grécia Antiga, quando da escrita do livro De Motu Animalium por Aristóteles (Nussbaum 1985). Na última década, esse interesse foi catalisado pelo desenvolvimento de análises matemáticas de dados de movimento e por avanços tecnológicos para o monitoramento à distância de animais, gerando uma grande quantidade de dados e de produção científica (Holyoak et al. 2008, Cagnacci et al. 2010, Kays et al. 2015) (veja Quadro 1). Os estudos do movimento foram unificados por Nathan et al. (2008) na disciplina nomeada Ecologia do Movimento, que descreve as rotas percorridas pelos organismos como resultado da interação entre fatores intrínsecos a eles – i.e., estado interno (por que mover-se), capacidade de deslocamento (como mover-se), e capacidade de navegação (para onde mover-se) – e fatores externos.

Como previsto, o rápido avanço na Ecologia do Movimento tem gerado oportunidades e evidenciado desafios (Holyoak et al. 2008) (Quadro 1). O monitoramento remoto de animais com equipamentos de telemetria, o maior aliado da disciplina, é um bom exemplo. Essas tecnologias estão em contínuo aperfeiçoamento e

inovação e permitem o registro sucessivo da posição dos animais com cada vez mais precisão e acurácia (Cagnacci et al. 2010, Kays et al. 2015). No entanto, o custo de um equipamento avançado de telemetria limita o número de indivíduos e espécies que podem ser monitorados (Cagnacci et al. 2010). Ainda são escassos os estudos que abordam, por exemplo, o movimento em âmbito de comunidades ou comparam de maneira eficiente o movimento em diferentes condições ambientais. Além disso, o peso desses equipamentos impede seu uso em organismos pequenos (Cagnacci et al. 2010). Essa restrição é especialmente importante no estudo do movimento das plantas dado por suas formas móveis, o pólen e as sementes, no caso de gimnospermas e angiospermas. Ferramentas da ecologia molecular, como a análise com microssatélites e o *DNA barcoding*, têm sido usadas, respectivamente, para desvendar a origem e destino de sementes (análise de maternidade) e seus dispersores (veja González-Varo et al. 2014 e 2017). No entanto, seu uso ainda apresenta limitações logísticas, principalmente quanto ao custo e à escala espacial passível de ser monitorada.

O potencial uso de dados de movimento para a solução de desafios da conservação de ecossistemas (Jeltsch et al. 2013) é um estímulo especial para a superação dessas limitações. A mudança do uso da terra promovida pelas atividades antrópicas altera a estrutura do meio no qual o movimento se dá, impondo novas barreiras e riscos e alterando a distribuição espacial de recursos (Haddad et al. 2015). Para que as espécies persistam e mantenham o uso ótimo do ambiente alterado é predito que seu comportamento de movimentação deve mudar, seja devido a mecanismos evolutivos ou à plasticidade comportamental (Fahrig 2007).

O movimento em paisagens degradadas

A forma de obtenção de recursos naturais para suprir as necessidades humanas tem alterado substancialmente as paisagens naturais. À medida que as florestas tropicais são substituídas por pastagem, agricultura e silvicultura, os habitat são perdidos e fragmentados (DeFries et al. 2004, Foley et al. 2005) resultando em numerosos fragmentos de pequeno tamanho e em um aumento das áreas de borda e do isolamento desses fragmentos (Fahrig 2003). Como consequência, alterações bióticas e abióticas – e.g. mudanças nas pressões de competição e predação, mudanças na disponibilidade de nutrientes, redução do tamanho das populações – causam perda e substituição de espécies nos fragmentos resultantes (Pardini et al. 2010, Beca et al. 2017).

Um efeito consistente do isolamento de florestas, decorrente do processo de fragmentação, é a redução do movimento entre fragmentos (Fahrig 2007, Cosgrove et al. 2017). As populações de espécies normalmente são reduzidas e divididas pela matriz produtiva hostil (Sekercioglu et al. 2007, Haddad et al. 2015). Ao mesmo tempo, a possibilidade de recolonização é reduzida, o que aumenta a probabilidade de extinções locais (Fahrig 2007, Sekercioglu et al. 2007). Essa falta de movimento de indivíduos também pode alterar os processos evolutivos e limitar o fluxo de genes, reduzindo a variabilidade genética e a capacidade de adaptação das espécies (Clark et al. 2010, Lancaster et al. 2011). Todos esses efeitos culminam em menor capacidade de persistência das espécies em paisagens fragmentadas. Empobrecidos em diversidade genética e de espécies, processos ecológicos essenciais e serviços ecossistêmicos podem ser comprometidos nos fragmentos remanescentes (Turner 1996, Hooper et al. 2005).

Em contraposição a essas tendências, alguns animais possuem alta capacidade de deslocamento e podem conectar ativamente habitats espacialmente segregados. Ao se moverem na paisagem, essas espécies carregam nutrientes, pólen e propágulos de plantas, micorrizas, e são responsáveis por funções ecológicas fundamentais aos ecossitemas, especialmente após distúrbios (Lundberg and Moberg 2003, Kremen et al. 2007, Jeltsch et al. 2013). Esses animais atuam como agentes de conexão ("mobile links", Gilbert 1980, Lundberg and Moberg 2003) e são representados principalmente por espécies que voam, como insetos, morcegos e aves (Lundberg and Moberg 2003, Sekercioglu 2006). Além de terem alta capacidade de deslocamento, os agentes de conexão normalmente também possuem grande habilidade de sobreviver e se mover em áreas dominadas pelas atividades humanas (Jeltsch et al. 2013), o que permite seu papel no fluxo de espécies, serviços e funções entre os diferentes ambientes de paisagens fragmentadas.

A dispersão de sementes por aves assume uma importância chave nesse contexto. Ela é diretamente responsável pelo sucesso reprodutivo das plantas (Howe and Smallwood 1982, Wunderle Jr 1997, Peterson et al. 1998, da Silva and Tabarelli 2000) e promove o fluxo de genes intra e interpopulacional, influenciando a diferenciação genética e a capacidade de adaptação das espécies (Sork and Smouse 2006, Jeltsch et al. 2013, Galetti et al. 2013). A dispersão também determina o padrão de distribuição espacial das sementes e quais espécies podem coexistir (Jordano et al. 2011). A partir dessa interação ocorrem os demais eventos populacionais, como a germinação, estabelecimento de plântulas e subsequente crescimento e mortalidade das plantas (Nathan e Muller-Landau 2000, Howe e Miriti 2004). Por sua vez, é o movimento dos

agentes dispersores que determina o padrão espacial de deposição das sementes no ambiente (Jordano et al. 2011).

Em florestas tropicais, ao menos 50% e frequentemente 75% ou mais das espécies arbóreas produzem frutos adaptados ao consumo por aves ou mamíferos (Howe and Smallwood 1982). Como em áreas alteradas pelas atividades antrópicas grandes vertebrados normalmente estão ausentes ou são raros, aves e morcegos desempenham o papel principal de dispersão de sementes (Nepstad et al. 1996, Galindo-González et al. 2000, Martínez-Garza and González-Montagut 2002, Cole et al. 2010). Embora os morcegos frequentem áreas abertas, parte das aves as evita, em particular aves florestais (Cardoso da Silva et al. 1996, Nepstad et al. 1996, Medina et al. 2007, Muscarella and Fleming 2007, Martin et al. 2009, Pizo and dos Santos 2011). Mesmo não sendo seus locais preferenciais, muitas espécies de aves utilizam de alguma forma tais habitats em busca de recursos necessários à suas sobrevivências (Guevara and Laborde 1993, Pizo 2004, Sekercioglu et al. 2007) e esses movimentos podem ser suficientes para imigração e redução das taxas de extinção nos fragmentos remanescentes (Ricketts 2001, Antongiovanni and Metzger 2005).

Ao se movimentarem na paisagem carregando sementes, as aves se contrapõem ao efeito negativo da fragmentação, promovendo o fluxo gênico entre população de plantas, favorecendo a diversidade genética e a persistências dessas populações (da Silva and Tabarelli 2000, Jordano et al. 2006, Pizo and dos Santos 2011, Jeltsch et al. 2013). Somado a isso, em paisagens intensamente fragmentadas, a conservação das florestas remanescentes não é suficiente para garantir a perpetuação do bioma e de suas espécies (Jakovac 2007) e deve estar aliada à restauração ecológica de áreas degradadas (Duncan and Chapman 2002, Barbosa 2004, Rodrigues et al. 2009). Nesse contexto, o

comportamento do animal em transportar as sementes e então "plantá-las" em novos ambientes é um serviço prestado a custo zero (Reis e Kageyama 2003). A presença de agentes dispersores não apenas garante a disseminação das espécies locais na área em restauração, mas também adiciona diversas outras espécies alóctones importantes para o processo de regeneração (Wunderle Jr 1997, Silva 2003, Jordano et al. 2006).

Efeito da estrutura de paisagens no movimento de aves

Dada a sua grande movimentação, a distribuição espacial dos recursos e a heterogeneidade das paisagens têm um papel particularmente importante na biologia dos agentes de conexão (Kremen et al. 2007). A habilidade dessas espécies se moverem varia de acordo com as características de percepção e comportamento intrínsecas de cada indivíduo e com a composição e localização dos elementos ou habitats na paisagem (Hansbauer et al. 2010). Paisagens são heterogêneas e seus diferentes elementos são favorecidos ou evitados em graus distintos por cada espécie (Graham and Blake 2001, Sekercioglu et al. 2007, Hansbauer et al. 2010, Zurita and Bellocq 2012). Sekercioglu et al. (2007), por exemplo, observaram na Costa Rica que indivíduos de *Tangara icterocephala* buscavam corredores de mata ripária em paisagens dominadas por plantação de café e pasto devido ao microclima ser mais parecido com o de fragmentos florestais, diferente de *Catharus aurantiirostris*, encontrado em locais com microclima mais quente e seco inclusive dentro dos mesmos tipos de vegetação. Os autores também encontraram uma correlação positiva entre a dependência por florestas e o tamanho da área de vida e distâncias de voo. Zurita e Bellocq (2012) demonstraram que o uso de diferentes elementos da paisagem por aves depende da complexidade de sua estrutura vertical, de forma que silviculturas e agroflorestas são preferidas a ambientes abertos.

Outra fonte de variação para o movimento de agentes de conexão é a própria capacidade de adaptação das espécies, que podem apresentar diferentes comportamentos para otimizar seu movimento dependendo do contexto ambiental. No caso das aves, a heterogeneidade das matrizes, o isolamento e tamanho de fragmentos florestais, a densidade de stepping-stones e a cobertura florestal alteram a disponibilidade de recursos e consequentemente o custo do deslocamento e definem padrões diferentes de movimento (Graham 2001, Sekercioglu et al. 2007, Silva 2012). Levey et al. (2008) constataram que o comportamento de aves dispersoras de sementes se modificou em paisagens heterogêneas em comparação com paisagens com um único tipo de habitat devido à busca por locais preferenciais (bordas de fragmentos). Como consequência, a dispersão de sementes foi irregular e adensada em áreas fragmentadas. Hansbauer et al. (2008) observaram que indivíduos de *Chiroxiphia caudata* possuíam cerca do dobro da área de vida em paisagens fragmentadas se comparada a áreas de floresta contínua devido à necessidade de busca de recursos nos diversos fragmentos.

Tendo esses conhecimentos em vista, ao invés de considerar paisagens modificadas pelo homem como fragmentos imersos em uma matriz agressiva, uma melhor perspectiva para o planejamento de projetos de preservação de ecossistemas é tratá-las como mosaicos de diferentes tipos de coberturas vegetais nativas ou antrópicas (Hansbauer et al. 2009), comunidades interativas e usos do solo, com valores para a conservação de ecossistemas naturais (Wiens 2008). Com essa abordagem, as necessidades humanas e a biodiversidade deixam de serem inimigas e as potenciais consequências dos diferentes usos do solo sobre as espécies e suas interações podem ser melhor compreendidas visando à conciliação entre os interesses econômicos, sociais e ambientais (Ricketts 2001, Lindenmayer et al. 2008, Wiens 2008).

Objetivos gerais e específicos

Dentro do contexto descrito acima, o objetivo geral desta tese de doutorado é explorar os efeitos da estrutura de paisagens rurais modificadas pelo homem sobre o movimento de aves. Para abordar essa questão, coletamos um conjunto de dados de movimento de 80 espécies de aves abundantes em paisagens fragmentadas com um gradiente de variáveis estruturais. Unimos a esse esforço de campo métodos inovadores de análise de movimento de comunidade de aves e simulações espacialmente explícitas para inferir sobre as possíveis consequências dos comportamentos de voo das aves sobre funções ecossistêmicas, particularmente a dispersão de sementes.

A estrutura de paisagens é determinada, em grande parte, por políticas de uso do solo que agem em escalas locais, como no interior de propriedades individuais, ou em escalas maiores e regionais (Kremen et al. 2007). Dessa forma, discutimos ao longo da tese potenciais aplicações de nossos resultados para o manejo adequado de paisagens visando o aumento da conectividade e de serviços ecossistêmicos gerados por aves. Especificamente, os seguintes objetivos foram abordados, estruturados em três capítulos redigidos em formato de artigo científico internacional:

1. Construir um modelo de movimento conjunto para espécies (*joint-species movement model*, JSMM), de forma a permitir a análise eficiente de dados de movimento multi-espécies, e prover um entendimento sintetizado das causas e consequências da variação de movimento entre organismos em função de suas características funcionais (Capítulo 1).
2. Em uma abordagem conjunta para dados de comunidades, quantificar como a cobertura florestal e o isolamento de paisagens alteram o comportamento de

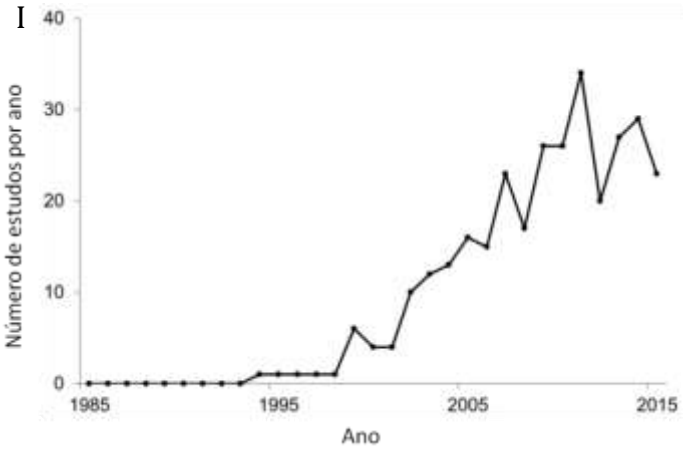
movimento de aves em consequência de suas características funcionais (Capítulo 2).

3. Distinguir os efeitos de características dos fragmentos florestais fontes de espécies – disponibilidade de frutos e abundância de aves – e da estrutura da matriz sobre a chuva de sementes em áreas degradadas (Capítulo 3). Abordamos esse objetivo com uso de modelos de simulação de movimento de aves e sementes, parametrizados com dados de observação em campo e em experimentos.

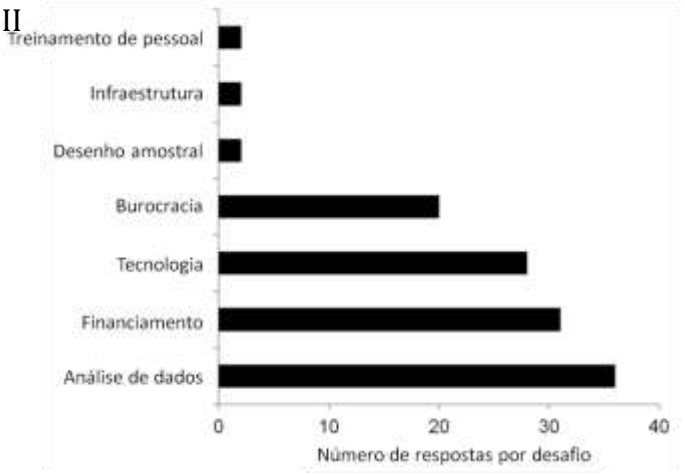
Quadro 1. Diagnóstico do crescimento e dos desafios da Ecologia do Movimento no Brasil

O estudo do movimento de animais no Brasil teve um crescimento acentuado nos últimos 30 anos (Fig. I). Esse aumento foi quantificado a partir de buscas por literatura (na plataforma Web of Science) utilizando as expressões "movement* ecolog* Brazil", "animal* movement* Brazil", "animal* track* Brazil", "telemetry Brazil", e "model* movement* Brazil". Também foram buscadas as expressões "movement* ecolog*", "simulat* OR model*", e "random search* AND Lévy", com "Brazil" no campo de filiação dos autores. Foram encontrados 310 estudos que abordaram temas da Ecologia de Movimento no país desde 1999. Destes, 158 foram realizados a partir de 2010 (cerca de 51%).

I



II



Apesar do crescente interesse e do consequente aumento de estudos sobre esse tema, ainda são grandes os desafios para que os movimentos dos animais sejam adequadamente monitorados e analisados. Para fazer um diagnóstico das principais dificuldades encontradas, realizou-se uma pesquisa com 97 pesquisadores brasileiros com uso de questionário online. O principal desafio apontado no questionamento foi a análise dos dados de movimento, seguido por falta de aceso a financiamento e tecnologia adequada (veja Fig. II). Esses dados evidenciam a importância não só do preenchimento de lacunas metodológicas para coleta e análise de dados de movimento, como também do treinamento adequado de pesquisadores e do desenvolvimento de métodos mais econômicos para monitorar animais em campo.

Fonte dos dados e figuras: Alves-Eigenheer et al. in prep..

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CAPÍTULO 1

Joint species movement modelling: how do species´ traits influence movement?

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Abstract

Recent advances in joint species distribution modelling have enabled researchers to move from species-level analyses to community-level analyses, leading to statistically more efficient and ecologically more informative use of data. Here we propose joint species movement modelling (JSMM) as an analogous approach that enables one to infer both species- and community-level movement parameters from multi-species movement data. The species-level movement parameters are modelled as a function of species traits and phylogenetic relationships, allowing one to ask how species traits influence movements, and whether phylogenetically related species are similar in their movement behaviour. We illustrate the performance of the modelling framework with bird movement data in a heterogeneous landscape in Brazil. The JSMM approach increased the precision of species-specific parameter estimates by modelling shared responses among the species to the environment, especially for those species with limited data. At the community level, we found both specialisation to forest habitats, as well as movement distances to be greatest for large birds and for frugivorous birds. The JSMM approach is applicable for many kinds of movement data, and it facilitates a synthetic understanding of the causes and consequences of variation in movement behaviour.

Introduction

Statistical ecologists are increasingly recognising that ecological and evolutionary processes are structured across many kinds of hierarchical levels, as reflected by the increasing popularity of hierarchical Bayesian modelling (Newman 1998, Clark 2005, Royle and Dorazio 2009, Parent and Rivot 2013, Gimenez et al. 2014, Kéry and Royle 2015). As one example, joint species distribution modelling (JSDM) is revolutionising the field of statistical community ecology, as it allows one to derive simultaneously species- and community-level inference by integrating data on species occurrences, environmental covariates, species traits, and their phylogenetic relationships (Warton et al. 2015, Johnson and Sinclair 2017, Ovaskainen et al. 2017). In movement ecology, the need for hierarchical modelling arises from variation in movement characteristics expressed within individuals, among individuals and among species, as well as from the need to account for measurement error (Patterson et al. 2008). Within an individual, movement characteristics may vary over space, e.g. depending on the habitat type, or over time, e.g. depending on the prevailing weather conditions, reproductive phase or temporal variation in the individual's motivation to move. Such variation has been accounted for in statistical models e.g. by assuming that the movement characteristics depend on the measured environmental parameters (Morales et al. 2004, Ovaskainen et al. 2008), or by modelling switches among different movement modes, e.g. via hidden Markov models (Morales et al. 2004, Gurarie et al. 2009, Langrock et al. 2012). Variation among individuals has been accounted either by fitting a movement model to each individual separately and then making population-level inferences in a separate second step (Hanks et al. 2011, Hooten et al. 2016), or by adding random effects to parameters

governing e.g. step lengths or turning angles (Jonsen et al. 2003, Jonsen et al. 2006, Langrock et al. 2012, Hopcraft et al. 2014, Hooten et al. 2017).

In this work, our interest is in variation in movement characteristics among species. Such variation has typically been analysed in a post hoc manner using a two-step approach: 1) fitting a movement model separately for each species; 2) comparing the model structures or parameter estimates among the species (Morales et al. 2013). Such a two-step approach is likely to lead to compromised statistical efficiency especially in the analysis of sparse data. Here we borrow from the recent developments in JSDM (Warton et al. 2015, Ovaskainen et al. 2017) to build a joint species movement model (JSMM) that enables statistically efficient use of multi-species movement data. In species distribution modelling, regression approaches are commonly used to describe how species occurrence depends on the environmental covariates (Elith and Leathwick 2009). JSDMs can greatly facilitate the more accurate estimation of such parameters, especially for rare species with sparse data, by incorporating hierarchical layers modelling shared responses among the species to environmental covariates (Ovaskainen and Soininen 2011). Such models can be further extended to yield community-level inference by assuming that the responses of the species to their environment depend on their traits or phylogenetic relationships (Ovaskainen et al. 2017). Here, we transfer these ideas into movement ecology, with the aim of building a JSMM that models species-specific movement parameters as a function of their traits, phylogenetic relationships, or both. We expect that JSMMs provide a statistically efficient framework for analysing multi-species movement data, and in particular for providing a synthetic understanding of the causes and consequences of variation in movement characteristics.

Material and methods

The data

While our approach for the joint-estimation of species- and community-level movement parameters applies to many kinds of movement models and many types of movement data, we illustrate the approach here with a simple stochastic redistribution model applied to direct observations of bird movements. The movement data are based on binocular observations of birds moving within a 600 m x 600 m landscape, which we divided into a regular 10 m x 10 m grid with 3600 cells, with method adapted from Morales et al. (2013). We collected the data from September to December of 2014 and 2015, during 72 hours of observation. The locations of the birds were recorded at the level of the grid cell by comparing the observed location to a grid overlaid on a high-resolution Google Maps image. We considered the movements as discrete steps in which the bird left one location where it had been stationary and flew to another location, possibly within the same grid cell or one to several grid cells away. We ignored here the time dimension, i.e. when the bird makes the next move or how long it takes to perform each move. We classified the grid cells into three habitat types: (i) forest habitat, (ii) open habitat (mainly pasture), and (iii) semi-open habitat (narrow corridors of trees, single trees and small groups of trees outside forest patches). Fig. 1 illustrates the structure of the landscape and exemplifies movement data. The studied landscape is fragmented, having ca. 40% of arboreal cover, and most observed species were abundant habitat generalists that show high mobility. The recorded tracks were short sequences of steps (1 to 7 steps) and the same bird individual was observed for more than one sequence of steps only rarely.

As species traits, we acquired information on body size and feeding type. Birds were classified into four diet types, based on Wilman et al. (2014) and on the authors' experience: granivorous, frugivorous, insectivorous, or omnivorous birds (for the trait values, see Supporting Information). We constructed a phylogenetic correlation matrix **C** from the mean phylogenetic tree provided by Jetz et al. (2014) with the package ape 4.0 (Paradis et al. 2004) by assuming the diffusion model of trait evolution, and thus defining correlation between two species as the proportion of shared evolutionary history.

The joint species movement model

We denote the number of species by n_s, the number of species traits by n_t and the number of species-specific movement parameters by n_p. Assuming that an individual of species $s = 1, \dots, n_s$ is currently at grid cell $i = 1, \dots, 3600$, we model the probability p_{sji} that it will next move to grid cell j by

$$p_{sji} = K_{is}\exp(-d_{ij}/\alpha_s)\exp(\beta_s^{(1)}h_j^{(1)})\exp(\beta_s^{(2)}h_j^{(2)}). \quad \text{Eq. 1}$$

In Eq. 1, d_{ij} is the Euclidian distance between the grid cells i and j, and the parameter $\alpha_s > 0$ models the typical step length of species s. The variable $h_j^{(1)} \in \{0,1\}$ (respectively, $h_j^{(2)}$) is an indicator of whether grid cell j belongs to the semi-open habitat (respectively, forest) and the parameter $\beta_s^{(1)}$ (respectively, $\beta_s^{(2)}$) measures the affinity of the species to semi-open (respectively, forest) habitats compared to open habitat. The normalising constant K_{is} is defined so that the probabilities sum to unity over the target cells, i.e. that $\sum_j p_{sji} = 1$ for all i and s. As the model does not include the possibility of the individual leaving the study area, it models the next location conditional on the

individual not leaving the study area. Thus, we truncated the data so that they did not involve steps outside of the study area.

The parameters α_s, $\beta_s^{(1)}$ and $\beta_s^{(2)}$ describe the movement behaviour of the species s. We combined these into the $n_s \times n_p$ matrix $\mathbf{\Theta}$, where $n_p = 3$ is the number of movement parameters. Each row of $\mathbf{\Theta}$, i.e. the vector $\mathbf{\Theta}_{k\cdot} = \begin{pmatrix} \log(\alpha_s) & \beta_s^{(1)} & \beta_s^{(2)} \end{pmatrix}$, contains the movement parameters for species s. We log-transformed the movement scale α_s so that all elements of the matrix $\mathbf{\Theta}$ can attain any (positive or negative) real values. To determine how the movement characteristics of the species depend on their traits and phylogenetic relationships, we vectorised the matrix $\mathbf{\Theta}$ to the $n_s n_p \times 1$ vector $\boldsymbol{\theta} = \mathrm{vec}(\mathbf{\Theta})$, and modelled it using a multivariate normal distribution as

$$\boldsymbol{\theta} \sim N\left(\mathbf{m}, \mathbf{\Sigma} \otimes \left[\rho \mathbf{C} + (1-\rho)\mathbf{I}_{n_s}\right]\right). \quad \text{Eq. 2}$$

Here the $n_s n_p \times 1$ vector $\mathbf{m} = \mathrm{vec}(\mathbf{M})$ is the vectorised version of the $n_s \times n_p$ matrix $\mathbf{M}$ (with elements m_{sp}, where $p = 1, \ldots, n_p$ is the index for the movement parameter), and it gives the expected movement parameters for each species based on its traits. The influence of the species traits is modelled with a linear regression model $m_{sp} = \sum_t t_{st}\zeta_{tp}$, where the index t runs over the selection of n_t traits included, t_{st} is the trait t for species s, and the parameter ζ_{tp} measures the influence of trait t on movement parameter p. Arranging the regression parameters ζ_{tp} into a $n_t \times n_p$ matrix $\mathbf{Z}$ and the trait values t_{st} into a $n_s \times n_t$ matrix $\mathbf{T}$, we may write in matrix form $\mathbf{M} = \mathbf{TZ}$. To include the intercept into the model, we set $t_{s1} = 1$ for all species s. In the absence of trait information, only the intercept is included, in which case the expectation $\mathbf{M}_{s\cdot}$ is the same for all species s. The $n_p \times n_p$ variance-covariance matrix $\mathbf{\Sigma}$ models the species-specific deviations around the expectation based on species traits, and $\otimes$ is the Kronecker

(outer) product. The $n_s \times n_s$ matrix $\mathbf{C}$ is a phylogenetic correlation matrix that is usually derived from a phylogenetic tree based on genetic data (like in our empirical case study, see above), $\mathbf{I}_{n_s}$ is the identity matrix (ones at the diagonal and zeros at the off-diagonal) of dimension n_s (hence corresponding to independent species), and the parameter $0 \leq \rho \leq 1$ measures the strength of the phylogenetic signal.

To fit the model to the data with Bayesian inference, we developed a Markov chain Monte Carlo (MCMC) sampling scheme that uses a Metropolis-Hastings step to sample the species-specific parameters $\boldsymbol{\Theta}$, whereas the parameters $\mathbf{Z}$, $\boldsymbol{\Sigma}$ and ρ are sampled directly from their full conditional distribution (for technical details and prior distributions, see Supporting Information). We tested the validity of the estimation scheme by generating simulated data sets of various sizes and examining whether the parameter estimates converged to the true values as the data size increased (see Supporting Information). We provide the code, instructions on how to use it, and the study case data at the GitHub server: https://github.com/LEEClab/JSMM.

Testing the performance of the modelling framework with real data

The data consist of the movements of $n_s = 43$ species, with an average (min…max) of 12 (1…109) observed movement steps per species. To examine the potential utility of using shared information across the species, we fitted three versions of the JSMM to the data, called (i) the full model, (ii) the single-species models, and (iii) the leave-one-out models. In the full model, the parameter estimates for each focal species are based both on the movement data for the focal species as well as information that can be borrowed from the other species. In the single-species models, the parameter estimates are based solely on the movement data for the focal species. In the

leave-one-out models, the parameter estimates are based solely on the information that can be borrowed from the other species. The full model was thus fitted simultaneously to movement, trait and phylogenetic data on all species, whereas the single-species models were fitted separately to movement data on each focal species at a time. The leave-one-out models were also parameterised separately for each focal species, including in model fitting trait and phylogenetic data for all species, and movement data for all except the focal species.

Results

The performance of the estimation scheme was successfully validated with simulated data in the sense that the posterior distributions became increasingly concentrated around the true values with increasing amount of data. As expected, the accurate estimation of the community-level parameters required data on many species, whereas the accurate estimation of species-specific parameters required many movement steps for the focal species (Supporting Information).

The model fitted to the bird data was able to create movement tracks that visually resembled the real ones (Fig. 1AB, Supporting Information). The parameter estimates from the full model showed that all birds generally preferred semi-open and forest habitats over the open habitats (Fig. 1). Affinity to both semi-open and forest habitats was stronger for frugivorous birds, and both of these affinities increased with increasing body size. Granivorous birds moved larger distances on average than birds from the other groups, and movement distances increased with body size (Fig. 1). The data were not informative about a possible phylogenetic signal in the movement parameters in the sense that the posterior distribution of the parameter ρ closely resembled its prior

distribution: the prior was uniform in [0,1], and the posterior mean was 0.51, with (0.30, 0.72) as 50% credible interval and (0.03, 0.96) as 95% credible interval.

The comparison between the full model, the single-species models, and the leave-one-out models showed that borrowing information from other species increases the precision of parameter estimates, especially for species with limited data (Fig. 2). For those eleven species for which only one movement step was observed, the parameter estimates based on the single-species models (black dots and lines in Fig. 2) remained highly uncertain, and the estimates based on the full model (red dots and lines in Fig. 2) closely resembled those of the leave-one-out models (grey dots and lines in Fig. 2). In contrast, for species with many observations, the parameter estimates based on the full model closely resembled those based on the single-species models. The effect of utilising shared information among the species is especially clear for the parameters measuring affinity to semi-open areas (Fig. 2C) and forests (Fig. 2D). For these parameters, in the single-species models the data were not informative about habitat affinities for many species, as the posterior distributions overlapped with zero and thus resembled the prior distributions that were symmetric around zero. However, both of the affinity parameters were estimated to be positive for most species in the full model (Figs. 1 and 2), including species with very sparse data. This is because these parameters were consistently estimated to be positive for those species with many observations, and thus, by borrowing this information, in the full model these parameters were estimated to be positive also for species with sparse data.

Discussion

The increasing interest in movement ecology, fuelled by methodological advances in data collection and analysis, is promoting an unprecedented availability of movement

data on individuals and species in numerous environmental contexts (Nathan et al. 2008, Cagnacci et al. 2010, Kranstauber et al. 2011, Kays et al. 2015). In this study, we have developed joint species movement modelling (JSMM) to help researchers make more out of multi-species movement data. As we have demonstrated using both simulated and real data on bird movements in a heterogeneous landscape, the JSMM approach can be used to estimate and predict movement parameters as a function of species traits and phylogenetic relationships. This approach is promising for answering many kinds of questions in movement ecology, in particular tackling the challenge on how to best use the large amount of sparse data that is currently building up in various databases (e.g. Kranstauber et al. 2011).

Previous research assessing how functional traits affect bird movement (Spiegel and Nathan 2007, Neuschulz et al. 2013, Betts et al. 2014) has been based on two-step analyses where each species is first modelled separately. As species-specific analyses require several observations, these analyses have been restricted to the few most dominant species only. In contrast, our approach allowed us to utilise data on a large number of species, including species for which just a single movement step was observed. The comparison between the full model, single-species models, and leave-one-out models showed that the amount of data available for each focal species influenced how accurately the species-specific parameters could be estimated, and how much the data on the focal species influenced the community-level parameters. The results from our case study showed that bird movement behaviour can, to a large extent, be related to species traits. In contrast, in our study case the phylogenetic relationships turned out to be poor predictors of movement, probably because diet can vary substantially among closely-related species (Wilman et al. 2014), and because diet strongly influences

movement patterns. Granivorous birds, for instance, feed on the seeds of herbaceous plants growing in open areas, explaining their low affinity to semi-open habitats and forest fragments. Frugivorous and granivorous birds do not maintain territories, possibly explaining why we found them to move larger distances than insectivores, which typically are territorial (Hansbauer et al. 2010, Neuschulz et al. 2013). We further found large birds to move larger distances than small birds, which is in line with other studies showing that larger animals generally have higher movement capacity (Spiegel and Nathan 2007, Neuschulz et al. 2013). Besides moving larger distances, large birds showed lower affinity to open habitat, possibly because such habitat do not offer shelter against their predators. In fact, within landscapes under high levels of habitat fragmentation, many of the large-sized forest species have disappeared as a consequence of habitat loss and hunting. This has resulted in a decline in bird species diversity in fragmented landscapes, such as the Atlantic Forest (Galetti et al. 2013).

While we applied here the JSMM approach to a simplistic three-parameter movement model, the approach itself is very generally applicable to almost any kind of multi-species movement data, such as GPS-based tracking data (e.g. Reisinger et al. 2018) or spatial capture-recapture (SCR) data. Traditional methods to acquire community-level SCR data include bird ringing (e.g. Paradis et al. 1998) and trapping of small mammals (e.g. Puttker et al. 2012) or insects (e.g. Slade et al. 2013). New kinds of SCR data include e.g. camera-trapping data and non-invasive genetic sampling data (Royle et al. 2018). The JSMM approach can be applied to any likelihood-based analyses of multi-species movement data by adding a hierarchical layer that models species-specific parameters as a function of their traits as phylogenetic relationships (Eq. 2). The model can involve any kind of movement parameters, such as the level of temporal

autocorrelation, size of home-range, or tendency to return to familiar sites, to name a few examples. Studying movement at the community level helps one to relate data on theory, such as the movement ecology paradigm (Nathan et al. 2008). For example, if proxies of species-specific navigation and motion capacities are available, one may incorporate them into the analyses as species traits and thus statistically link such traits to observed movement behaviour.

The movements of organisms greatly influence which individuals, species, and environmental factors they will interact with and, consequently, both their ecological and evolutionary dynamics (Nathan et al. 2008, Morales et al. 2010, Jeltsch et al. 2013). Thus, identifying how species traits influence organismal movement is crucial for building links from movement ecology to population and evolutionary ecology, and for assessing the consequences of movement on ecosystem functioning and management. We thus expect that the JSMM framework developed here will find applications not only in basic ecological research, but also in biodiversity conservation and restoration projects. As one example, a key challenge for conservation is to quantify the effects of agricultural systems on biodiversity and ecosystem services (Rands et al. 2010, Blitzer et al. 2012). One approach for predicting the resilience, connectivity, and restoration potential of altered landscapes is the modelling of seed dispersal (Levey et al. 2005, Hougner et al. 2006, Morales et al. 2013, Perez-Hernandez et al. 2015). In highly diverse environments, such as tropical forests, comprehensive understanding of seed dispersal is not possible at the species level, and thus synthetic analyses need to be derived at the community level. While we have focused here on movements at the level of a single landscape, an exciting challenge for further research is to acquire and analyse multi-species data from multiple landscapes, with the aim of asking how the movement

behaviour of species communities respond to forest fragmentation or other anthropogenic perturbations.

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Figures

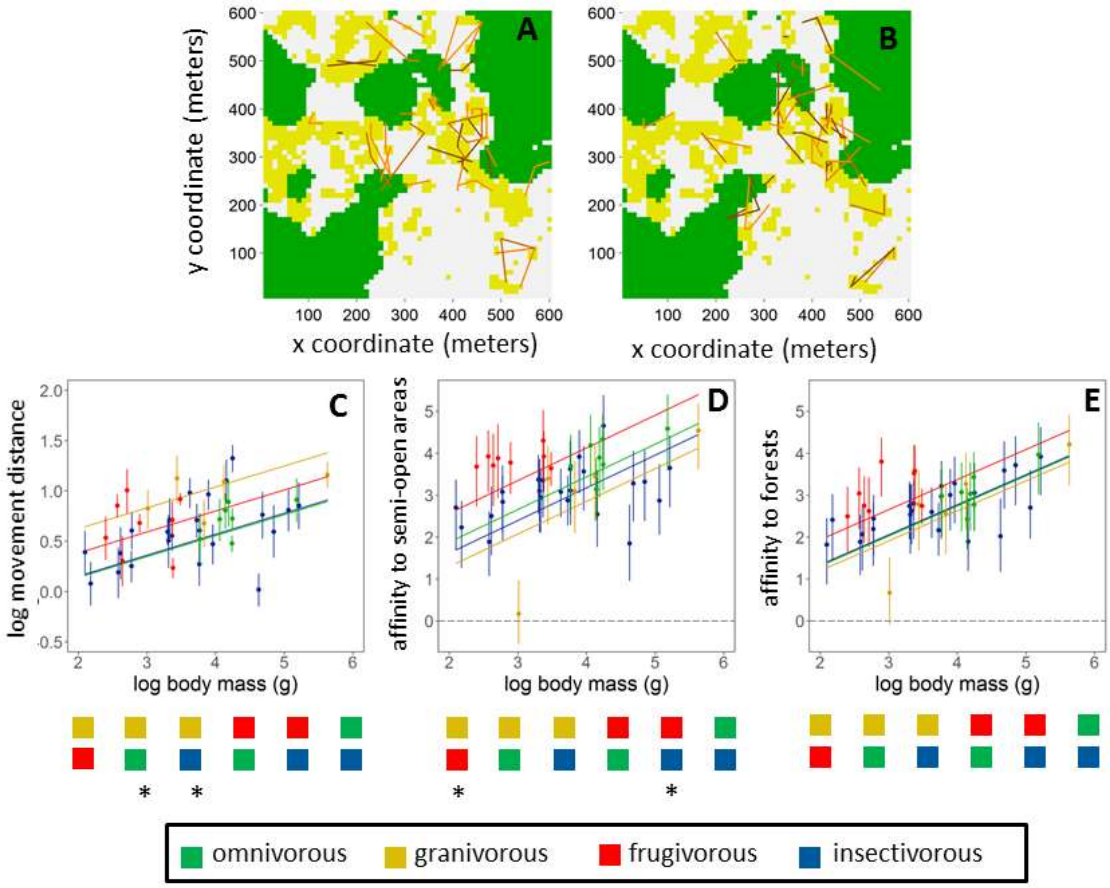


Figure 1. A map of the study area, examples of real and simulated movement data, and influence of species traits on species-specific movement parameters. The 600 m x 600 m landscape is divided into a 10 m x 10 m grid, with the habitat type of each grid cell classified as open (grey), semi-open (yellow), or forest habitat (green). Panel A shows the movement data observed for *Tangara sayaca* and panel B shows data simulated for the same species. Tracks of different colours correspond to different individuals. The panels CDE show the posterior mean (dot) and 95% credible intervals of the movement parameters describing the log of the mean movement distance $\log(\alpha_s)$ (panel C), affinity to semi-open areas $\beta_s^{(1)}$ (panel D), and affinity to forest $\beta_s^{(2)}$ (panel E) for each species s. The continuous lines show the posterior mean prediction of expected movement parameters based on species traits. The colours indicate omnivorous (green),

granivorous (yellow), frugivorous (red), and insectivorous birds (blue). For the pairs of feeding classes marked with *, the posterior probability for one feeding class having a higher parameter value than the other feeding class (measured as the difference in the ζ parameters being either positive or negative) was at least 0.9. For all movement parameters p, the posterior support for the movement parameter increasing with body size was high: $\Pr(\zeta_{tp} > 0)$>0.99, where $t = 5$ corresponds to body size.

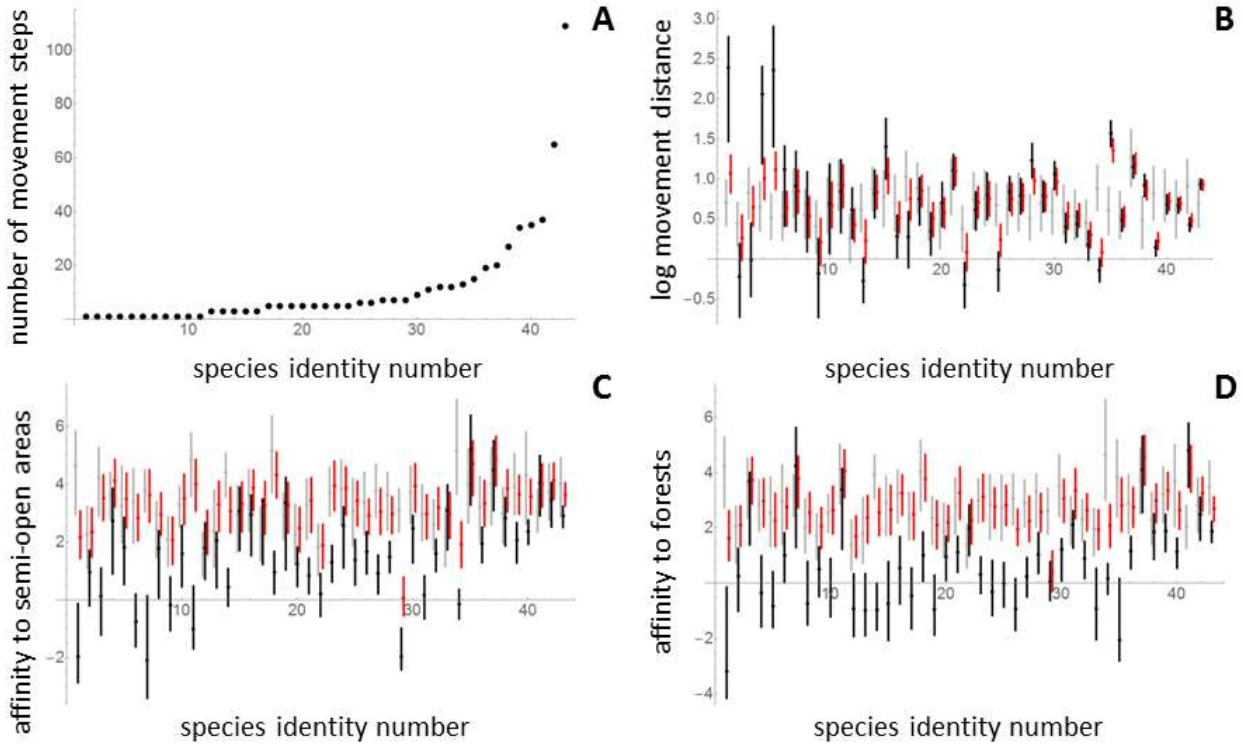


Figure 2. A comparison of parameter estimates based on single and joint species movement models. In all panels, the species have been ordered according to increasing amount of movement steps, shown in panel A. Panels BCD show the posterior means (the dots) and the posterior interquartile ranges (the lines) for the parameters modelling movement distance $\log(\alpha_s)$ (panel B), affinity to semi-open areas $\beta_s^{(1)}$ (panel C), and affinity to forest $\beta_s^{(2)}$ (panel D). In the order from left to right, the estimates are based on the leave-one-out models (grey colour), single species models (black colour), and the full joint species movement model (red colour).

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Supporting Information

As described in the main text, the model to be fitted is

$$\boldsymbol{\theta} \sim \mathrm{N}\left(\mathbf{m}, \boldsymbol{\Sigma} \otimes \left[\rho \mathbf{C} + (1-\rho)\mathbf{I}_{n_s}\right]\right),$$

where the likelihood of the movement data depends on the parameters $\boldsymbol{\Theta}$. The mean $\mathbf{m}$ is a vectorised version of the matrix $\mathbf{M} = \mathbf{TZ}$, where the matrix $\mathbf{T}$ consists of the elements t_{st}. We denote by $\mathbf{z} = \mathrm{vec}(\mathbf{Z})$ the vectorisation of the matrix $\mathbf{Z}$.

Prior distributions

The parameters for which prior distributions need to be defined are $\mathbf{z}$, $\boldsymbol{\Sigma}$ and ρ.

- For the vector $\mathbf{z}$, we assumed the multivariate normal prior $\mathbf{z} \sim \mathrm{N}(\boldsymbol{\mu}_z, \boldsymbol{\Sigma}_z)$, where we set the mean $\boldsymbol{\mu}_z$ to a zero vector and the variance-covariance matrix $\boldsymbol{\Sigma}_z$ to an identity matrix. We note that as the mean is set to zero, we do not make any a priori assumptions about directions of habitat preferences.
- For $\boldsymbol{\Sigma}$ we assumed an Inverse-Wishart prior $\mathrm{W}^{-1}(\boldsymbol{\Psi}, \nu)$, where we set the degrees of freedom to the number of parameters ($\nu = n_p$) and the scale matrix $\boldsymbol{\Psi}$ to the identity matrix.
- For the phylogenetic signal parameter ρ, we assumed a discrete prior, with the probability uniformly distributed in the range [0,1], discretised to 100 values.

Posterior sampling by MCMC

To fit the model to the data, we developed a Markov chain Monte Carlo (MCMC) sampling scheme in which we updated each of the following parameters in turn: $\boldsymbol{\theta}$, $\mathbf{z} = \mathrm{vec}(\mathbf{Z})$, $\boldsymbol{\Sigma}$ and ρ.

- The species-specific parameters $\boldsymbol{\theta}$ were sampled one at a time using a Metropolis-Hastings step in which the proposal distribution was adapted during the burn-in to reach an optimal acceptance ratio of 0.44.

- The parameter $\mathbf{z}$ was sampled directly from its full conditional which is $\mathbf{z} \sim \mathrm{N}(\boldsymbol{\mu}_{z*}, \boldsymbol{\Sigma}_{z*})$, where

$$\boldsymbol{\Sigma}_{z*} = (\boldsymbol{\Sigma}_z^{-1} + \mathbf{X}^{\mathrm{T}}(\boldsymbol{\Sigma} \otimes \mathbf{W})^{-1}\mathbf{X})^{-1},$$

$$\boldsymbol{\mu}_{z*} = \boldsymbol{\Sigma}_{z*}(\boldsymbol{\Sigma}_z^{-1}\boldsymbol{\mu}_{\mathrm{z}} + \mathbf{X}^{\mathrm{T}}(\boldsymbol{\Sigma} \otimes \mathbf{W})^{-1}\boldsymbol{\theta}),$$

$$\mathbf{X} = \mathbf{T} \otimes \mathbf{I}_{n_p},$$

$$\mathbf{W} = \left[\rho\mathbf{C} + (1-\rho)\mathbf{I}_{n_s}\right].$$

- The parameter $\boldsymbol{\Sigma}$ was sampled directly from its full conditional $W^{-1}(\boldsymbol{\Psi}_*, \nu_*)$, where

$$\nu_* = \nu + n,$$

$$\boldsymbol{\Psi}_* = \boldsymbol{\Psi} + \mathbf{A},$$

$$\mathbf{A} = (\boldsymbol{\theta} - \mathbf{m})^{\mathbf{T}}\mathbf{W}^{-1}(\boldsymbol{\theta} - \mathbf{m}),$$

$$\mathbf{m} = \mathrm{vec}(\mathbf{TZ}).$$

- The parameter ρ was sampled directly from its full conditional by using a discrete grid sampler. By Eq. 2, the density of the full conditional for ρ follows

$$p(\rho|\boldsymbol{\theta}) \propto p(\rho)(\boldsymbol{\Sigma}\otimes\mathbf{W})^{-\frac{1}{2}} \exp(-(\boldsymbol{\theta}-\mathbf{m})^{\mathbf{T}}(\boldsymbol{\Sigma}\otimes\mathbf{W})^{-1}(\boldsymbol{\theta}-\mathbf{m})/2).$$

To increase computational speed, in the beginning of the MCMC approach, we pre-computed the determinants and inverses of the variance-covariance matrices **W** for all ρ values included in the discrete grid prior (see above).

To estimate the parameters for the real dataset with 43 bird species (Supporting Table 1), we ran a total of 100,000 iterations, with a 20,000 burn-in period and thinning interval of 10. We ran three chains and checked the convergence of the posteriors using the Gelman-Rubin convergence statistic (Gelman and Rubin, 1992), with the package CODA (Plummer et al., 2006) (Supporting Table 2).

The ability of the model to create realistic movement tracks

To examine the ability of the model to generate realistic movement tracks, we simulated movements for each species, based on the parameters sampled from the posterior distribution of the full model. We initiated these simulations from the same locations where the individuals were first recorded in the field, and simulated for each individual the same number of steps as in the data. For each species, we generated a pair of maps (such as the ones shown in Fig. 1AB in the main manuscript), one of which represented real data and the other one simulated data. We then ordered the maps

randomly and asked six researchers with much experience in bird ecology to make their best guess at which of the two maps represented real data. We then examined whether the researchers were able to pinpoint the real data more often than expected by chance.

The model was able to create simulated movement tracks that visually resembled real movement tracks (Fig. 1B vs. 1A in the main manuscript). The difference between real and simulated movement tracks was invisible to the six bird experts who tried to guess which of the provided maps showed real data: the average number of correct answers per researcher was 19.5, which is slightly below the random expectation of 21.5 (50% of the 43 species). Restricting the analysis to the ten species with at least 13 movement steps (and hence the most information to distinguish the true map from the simulated ones), the average number of correct answers per researcher was 3.7, which was clearly below the random expectation of five correct answers.

Testing the validity of the posterior sampling scheme

To test the validity of the posterior sampling scheme, we applied it to datasets generated by known parameter values. In these data, we assumed that there are n species, for each of which we simulated m movement steps. We assumed that the species belonged to two feeding types (frugivores vs. insectivores), and that they showed variation in their body size. We randomised the log-transformed body sizes from uniform distribution in the range [2, 6], and assigned each species with equal probability to frugivores or insectivores. We constructed a $n \times 3$ trait matrix by letting the first column (i.e., values of t_{sp} with $p = 1$) correspond to intercept (all values set to one), the second column (i.e., values of t_{sp} with $p = 2$) indicator variable describing if the species is a frugivore (with value one) or not (with value zero), and the third column

(i.e., values of t_{sp} with $p = 3$) log-body size. We generated a phylogenetic correlation matrix by grouping the n species into $n/2$ groups, each of which contained two species. We assumed that the phylogenetic correlation within a group is 0.9, whereas the phylogenetic correlation is zero for species that do not belong to the same group.

As true parameter, we set the value of the matrix $\mathbf{Z}$ (with elements ζ_{tp}) to

$$\mathbf{Z} = \begin{pmatrix} -2 & 0 & 0 \\ 1 & 0 & 2 \\ 0.5 & 0.5 & 0 \end{pmatrix}.$$

Thus, as illustrated by Supporting Fig. 1, we assumed that t movement distance is greater for frugivores than insectivores and that it increases with body size, that semi-open habitats affinity increases with body size but is not influenced by feeding type, and that forest affinity is greater for frugivores than insectivores but it is not influenced by body size. We set the matrix $\mathbf{\Sigma}$ to diagonal matrix with diagonal values 0.2, 1 and 0.5. Thus, we assumed the smallest amount of variation (not explained by traits) in the parameter measuring movement distance, the largest for semi-open habitats affinity, and the second largest amount to forest affinity. We set the strength of the phylogenetic signal to $\rho = 0.7$. The realised parameter values of the species are shown at the lower row of panels in Supporting Fig. 1.

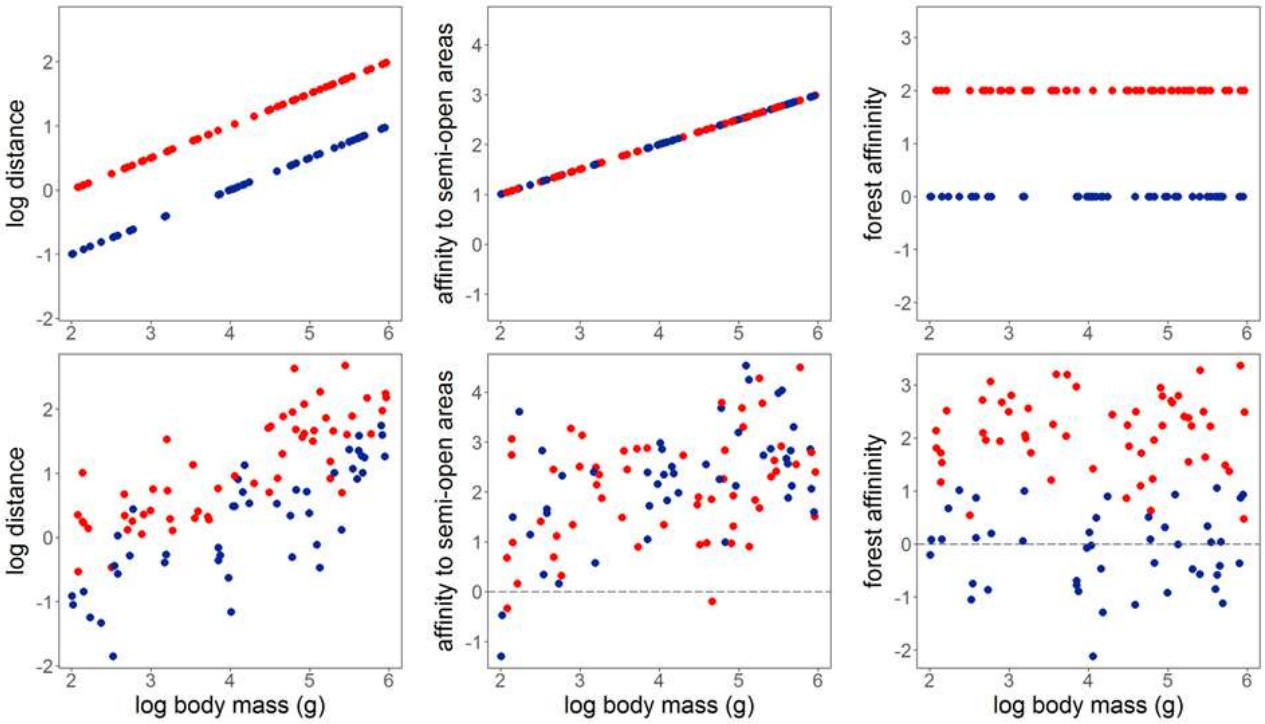
We generated simulated movement data for each species using the same landscape as we did in the empirical study, randomising the initial condition with equal probability among all cells, simulating $m + 10$ movement steps as a single track, and ignoring the first 10 positions. Supporting Fig. 2 illustrates such tracks for species 1-6.

We generated a large dataset (called the full data) by setting $n = 100$ and $m = 100$. We then subsampled the full data in three ways to form datasets with $(n = 100, m = 10)$, $(n = 10, m = 100)$, and $(n = 10, m = 10)$. We fitted the model to

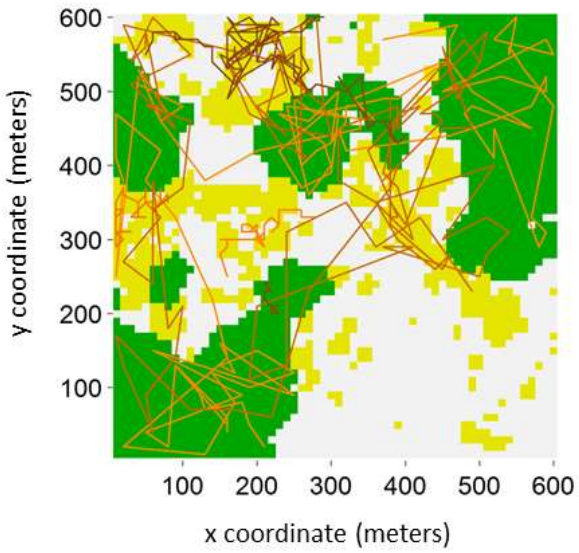
each of the datasets, and compared the posterior distributions of the model parameters to the true values. To examine how borrowing information from other species influences estimation of species-specific parameter, we also fitted leave-one-out models as well as single-species models (as described in the main manuscript).

Supporting Figs. 3-6 compare posterior distributions to the true values for the community-level parameters ζ (Supporting Fig. 3), $\mathbf{\Sigma}$ (Supporting Fig. 4), ρ (Supporting Fig 5), as well as the species-level parameters $\boldsymbol{\theta}$ (Supporting Fig. 6). In all cases, the posterior distributions become increasingly concentrated around the true values with increasing amount. Further, as expected, the accurate estimation of the community-level parameters requires data on many species, whereas the accurate estimation of species-specific parameters requires many movement steps for the focal species. To see this, let us first make the trivial observation that for all parameters the most accurate estimates are achieved for the case with most data, i.e. $n = 100$ and $m = 100$. For the community-level parameters (Supporting Figs. 3-5), the second most accurate parameter estimates are obtained for $n = 100, m = 10$, and thus reducing the number of data points per species is less harmful than reducing the number of species. In contrast, for the species-level parameters (Supporting Fig. 6), the second most accurate parameter estimates are obtained for $n = 10, m = 100$, and thus reducing the number of species is less harmful than reducing the number of data points per species, naturally assuming that the species of interest are still included in the data. A comparison between the single-species models, leave-one-out models and full model in Supporting Fig. 6 shows that the benefit of borrowing information from other species can strongly depend on the parameter in question. In particular, while with these simulated data the estimation of the movement length required species specific data (single species models performed better than

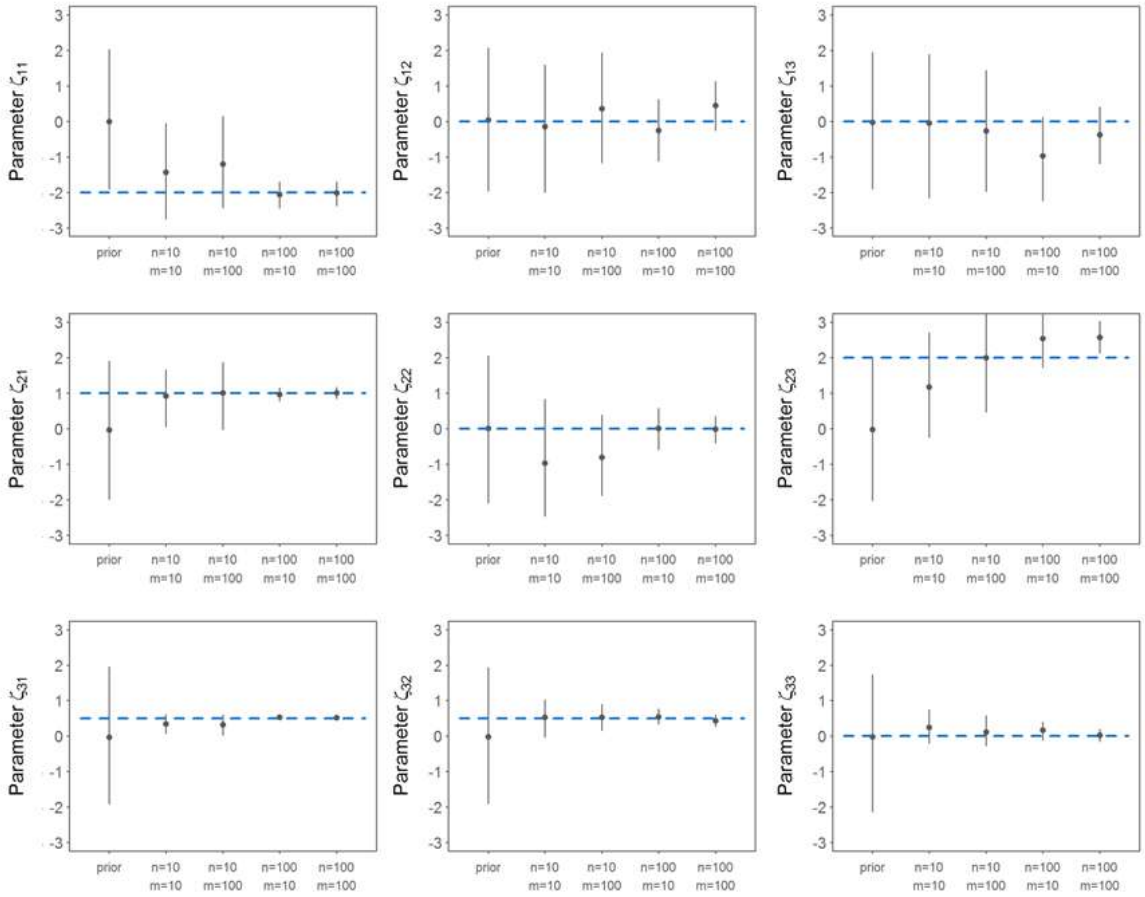
leave-one-out models), borrowing information from other species greatly improved the estimation of the habitat affinity parameters (leave-one-out models performed better than single species models).



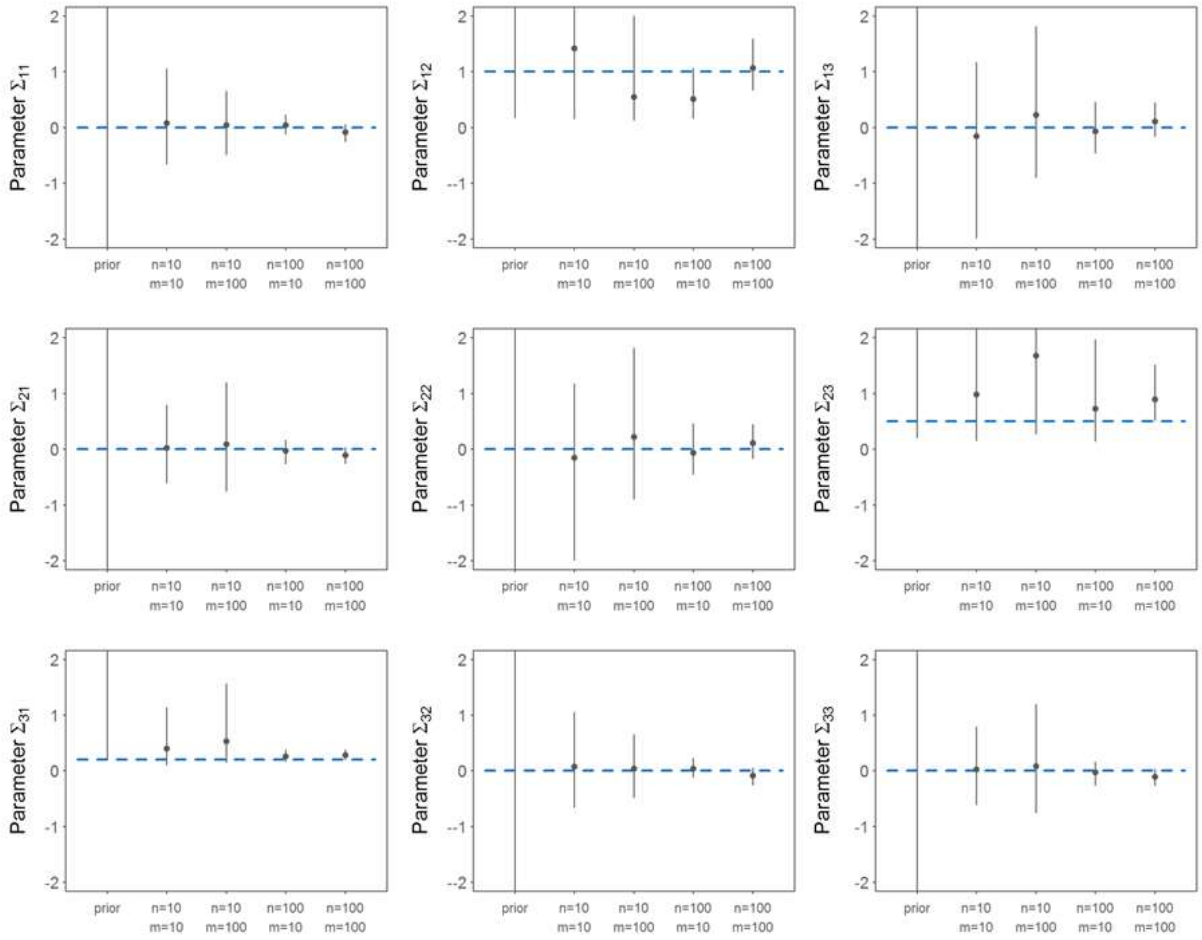
Supporting Figure 1. Species-specific movement parameters and their relationship to species traits assumed in the simulated case study. In each panel, one dot corresponds to one species. The upper row of panels shows the expected movement parameters based on the species traits, and the lower row of panels the realised movement parameters, based on both traits and the residual variation that is structured by phylogenetic relationships. Frugivores are depicted by red and insectivores by blue colour.



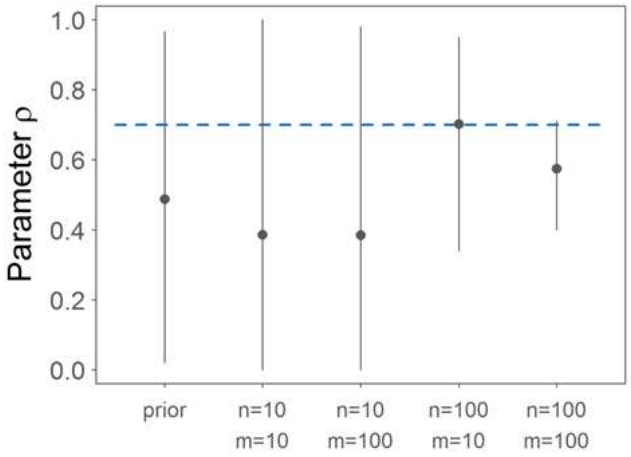
Supporting Figure 2. Illustration of simulated movement tracks. Each line shows $m = 100$ simulated movement steps. Out of the full community with $n = 100$ species, the data are shown for species 1-6, each species being shown by one colour.



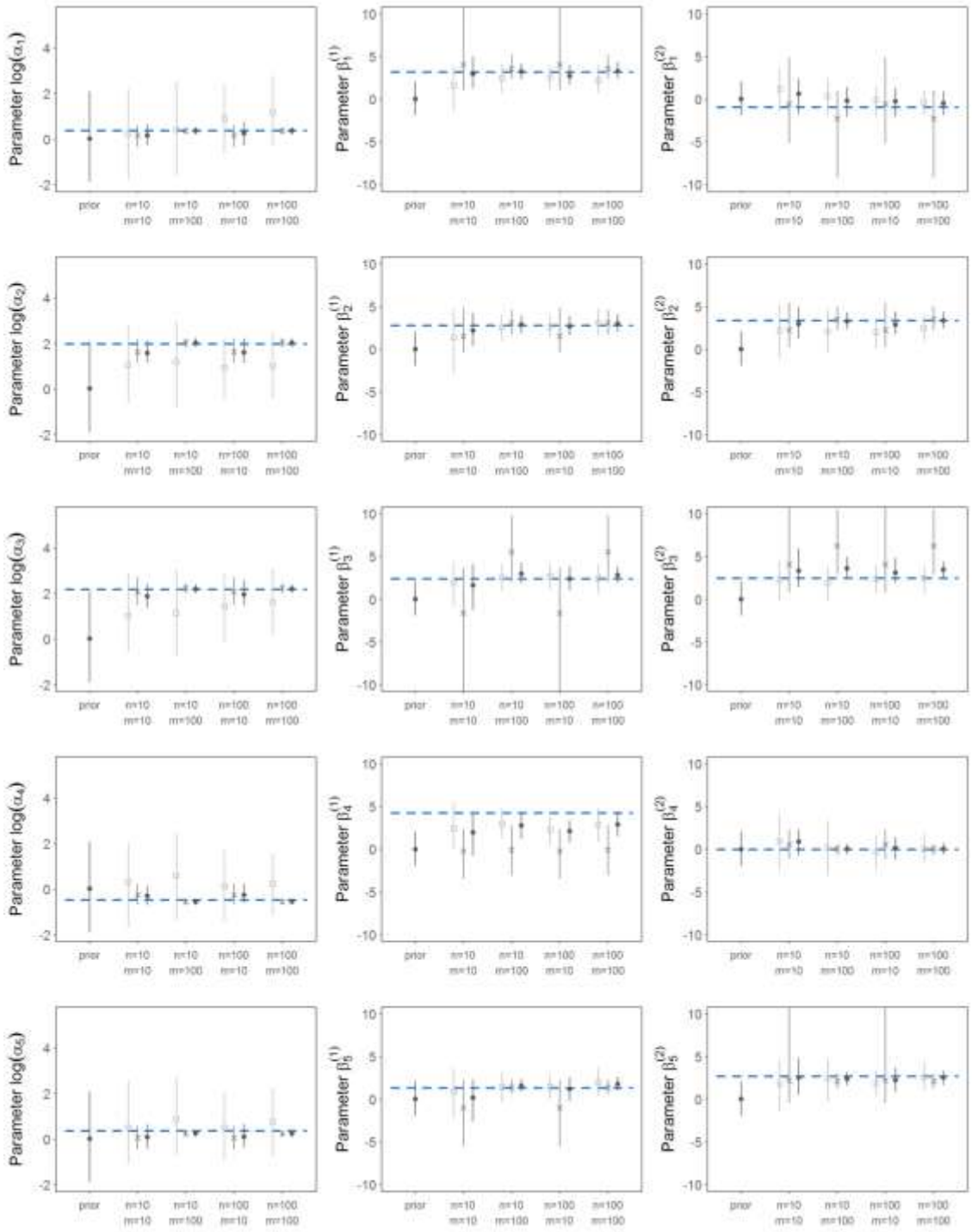
Supporting Figure 3. The ability of the model to identify the true values of the parameters ζ measuring the influence of species traits on movement parameters. In each panel, the dashed line shows the true value, and the dots and the lines show the mean and 95% quantile of the prior and posterior distributions. The posterior distributions are shown for four scenarios for data availability, with either $n = 10$ or $n = 100$ species, and with either m= 10 or $m = 100$ movements steps per species.



Supporting Figure 4. The ability of the model to identify the true values of the parameters **Σ** measuring the amount of variation in movement parameters among the species not explained by traits. In each panel, the dashed line shows the true value, and the dots and the lines show the mean and 95% quantile of the prior and posterior distributions. The posterior distributions are shown for four scenarios for data availability, with either $n = 10$ or $n = 100$ species, and with either m= 10 or $m = 100$ movements steps per species.



Supporting Figure 5. The ability of the model to identify the true value of the parameter ρ measuring the strength of phylogenetic signal in variation of the movement parameters among the species. The dashed line shows the true value, and the dots and the lines show the mean and 95% quantile of the prior and posterior distributions. The posterior distributions are shown for four scenarios for data availability, with either $n = 10$ or $n = 100$ species, and with either m= 10 or $m = 100$ movements steps per species.



Supporting Figure 6. The ability of the model to identify the true values of the species-level movement parameters $\boldsymbol{\theta}$. In each panel, the dashed line shows the true value, and the dots and the lines show the mean and 95% quantile of the prior and posterior distributions. The posterior distributions are shown for four scenarios for data availability, with either $n = 10$ or $n = 100$ species, and with either m= 10 or $m = 100$

movements steps per species. The bars (from left to right) show the results for the leave-one out models (light grey bar with circle), for single species models (grey bar with cross), and for the full model (black bar and dot). The parameter estimates are shown for five species included in all data sets.

Supporting Table 1. Bird species numerical identification (ID), name, feeding class, body size (g), and number of steps (N. steps) observed.

ID	Species name	Feeding class	Body size	N. steps
1	*Empidonomus varius*	Insectivorous	27.1	19
2	*Columbina talpacoti*	Granivorous	46.0	5
3	*Tangara cayana*	Frugivorous	18.0	37
4	*Tachyphonus coronatus*	Frugivorous	29.3	34
5	*Pachyramphus validus*	Insectivorous	43.0	6
6	*Cyanocorax cristatellus*	Omnivorous	178.0	5
7	*Camptostoma obsoletum*	Insectivorous	8.1	3
8	*Myiodynastes maculates*	Insectivorous	43.2	11
9	*Euphonia chlorotica*	Frugivorous	11.0	5
10	*Mimus saturninus*	Insectivorous	63.7	1
11	*Cnemotriccus fuscatus*	Insectivorous	13.6	1
12	*Pitangus sulphuratus*	Omnivorous	62.9	7
13	*Cyclarhis gujanensis*	Insectivorous	28.8	12
14	*Dacnis cayana*	Frugivorous	13.0	27
15	*Xolmis velatus*	Insectivorous	49.1	9
16	*Vireo chivi*	Insectivorous	16.1	5
17	*Tyrannus melancholicus*	Insectivorous	37.4	7
18	*Brotogeris chiriri*	Granivorous	61.6	5
19	*Colaptes melanochloros*	Insectivorous	127.3	1
20	*Zonotrichia capensis*	Granivorous	20.3	7
21	*Megarynchus pitangua*	Insectivorous	69.9	15
22	*Piaya cayana*	Insectivorous	102.0	13
23	*Gnorimopsar chopi*	Omnivorous	65.9	1
24	*Molothrus bonariensis*	Insectivorous	41.5	6
25	*Nemosia pileata*	Insectivorous	16.0	12
26	*Euphonia violacea*	Frugivorous	15.0	1
27	*Euphonia cyanocephala*	Frugivorous	14.0	3
28	*Conirostrum speciosum*	Insectivorous	8.8	5
29	*Myiozetetes similis*	Insectivorous	28.0	1
30	*Tersina viridis*	Frugivorous	29.0	5
31	*Melanerpes candidus*	Insectivorous	108.0	1
32	*Colaptes campestris*	Insectivorous	158.0	3
33	*Myiarchus ferox*	Insectivorous	27.5	1
34	*Basileuterus flaveolus*	Insectivorous	13.2	1
35	*Forpus xanthopterygius*	Granivorous	31.0	3
36	*Saltator similis*	Omnivorous	43.3	1
37	*Nystalus chacuru*	Insectivorous	52.3	3
38	*Dryocopus lineatus*	Insectivorous	183.2	1
39	*Turdus leucomelas*	Omnivorous	69.1	65
40	*Turdus rufiventris*	Omnivorous	69.4	35

41	*Tangara sayaca*	Frugivorous	32.5	109
42	*Turdus amaurochalinus*	Omnivorous	57.9	5
43	*Patagioenas picazuro*	Granivorous	279.0	20

Supporting Table 2. Parameters estimates and convergence diagnostics of the MCMC approach used to sample the posterior distribution for the case study with real data. The estimated parameters are ρ, $\mathbf{\Sigma}$, ζ_{ls}, α_k, β_k^S and β_k^F, where $l = 1, \dots, 5$ represents the trait, $k = 1, \dots, 43$ the species, and $s = 1,2,3$ the movement parameter. We show for each parameter the posterior mean, the 0.025 and 0.975 quantiles, the potential scale reduction factor (Rhat), the upper 95% confidence limit (95% C.I.) and the effective sample size (n.eff) for each parameter.

Parameter	Mean	0.025 quantile	0.975 quantile	Rhat	95% C.I.	n.eff
ρ	0.50	0.03	0.96	1.00	1.00	5085.6
Σ_{11}	0.21	0.10	0.42	1.00	1.00	15235.9
Σ_{12}	0.11	-0.46	0.66	1.00	1.00	2351.4
Σ_{13}	-0.05	-0.68	0.42	1.00	1.01	2058.7
Σ_{21}	0.11	-0.46	0.66	1.00	1.00	2351.4
Σ_{22}	2.84	0.22	11.77	1.02	1.02	297.5
Σ_{23}	2.13	-0.26	10.85	1.02	1.02	270.4
Σ_{31}	-0.05	-0.68	0.42	1.00	1.01	2058.7
Σ_{32}	2.13	-0.26	10.85	1.02	1.02	270.4
Σ_{33}	2.52	0.18	12.16	1.01	1.01	313.6
ζ_{11}	-0.03	-0.77	0.69	1.00	1.00	17555.4
ζ_{21}	-0.26	-0.99	0.46	1.00	1.00	17411.7
ζ_{31}	-0.28	-1.16	0.59	1.00	1.00	18130.0
ζ_{41}	0.21	-0.60	1.06	1.00	1.00	20235.5
ζ_{51}	0.21	0.03	0.39	1.00	1.00	20381.7
ζ_{12}	1.02	-0.39	2.35	1.00	1.01	4492.1
ζ_{22}	0.07	-1.15	1.29	1.00	1.00	5843.4
ζ_{32}	0.33	-1.08	1.73	1.00	1.00	8783.2
ζ_{42}	-0.25	-1.75	1.22	1.00	1.00	8143.2
ζ_{52}	0.78	0.38	1.20	1.00	1.00	2760.9
ζ_{13}	0.51	-0.87	1.83	1.00	1.01	3936.9
ζ_{23}	-0.09	-1.34	1.19	1.00	1.00	4934.9
ζ_{33}	-0.12	-1.64	1.34	1.00	1.00	6431.1
ζ_{43}	-0.24	-1.74	1.30	1.00	1.01	5660.4
ζ_{53}	0.72	0.32	1.14	1.00	1.00	2846.7
α_1	0.60	0.23	0.97	1.00	1.00	18786.8
α_2	0.68	0.00	1.40	1.00	1.00	18038.7

α_3	0.68	0.42	0.95	1.00	1.00	22229.7
α_4	0.24	-0.04	0.53	1.00	1.00	21678.9
α_5	0.27	-0.32	0.92	1.00	1.00	20023.0
α_6	0.91	0.32	1.56	1.00	1.00	17435.8
α_7	0.39	-0.20	1.07	1.00	1.00	19549.3
α_8	0.61	0.12	1.11	1.00	1.00	16114.5
α_9	0.53	-0.05	1.19	1.00	1.00	19642.6
α_{10}	1.11	0.49	1.80	1.00	1.00	14755.9
α_{11}	0.38	-0.38	1.14	1.00	1.00	17321.7
α_{12}	0.81	0.32	1.35	1.00	1.00	19714.5
α_{13}	0.55	0.16	0.99	1.00	1.00	22094.3
α_{14}	0.85	0.53	1.20	1.00	1.00	21367.4
α_{15}	0.97	0.55	1.43	1.00	1.00	20895.5
α_{16}	0.61	0.09	1.15	1.00	1.00	19626.5
α_{17}	0.98	0.58	1.45	1.00	1.00	19383.8
α_{18}	1.09	0.57	1.65	1.00	1.00	20796.0
α_{19}	0.60	-0.17	1.33	1.00	1.00	12912.9
α_{20}	0.83	0.30	1.41	1.00	1.00	11564.3
α_{21}	1.33	0.96	1.74	1.00	1.00	18303.6
α_{22}	0.02	-0.41	0.52	1.00	1.00	17073.3
α_{23}	0.89	0.28	1.61	1.00	1.00	14866.0
α_{24}	0.71	0.27	1.24	1.00	1.00	19737.1
α_{25}	0.26	-0.18	0.73	1.00	1.00	18928.3
α_{26}	1.01	0.39	1.73	1.00	1.00	16403.5
α_{27}	0.31	-0.39	1.03	1.00	1.00	16297.4
α_{28}	0.08	-0.53	0.71	1.00	1.00	13522.9
α_{29}	0.71	0.09	1.38	1.00	1.00	17691.3
α_{30}	0.71	0.20	1.26	1.00	1.00	18418.8
α_{31}	0.76	0.12	1.45	1.00	1.00	15880.4
α_{32}	0.81	0.23	1.44	1.00	1.00	13701.3
α_{33}	0.51	-0.23	1.32	1.00	1.00	18891.9
α_{34}	0.19	-0.53	0.92	1.00	1.00	17031.9
α_{35}	1.12	0.50	1.85	1.00	1.00	17907.4
α_{36}	0.52	-0.20	1.28	1.00	1.00	16127.4
α_{37}	0.47	-0.07	1.06	1.00	1.00	18896.0
α_{38}	0.86	0.20	1.55	1.00	1.00	13348.0
α_{39}	0.48	0.26	0.72	1.00	1.00	22304.2
α_{40}	0.73	0.44	1.02	1.00	1.00	21924.7
α_{41}	0.92	0.75	1.10	1.00	1.00	22547.7
α_{42}	0.72	0.14	1.37	1.00	1.00	18993.9
α_{43}	1.16	0.80	1.55	1.00	1.00	18793.6
$\beta^{(1)}{}_1$	3.37	1.60	6.24	1.01	1.01	1068.5
$\beta^{(1)}{}_2$	3.09	0.73	6.76	1.00	1.01	1738.4

$\beta^{(1)}_3$	3.78	2.16	6.63	1.00	1.01	782.6
$\beta^{(1)}_4$	3.93	1.96	7.15	1.00	1.00	662.0
$\beta^{(1)}_5$	3.62	1.05	8.03	1.00	1.01	1171.0
$\beta^{(1)}_6$	4.59	2.02	8.11	1.00	1.01	1396.0
$\beta^{(1)}_7$	2.71	0.39	6.77	1.00	1.01	1818.5
$\beta^{(1)}_8$	3.11	0.80	6.17	1.00	1.01	1179.8
$\beta^{(1)}_9$	3.68	1.11	7.22	1.01	1.01	1827.0
$\beta^{(1)}_{10}$	2.55	-1.49	5.14	1.00	1.01	907.4
$\beta^{(1)}_{11}$	2.51	-0.20	6.23	1.00	1.01	2022.1
$\beta^{(1)}_{12}$	3.14	0.84	5.40	1.00	1.00	4021.9
$\beta^{(1)}_{13}$	3.36	1.40	6.95	1.01	1.01	939.0
$\beta^{(1)}_{14}$	3.93	2.00	7.11	1.00	1.01	1002.2
$\beta^{(1)}_{15}$	3.92	1.90	7.02	1.00	1.01	1039.6
$\beta^{(1)}_{16}$	2.84	0.65	6.66	1.01	1.01	963.9
$\beta^{(1)}_{17}$	3.08	1.40	5.07	1.00	1.01	4457.6
$\beta^{(1)}_{18}$	3.45	1.01	7.65	1.00	1.00	1123.8
$\beta^{(1)}_{19}$	3.32	0.59	6.98	1.00	1.00	1547.9
$\beta^{(1)}_{20}$	0.17	-2.24	2.20	1.00	1.01	1193.1
$\beta^{(1)}_{21}$	4.65	2.54	8.17	1.00	1.01	1406.7
$\beta^{(1)}_{22}$	1.85	-0.58	4.18	1.00	1.01	1210.5
$\beta^{(1)}_{23}$	3.90	1.48	7.25	1.00	1.00	2102.6
$\beta^{(1)}_{24}$	2.88	1.00	4.93	1.00	1.00	4710.5
$\beta^{(1)}_{25}$	3.08	1.03	6.81	1.00	1.01	1114.3
$\beta^{(1)}_{26}$	3.88	0.90	7.49	1.00	1.00	2471.7
$\beta^{(1)}_{27}$	3.71	1.14	7.49	1.00	1.01	1997.3
$\beta^{(1)}_{28}$	2.24	-0.03	6.19	1.00	1.00	999.3
$\beta^{(1)}_{29}$	2.94	0.59	5.99	1.01	1.01	2136.0
$\beta^{(1)}_{30}$	4.30	1.91	7.76	1.00	1.00	1082.7
$\beta^{(1)}_{31}$	3.28	0.58	6.84	1.00	1.00	1914.1
$\beta^{(1)}_{32}$	2.87	-0.01	5.28	1.00	1.01	2005.5
$\beta^{(1)}_{33}$	3.10	0.37	6.79	1.00	1.00	2284.6
$\beta^{(1)}_{34}$	1.89	-0.84	5.06	1.00	1.00	2442.5
$\beta^{(1)}_{35}$	3.40	1.04	7.54	1.01	1.01	1101.9
$\beta^{(1)}_{36}$	3.70	1.21	7.68	1.00	1.01	1380.2
$\beta^{(1)}_{37}$	3.57	1.46	7.36	1.00	1.00	1192.5
$\beta^{(1)}_{38}$	3.65	0.94	7.05	1.00	1.00	1756.8
$\beta^{(1)}_{39}$	4.34	2.53	7.24	1.00	1.01	819.4
$\beta^{(1)}_{40}$	3.73	2.19	5.69	1.00	1.00	3328.8
$\beta^{(1)}_{41}$	3.64	2.56	4.87	1.00	1.00	3712.0
$\beta^{(1)}_{42}$	4.19	1.87	7.89	1.00	1.00	1673.8
$\beta^{(1)}_{43}$	4.54	2.51	8.01	1.00	1.01	826.9
$\beta^{(2)}_1$	2.74	1.01	5.57	1.01	1.01	1011.3
$\beta^{(2)}_2$	2.55	0.09	6.08	1.00	1.01	1525.9

$\beta^{(2)}_3$	3.80	2.08	6.77	1.00	1.01	830.6
$\beta^{(2)}_4$	3.58	1.70	6.87	1.00	1.00	737.0
$\beta^{(2)}_5$	2.97	0.47	7.33	1.00	1.01	1083.5
$\beta^{(2)}_6$	3.97	1.57	7.40	1.00	1.01	1526.9
$\beta^{(2)}_7$	1.82	-0.64	5.76	1.01	1.01	1505.0
$\beta^{(2)}_8$	3.22	1.25	6.28	1.01	1.02	1097.2
$\beta^{(2)}_9$	2.49	-0.21	5.93	1.01	1.01	1715.7
$\beta^{(2)}_{10}$	1.90	-2.20	4.35	1.00	1.01	817.5
$\beta^{(2)}_{11}$	2.07	-0.51	5.90	1.00	1.01	1477.8
$\beta^{(2)}_{12}$	2.43	-0.11	4.62	1.00	1.00	3555.5
$\beta^{(2)}_{13}$	2.81	0.84	6.35	1.01	1.01	901.6
$\beta^{(2)}_{14}$	3.04	1.04	6.19	1.00	1.01	948.1
$\beta^{(2)}_{15}$	3.01	0.95	6.11	1.00	1.01	1188.1
$\beta^{(2)}_{16}$	2.44	0.32	6.31	1.00	1.01	825.6
$\beta^{(2)}_{17}$	2.60	0.76	4.74	1.00	1.00	3494.4
$\beta^{(2)}_{18}$	3.26	0.88	7.37	1.00	1.00	971.8
$\beta^{(2)}_{19}$	3.72	1.33	7.34	1.00	1.00	1340.7
$\beta^{(2)}_{20}$	0.67	-1.99	2.80	1.00	1.01	974.3
$\beta^{(2)}_{21}$	3.06	0.74	6.26	1.01	1.01	1234.9
$\beta^{(2)}_{22}$	2.02	-0.44	4.25	1.00	1.01	1218.1
$\beta^{(2)}_{23}$	3.04	0.43	6.42	1.00	1.00	1987.2
$\beta^{(2)}_{24}$	2.16	-0.01	4.24	1.00	1.00	3257.6
$\beta^{(2)}_{25}$	2.20	-0.06	5.79	1.00	1.00	1079.0
$\beta^{(2)}_{26}$	2.62	-0.37	5.84	1.00	1.01	2351.8
$\beta^{(2)}_{27}$	2.75	0.18	6.32	1.01	1.01	1917.9
$\beta^{(2)}_{28}$	2.42	0.30	6.64	1.00	1.00	824.4
$\beta^{(2)}_{29}$	2.63	0.50	5.60	1.01	1.02	2020.1
$\beta^{(2)}_{30}$	3.52	1.20	6.91	1.00	1.00	1136.8
$\beta^{(2)}_{31}$	3.59	1.12	7.31	1.00	1.00	1837.3
$\beta^{(2)}_{32}$	2.71	-0.35	5.03	1.00	1.01	1600.4
$\beta^{(2)}_{33}$	2.54	-0.23	6.33	1.00	1.00	1866.0
$\beta^{(2)}_{34}$	1.89	-0.62	5.07	1.00	1.00	2390.6
$\beta^{(2)}_{35}$	2.78	0.12	6.90	1.01	1.02	1065.9
$\beta^{(2)}_{36}$	2.98	0.37	6.86	1.00	1.00	1353.2
$\beta^{(2)}_{37}$	3.29	1.11	7.13	1.00	1.00	1230.9
$\beta^{(2)}_{38}$	3.92	1.41	7.41	1.00	1.00	1796.7
$\beta^{(2)}_{39}$	3.43	1.62	6.35	1.00	1.01	784.1
$\beta^{(2)}_{40}$	2.78	1.02	4.84	1.00	1.00	2869.3
$\beta^{(2)}_{41}$	2.75	1.59	4.04	1.00	1.00	3351.7
$\beta^{(2)}_{42}$	3.07	0.62	6.63	1.00	1.00	1493.8
$\beta^{(2)}_{43}$	4.22	2.03	7.82	1.00	1.01	810.8

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CAPÍTULO 2

Forest and connectivity loss drive changes in movement behavior of bird species

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Abstract

The movement ecology paradigm states that external factors interact with intrinsic factors of the species to shape movement patterns. In a rapid changing world, to manage ecosystem functions and services it is important to understand how environmental modifications by humans affect species' behavior. This is not a simple task, since we need to address field survey and analysis limitations to deal with multitude of species, and the different external contexts that affect their behavior. Here, we investigate how movement behavior of common forest birds can be predicted by forest cover and forest isolation. We modeled bird movement parameters as a function of species traits – body mass and feeding habit – and phylogenetic relationships, using Joint Species Movement Models. We used field data collected in five 600 x 600 m plots in the southeastern part of Atlantic Forest. We show evidence that increasing forest cover reduces the flight distances of birds and the movement bias to forest patches and remnant trees, especially for insectivores. Increasing forest isolation, in turn, increases the movement bias to forest patches for most species, and the perching time of granivores and omnivores. These changes have direct effects on habitat connectivity and ecosystem services provision, which we summarized in a conceptual framework.

Introduction

The increasing influence of humans on the environment is progressively changing tropical forests. Either directly, by deforestation, or indirectly, by changing the atmospheric composition and biogeochemical cycles, we are modifying natural communities and causing species loss (Lewis 2006, Ceballos et al. 2015). In fragmented landscapes, native vegetation share space with a diverse array of human land uses, and the species that persist may show evolutionary changes (Galetti et al. 2013), changes in biotic interactions (Tylianakis et al. 2008), and behavioral changes (Kremen et al. 2007, Tucker et al. 2018).

Although subtle, changes in movement behavior are widespread responses to environmental alterations, mostly due to the behavioral plasticity of species (Sih et al. 2011, Tucker et al. 2018). Individuals in a context of abundant and predictable resources, for instance, forage in small-range areas, with sinuous paths, short step lengths and low speed (McIntyre and Wiens 1999, Nolet and Mooij 2002, Weimerskirch et al. 2007, Roshier et al. 2008, de Jager et al. 2011). In contrast, if resources are heterogeneously distributed in space or movement risks are high, foraging areas, step lengths, and movement speed can be increased (McIntyre and Wiens 1999, Nolet and Mooij 2002, Weimerskirch et al. 2007, Roshier et al. 2008, Sih et al. 2011). These behavioral responses, and their intensities, are related to species traits (Sih et al. 2011, Spiegel et al. 2017). Large-bodied species, for example, may exhibit higher movement capacity (Spiegel and Nathan 2007, Neuschulz et al. 2013) and, to ensure sufficient resources, should be more likely to change their behavior in response to variation in resource distribution than small-bodied species (Buchmann et al. 2012). Dietary specialization can also affect species movement, since resources have different spatial distribution, spatial predictability, and nutritional values. Frugivorous

birds, for instance, move more than insectivorous birds, probably because they are not able to predict where are the fruit sources and due to the necessity of birds to track fruits over large areas (Graham 2001, Neuschulz et al. 2013).

Although it is known that external factors can shape the movement of species, there is still a lack of empirical data to understand how human-modified environments drive behavioral changes. Filling this knowledge gap is crucial, particularly because the movements of animals are tightly linked to their ecosystem functions and the services they provide (Kremen et al. 2007, Nathan et al. 2008). Assessing community-wide changes in the movement behavior of species is a hard task, since we need to address field work and analytical limitations to deal with a multitude of species and the different external contexts that affect their behavior. Here, we present a community-based study investigating how the movement behavior of common forest birds can be predicted by landscape structure. Considering that movement is intrinsically related to allometric relationships and particular species needs, we use a Joint Species Movement Models (Chapter 1), which estimates movement parameters as a function of species traits and phylogenetic relationships. We extended this framework to a multiple-landscape model to enable estimating the mean flight distance, the movement bias to forest and to remnant trees in pasture, and the mean perching time of 65 forest bird species in five fragmented landscapes in the Atlantic Forest (Brazil).

We hypothesized that (1) flight distance should increase with decreasing forest cover and increasing mean forest isolation, while perching time should decrease, since movement is expected to be faster in hostile environments; (2) the movement bias towards

remnant trees should increase with decreasing forest cover and increasing mean isolation, since these trees can serve as stepping-stones between forest patches and additional sources of resources (Prevedello et al. 2017); and (3) The intensity of changes in movement across forest cover and isolation gradients, described in (1) and (2), should be higher for more mobile species – large bodied birds and frugivores. Finally, we build a conceptual framework to summarize how the main effects of forest cover and isolation on the movement of forest birds can change habitat connectivity and ecosystem services provided by birds.

Methods

Study area

We conducted this study in the Cantareira-Mantiqueira Corridor in southeastern Brazil (Fig. 1a). The region is considered a priority area for conservation of the Atlantic Forest, since it connects two large blocks of forest remnants: Serra da Cantareira and Serra da Mantiqueira. Moreover, the region surrounds the water supply system responsible for providing water for the largest metropolitan areas of São Paulo State (Brasil 2007, Rodrigues and Bononi 2008). The region features a hilly to strongly hilly relief and its elevation ranges from 600 to 2000 m a.s.l. (São Paulo 2010). Although the region still harbors many forest patches, the landscape is a mosaic mainly composed by cattle pasture, forestry, agriculture, and urban areas.

We selected five square plots of 600 x 600 m, located at least 3 km from each other (Fig. 1c). The criteria for selecting the plots were: (1) the presence of a hilly relief to make

possible the observation of bird movements (see below); (2) the predominance of cattle pasture as non-forest habitat; (3) the presence of a variety of arboreal vegetation within the pasture, such as scattered trees, hedgerows, riparian vegetation, and small patches of secondary forest (< 0.15 ha); (4) logistic facilities for data collection (for example: the landlord authorization to use the area). The plots were classified into three vegetation cover types: a) active pasture, open areas composed mainly by exotic grasses with or without sparse bushes; b) remnant trees, characterized by vegetation patches with one or more trees, within the pasture; and c) forest patches. We discriminated remnant trees and forest patches because birds can make an unequal use of these elements, as reported by previous studies in the region (see Pizo 2004, Pizo and dos Santos 2011). We classified as forest habitat only patches more than 40 m wide. Patches less than 40 m wide, which we also classified as remnant trees, usually showed lower diversity of plant species, presence of exotic grasses and absence of understory, probably due to edge effect and the incursion of cattle, since most of them were not fenced.

As landscape structure variables, we calculated the percentage of forest cover and the mean isolation (see the metrics values for each area in Supporting Table 1). Forest cover was quantified within a 1500 m radius around the centroid of each plot (Fig. 1b), and ranged from 20% to 70%. Home range sizes vary greatly among bird species, so we set this landscape size to encompass the area needed by most birds. Therefore, forest cover is a measure of the amount of resources available at the home range level. Mean isolation ranged from 18 m to 35 m, and was calculated for each plot as the average distance from 1000 random pasture points to the nearest forest patch or remnant tree (method adapted from Baddeley and Turner (2005) and Dale and Fortin (2014) by Ribeiro et al. (2009)).

Since forest birds usually avoid perching on pasture, mean isolation represents how much of open habitat birds need to fly to reach other perches.

We collected data on vegetation structure, bird community and bird species abundances to control for variation throughout the studied areas. We observed evidence of correlation between bird community similarity and forest cover, and homogeneity of vegetation structure variation over the studied plots. See Supporting Information for details about the methods and results.

Bird movement survey

We monitored bird movement in each landscape from September to December 2014 and 2015 (total of 72 hours of observation per landscape). We divided each landscape into a grid of 10 x 10 m, totalizing 3600 cells. We distributed vantage points on the plots from which we had a broad view of the landscape, and from which we could have homogeneously surveyed all landscape cells at the end of data collection. At sunrise, we started looking for birds from the vantage points for four and a half hours, with the help of 10 x 42 binoculars and a chronometer. Once a bird was spotted, we identified the species and tracked its movement, recording the time spent flying and perching (in seconds). In addition, we recorded the landscape cells used between consecutive flights until the bird was lost. To record the sequence of cells, we used a printed high resolution (0.5 x 0.5 m) satellite image of each plot. To control for variation in weather conditions, we didn't survey bird movements in rainy or windy days.

Modeling bird movements as a function of landscape structure and species traits

We analyzed the movement data using the Joint Species Movement Modeling (JSMM) framework proposed in the Chapter 1. The JSMM framework enables the simultaneous estimation of species- and community-level movement parameters by modelling movement activity and habitat affinities as a function of species traits and their phylogenetic relationships. In Chapter 1, we analyzed the dataset from one of the plots reported in this study. Here we extend the single-landscape version of JSMM to a multiple-landscape JSMM, enabling us to ask how landscape covariates influence bird movements.

We denote the number of landscapes by n_l, the number of species by n_s, the number of species traits by n_t, the number of landscape covariates by n_c, and the number of species-specific movement parameters by n_p. We used the log-transformed body size and feeding habit (granivorous, frugivorous, insectivorous, or omnivorous) as species traits, obtained from Wilman et al. (2014). We built a phylogenetic correlation matrix with the package ape 4.0 (Paradis et al. 2004) from phylogenetic trees provided by Jetz et al. (2014). As landscape covariates, we included forest cover and mean isolation. We standardized these to zero mean and unit variance, so that the intercept models movements in a typical landscape. We divided the movement parameters to be estimated into two components: (1) a spatial component, describing the typical flight distance and the movement bias to remnant trees and forest patches; and (2) a temporal component, describing the perching time. We estimated the parameters for the spatial and temporal components in separate models.

Assuming that an individual of species $s = 1, \dots, n_s$ is currently at grid cell $i = 1, \dots, 3600$ of landscape $l = 1, \dots, n_l$, we model the probability p_{klji} that it will next move to grid cell j by

$$p_{slji} = K_{isl}\exp(-d_{ij}/\alpha_{sl})\exp(\beta_{sl}^{(1)}h_{lj}^{(1)})\exp(\beta_{sl}^{(2)}h_{lj}^{(2)}). \quad \text{Eq. 1}$$

In Eq. 1, d_{ij} is the Euclidian distance between the grid cells i and j, and the parameter $\alpha_{sl} > 0$ models the typical flight distance of species s in landscape l. The variable $h_{lj}^{(1)}$ is an indicator of whether grid cell j of landscape l belongs to the remnant trees ($h_{lj}^{(1)} = 1$) or not ($h_{lj}^{(1)} = 0$), and the parameter $\beta_{sl}^{(1)}$ measures the movement bias of the species to remnant trees compared to pasture habitat. Similarly, the variable $h_{lj}^{(2)}$ is an indicator of whether grid cell j belongs to the forest habitat ($h_{lj}^{(2)} = 1$) or not ($h_{lj}^{(2)} = 0$), and the parameter $\beta_{sl}^{(2)}$ measures the movement bias of the species to forest habitats compared to pasture habitat. The normalizing constant K_{isl} is defined so that the probabilities sum to unity over the target cells, i.e. that $\sum_j p_{slji} = 1$ for all i, s and l. As the model does not include the possibility of the individual leaving the study plot, it models the next location conditional on the individual not leaving the study plot. Thus, we truncated the data so that they did not involve steps outside of the study plot.

The three ($n_p = 3$) parameters α_{sl}, $\beta_{sl}^{(1)}$ and $\beta_{sl}^{(2)}$ describe the movement behavior of the species s in landscape l. Next, we build a hierarchical structure that models these as a function of species traits. To do so in a simplified notation, we denote the movement parameters by $\hat{\theta}_{slp}$, where $p = 1, \dots, n_p$ is an index of the movement parameter:

$\hat{\theta}_{sl1} = \log(\alpha_{sl})$, $\hat{\theta}_{sl2} = \beta_{sl}^{(1)}$, and $\hat{\theta}_{sl3} = \beta_{sl}^{(2)}$. We model the movement parameters $\hat{\theta}_{slp}$ with the help of the regression model

$$\hat{\theta}_{slp} = \sum_{c=1}^{n_c} B_{lc}\theta_{scp} + \hat{\varepsilon}_{slp}, \quad \text{Eq. 2}$$

where B_{lc} denotes the covariate $c = 1, \dots, n_c$ for landscape l, and the parameter θ_{scp} measures how the landscape covariate c influences the movement parameter p of species s. We model the residuals $\hat{\varepsilon}_{slp}$ with a multivariate normal distribution with covariance structure

$$\text{Cov}\left(\hat{\varepsilon}_{slp}, \hat{\varepsilon}_{s'l'p'}\right) = \delta_{ss'}\delta_{ll'}V_{pp'}, \quad \text{Eq. 3}$$

where δ_{AB} is Dirac delta with $\delta_{AB} = 1$ if $A = B$ and $\delta_{AB} = 0$ if $A \neq B$, and the elements $V_{pp'}$ of the $n_p \times n_p$ matrix $\mathbf{V}$ model random variation in the landscape-specific movement parameters around the expectation set by landscape covariates.

The parameters θ_{scp} can be considered as general movement parameters of species s, as they describe the expected movement parameters of the species as a function of landscape structure. We further model these as a function of species traits and phylogenetic relationships with the regression model

$$\theta_{scp} = \sum_{t=1}^{n_t} T_{st}\zeta_{tcp} + \varepsilon_{scp}, \quad \text{Eq. 4}$$

where T_{st} denotes the trait t for species s, and the parameter ζ_{tcp} measures how the species trait t influences how landscape covariate c influences the movement parameter p.

We model the residuals ε_{scp} with a multivariate normal distribution with covariance structure

$$\mathrm{Cov}\left(\varepsilon_{scp}, \varepsilon_{s'c'p'}\right) = W_{ss'}\Sigma_{(cp)(c'p')}. \quad \text{Eq. 5}$$

Here $\mathbf{W}$ is a $n_s \times n_s$ matrix $\mathbf{W} = \rho\mathbf{C} + (1-\rho)\mathbf{I}_{n_s}$,where $\mathbf{C}$ is a phylogenetic correlation matrix, $\mathbf{I}_{n_s}$ is the identity matrix, and the parameter $0 \leq \rho \leq 1$ measures the strength of the phylogenetic signal. The matrix $\mathbf{\Sigma}$ is a $n_c n_p \times n_c n_p$ variance-covariance matrix that models random variation in species-specific movement parameters around the expectation set by species traits.

To fit the model to the observed data, we developed a Markov chain Monte Carlo (MCMC) sampling scheme (see Supporting Information for details). As observed flight distances, or movement steps, we used the Euclidean distance between the centroids of two consecutively-used cells.

Modelling perching times as a function of landscape structure and species traits

We adapted the above described multi-landscape JSMM to analyze data on perching times. We let $q = 1, \ldots, n_{sl}$ denote the set of perching time observations made for species s in landscape l. We model the perching time P_{slq} as

$$\log\left(P_{slq}\right) \sim N\left(\sum_{r=1}^{n_r} x_{lrsq}\beta_{slp}\,, \sigma_{sl}^2\right), \quad \text{Eq. 6}$$

where x_{lrsq} is the covariate $r = 1, \ldots n_r$ related to the observation q of species s in landscape l, and the β_{slp} are regression parameters to be estimated. We set as reference

habitat the intercept ($x_{lrsq} = 1, n_r = 1$) and estimated the typical perching time for bird species.

The species- and landscape-specific perching time models involve $n_p = n_r + 1$ parameters, which we denote by $\hat{\theta}_{slp}$. The first n_r parameters are the regression parameters, $\hat{\theta}_{slp} = \beta_{slp}$, and the additional parameter is the variance parameter, $\hat{\theta}_{sl(n_r+1)} = \log(\sigma_{sl}^2)$. While in the movement model (Eq. 1) the parameter $\hat{\theta}_{slp}$ models a specific movement behavior parameter p of species s in landscape l, in the perching time model (Eq. 6) it models a specific perching behavior parameter p of species s in landscape l. We built to the perching time model the same hierarchical structure as to the movement model (Eqs. 2-5), thus modeling the perching time parameters as a function of landscape covariates and species traits.

A summary with all coding in R and data are freely available under GLP2 at the following Github repository: https://github.com/leeclab/ MultipleLandscapes_JSMM .

Results

We recorded movement sequences of 1 to 9 steps (average 1.6 steps by track, and 44.8 steps by species). We also recorded 1 to 633 perching times by species (average of 35.7 perching times by species). See supporting material for details on quantity of data recorded by landscape and posterior values of the parameters.

We found evidence of the effect of forest cover and mean isolation on the species- and landscape-specific parameters of most bird species. Forest cover explained an average

of 47% of the variation in flight distances among the forest birds, 43% in movement bias to remnant trees, 39% in movement bias to forest patches, and 50% in perching times. Mean isolation explained less variability in the landscape- and species-specific parameters: average of 35% of the variation in flight distances, 30% in movement bias to remnant trees, 34% in movement bias to forest patches, and 50% in perching times. We found a small phylogenetic signal in the movement parameters, since the mean estimate of the parameter ρ was 0.05, with (0.01, 0.04) as 50% credible interval and (0.00, 0.15) as 95% credible interval for the spatial components of movement, and 0.03, with (0.01, 0.04) as 50% credible interval and (0.00, 0.10) as 95% credible interval for the temporal components of movement, while the prior distribution was uniform in the range from 0 to 1.

We found little evidence of correlation between body mass and the effect size of environmental covariates on movement parameters ($\Pr(\zeta_{tcp} < 0 \text{ or } \zeta_{tcp} > 0) < 0.9$, where t corresponds to body size, p corresponds to the slope parameters, and c are the landscape covariates). Increasing forest cover had a stronger negative effect on movement bias to remnant trees and forest patches for insectivorous birds. Increasing mean isolation had a stronger positive effect on perching time for granivorous and omnivorous birds than for frugivores (Fig. 2). The effects of forest cover on perching time and mean isolation on flight distance and movement bias were less dependent on bird traits ($r^2 \leq 0.45$). We found evidence of negative effects of forest cover on flight distance, and a positive effect of mean isolation on movement bias to forest patches. The effect of forest cover on perching time was mostly null, as well as the effect of mean isolation on typical flight distance and movement bias to remnant trees (Fig. 2).

Bird traits explained most of the variance ($r^2 > 0.50$) in estimated intercepts of landscape- and species-specific movement parameters. Perching time was the parameter most strongly predicted by bird traits ($r^2 = 0.78$) (Fig. 3). The intercept of typical flight distance was the parameter less dependent on bird traits ($r^2 \approx 0.35$). There was a strong evidence of a positive correlation between movement parameters and body mass ($\Pr(\zeta_{tcp} > 0) > 0.99$, where t corresponds to body size, p corresponds to the intercept parameters, and c are the landscape covariates). Typical flight distance were smaller for insectivorous than frugivorous birds when predicted by forest cover (Fig. 3). Movement bias towards remnant trees and forest patches was larger for frugivorous birds than for the other diet groups. Granivorous birds showed smaller movement bias to non-open areas, and insectivores showed intermediate values. Perching time was larger for insectivores than for omnivores and granivores. It is worthwhile to point out that the intercept values represent the movement parameters at a typical landscape with intermediate covariates values. Therefore, the relation between species and feeding classes varied throughout different landscapes, depending on the covariates effects on landscape- and species-specific parameters. In landscapes with larger percentage of forest cover, for example, insectivores tended to have a smaller bias to remnant trees and forest patches than other diet groups (Sup. Fig. 2). In landscapes with higher mean isolation, frugivores tended to show larger movement bias to remnant trees and forest patches than other groups.

Discussion

It has been long hypothesized that species should change their behavior to optimize the use of resources in habitat modified by human activities (Fahrig 2007, Buchmann et al.

2012). In this study, we showed that birds change their movement behavior in response to landscape structure. To our knowledge, this is the first empirical community-based report summarizing the effects of human landscape modifications on bird movement. Such effects were related to the species traits, especially birds' diets, while phylogenetic relationships were not good predictors of movement changes. Our results suggest that resources amount and spatial distribution, allometry, and short spatiotemporal decisions are the most important factors shaping the response of birds to landscape change.

We observed the same effects of forest cover and bird traits on flight distances than the ones described in literature for bird home ranges, even in a smaller level of single flights or short flight sequences. Researchers describe that frugivores have larger home ranges than other species, as insectivores, as a consequence of lack of spatial predictability of fruit production (Graham 2001, Hansbauer et al. 2008, Neuschulz et al. 2013). Similarly, the allometric relationships between body size and home range have been intensively studied (McNab 1963, Buchmann et al. 2012), and increase in animals' home range or territories due to reduction of resources, here represented by forest cover, have been described in several ecosystems (*e.g.* Hansbauer et al. 2008, Uriarte et al. 2011). To predict a correlation between the flight distance and the size of home ranges is not so straightforward. The spatial pattern of the area used by an individual for its life activities is a result of the interaction of multiple factors acting at different spatiotemporal scales (Börger et al. 2008, Powell and Mitchell 2012), either intrinsic – e.g. body size, memory capacity, sex, personality, breeding status, territorialism – or external – e.g. abundance and predictability of resources, intra- and inter-specific interactions, and nesting sites. We show evidence that

flight distances can be used to predict variation in home range sizes and that this movement component can help improving mechanistic models of home range behavior.

While the movement distance was more related to the movement capacity and energetic needs of the species, the perching time showed to be better predicted by the decision of the individuals at the local context of land cover and spatial distribution of perches. The percentage of forest cover didn't change perching time, whereas mean isolation caused an increase of perching time– mainly for omnivores and granivores. We expected that the perching time would be shorter in less appropriated habitat – low forest cover and high mean isolation, for forest species – since birds would need to move more to reach the demanded resources (Uriarte et al. 2011). However, perching time also seems to depend on allometric relationships and on the local context of perches. The smaller the organism, the highest the mass-specific metabolic rate, i. e. more energy is spent by unit of mass (Brown et al. 2004). Therefore, the necessity to find food resources should limit the perching time of small species. Besides, predation risk is predicted to increase the longer a bird stays in a perch, and small species are more vulnerable to predators (Wheelwright 1991).

The positive correlation between body size and movement bias towards remnant trees and forest is probably also a consequence of the avoidance of predators, since large species are more conspicuous in open habitat. Small birds, in contrast, can perch and shelter on bushes and small trees regenerating on pasture (Pizo and dos Santos 2011). In turn, and in contrast to our expectations, small insectivores were the birds most affected by forest cover, showing higher movement bias to non-open areas in landscapes with lower

percentage of forest cover. This result highlights the importance of remnant trees acting as stepping-stones between forest patches for species with relative lower mobility capacity.

Implications of changes in bird movement behavior

Movement determines the environmental context and the pool of individuals and species the organisms will interact with (Jeltsch et al. 2013). Due to its consequences for the ecological and evolutionary processes, understanding the movement of organisms has gained an increasing importance in the study of fragmented landscapes and habitat loss (Fahrig 2007, Mitchell et al. 2015, Cosgrove et al. 2017). We addressed the implications of the observed bird movement changes for ecosystem functioning by building a conceptual framework that expands the movement variation to the landscape level.

One of the most obvious implications of movement variation are changes in the habitat connectivity, *i.e*. the degree to which a landscape facilitates or hinders movements among habitat patches for a given species (Fischer and Lindenmayer 2007). Habitat connectivity and its relation with the conservation of biodiversity has been extensively studied and, thus, a logical bridge between movement and landscape ecology has been built. For practical purposes, we will split the habitat connectivity into two processes in this text: (1) cross-habitat spillover (spillover), which has place in the interface between different habitat types (Rand et al. 2006); and (2) habitat connectivity *per se* (connectivity), which we will use to refer to processes involving different patches of forest.

The parameters most affected by forest cover were the typical flight distance and the movement bias to remnant trees and forest patches, which decreased with increasing forest

cover (Fig. 2 and 4a). With shorter mean distances, birds should have a shorter displacement in landscapes with high forest cover (Fig. 4b). With this information, we could suppose that the connectivity would diminish. However, the landscape structural connectivity increases with forest cover, and could offset the reduced mobility. At the same time, birds should be more prompt to use pasture, and to cross forest edges, which can improve spillover (Fig. 4c). In turn, the increasing mean isolation mainly increased the movement bias to forest patches and the perching time (Fig. 2 and 4d). If perched for longer time intervals, birds should show a smaller displacement rate in landscapes with high isolation. Besides, they should use less open areas and be less prompt to leave forest. As a consequence, the connectivity should decrease with increasing mean isolation. In fact, empirical studies show an increase of spillover with increasing forest cover (Boesing et al. 2017), and the reduction of connectivity with increasing isolation (Giubbina et al. in press). We highlight that these effects have different intensities among species with different traits. The effect of forest cover is more pronounced for insectivores, while mean isolation effect on perching time affects mostly granivores and omnivores.

Changes in habitat connectivity and spillover have immediate consequences on ecosystem services and functions based on birds, particularly pest control, seed dispersal and pollination, in the case of agricultural landscapes (Kremen et al. 2007, Whelan et al. 2008). The increase in spillover means that these services will be better provided in high forest covered landscapes: pest control will increase (Boesing et al. 2017) and more seeds will reach degraded areas (González-Varo et al. 2017, Chapter 3). By the other hand, the same bird species should disperse pollen and seeds for shorter distances with increasing

forest cover and mean isolation (Fahrig 2017), since flight distance is shorter and perching time is longer, respectively.

Concluding remarks

It is known that landscape structure can change the flow of mobile agents and consequently the ecosystem processes (Mitchell et al. 2015). We show with empirical data how landscape structure changes bird movements. By this means, we contribute to fill the lack of information about the exact mechanisms of the ecosystem responses to fragmentation. We highlight that we do not address other landscape variables that can potentially hinder or enhance the effects of the observed movement behavior changes. Habitat loss, for example, is often linked to functional extinction (Galetti et al. 2013). The increase in movement distances caused by reduction in forest amount can either compensate or be surpassed by the loss of large species, which can be more efficient for the provision of ecosystem functions and services (Spiegel and Nathan 2007, Bello et al. 2015). Likewise, environmental variation can directly influence movement, regardless behavioral rules (Cosgrove et al. 2017, Chapter 3). Their relative importance shaping movement should be investigated for a correct diagnostic of movement impediments and for effectiveness of biodiversity management. We provide a good basis to predict the consequences of community movement change for major concerns of conservation science, as species loss, function loss and biodiversity extinction thresholds. Further studies should deal with the challenge of linking animal movement to empirical data on ecosystem services provision and s ecosystem functioning variation.

Acknowledgments

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Figures

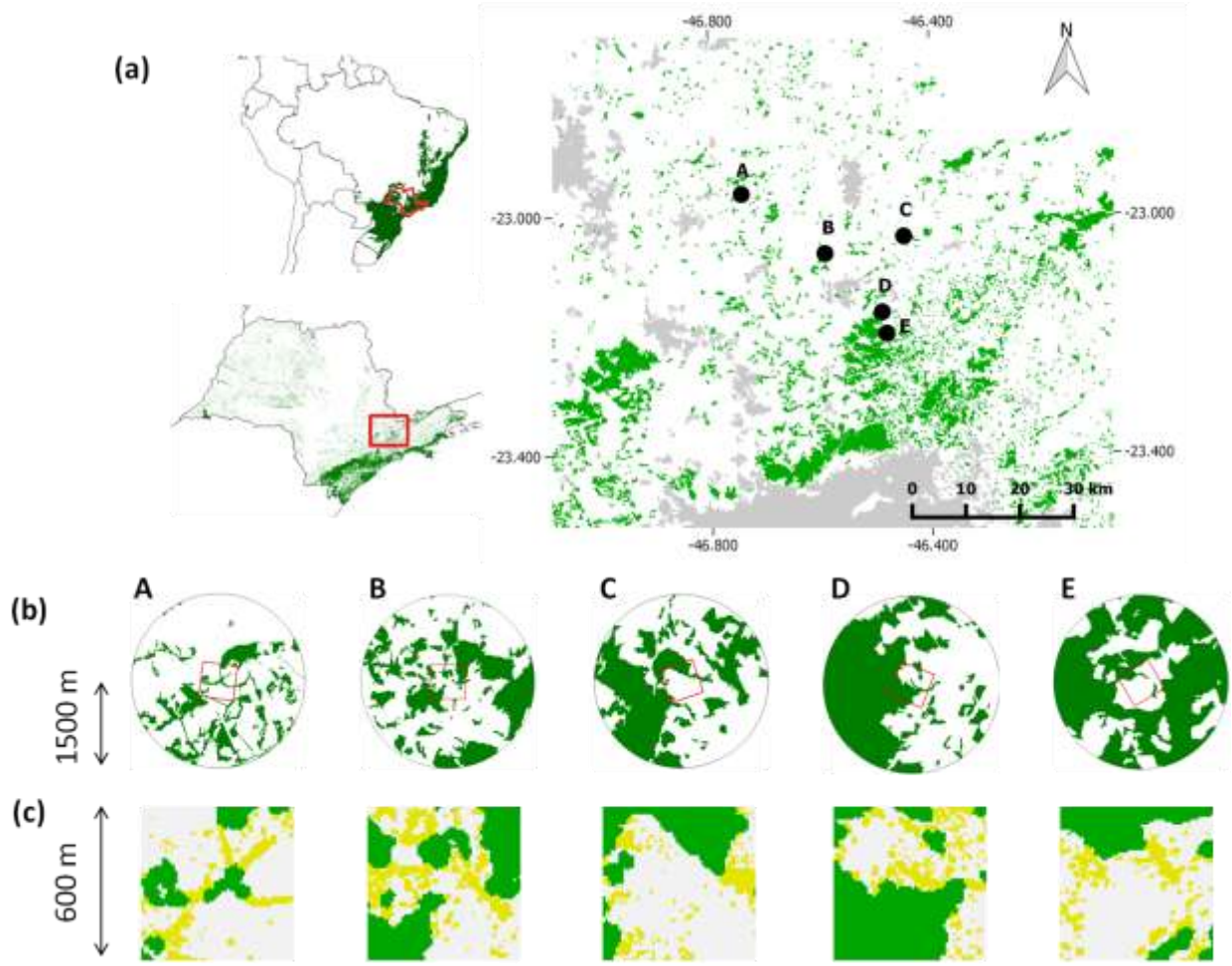


Figure 1. The Cantareira-Mantiqueira Corridor region (a) with the studied plots (dots A-E). The studied plots were 600 x 600 m squares (c), for which we show the surrounding circular landscape (A-E) used to calculate the forest cover percentage (b). The colors are: (a) urban areas (gray) and forest fragments (green); (b) forest fragments (green); and (c) forest fragments (green), remnant trees (yellow), and pasture (light gray).

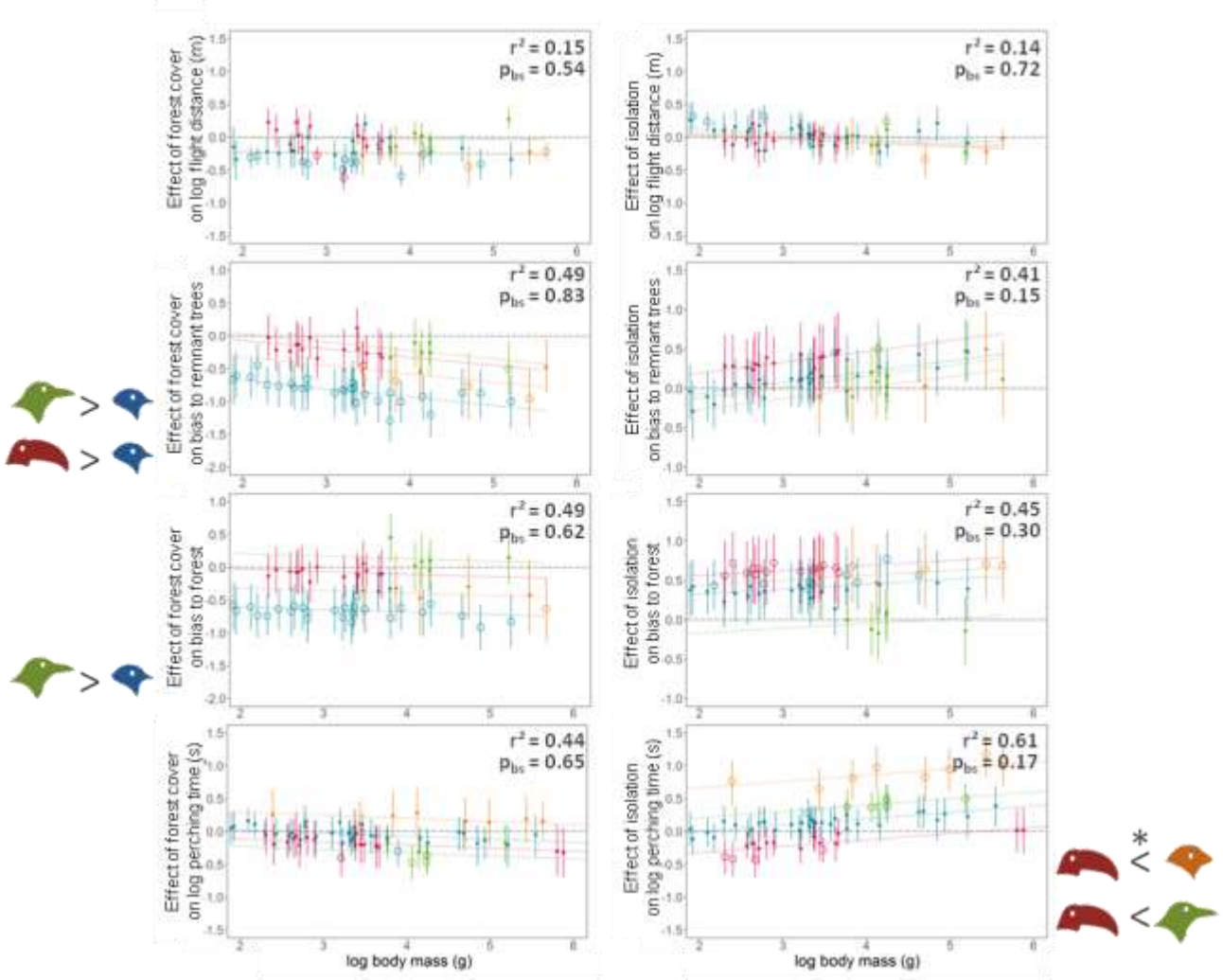


Figure 2. The influence of environmental covariates – forest cover and mean isolation – on the landscape- and species-specific movement parameters, as a function of bird functional traits. The dots represent the mean posterior values for each species, and the bars are the 25% and the 75% quantiles. The open dots show the slopes of the species with at least 80% of probability to be either positive or negative. The colors represent the diet groups: frugivores (red:), insectivores (blue:), granivores (orange:), and omnivores (green:). The pairs of images beside the panels indicate statistical support for a difference between each pair of feeding classes ($p > 0.9$). The colors represent the same diet

groups described above, and the asterisks (*) indicate difference probability of at least 0.95. The dashed lines show the posterior mean prediction of expected slopes based on species body size, for each diet group. For all slopes we also show the variability explained by the traits (r^2), and the posterior support for the slope decrease with body size ($p_{bs} = \Pr(\zeta_{tcp} < 0)$, where t corresponds to body size, p corresponds to the slope parameters, and c are the landscape covariates).

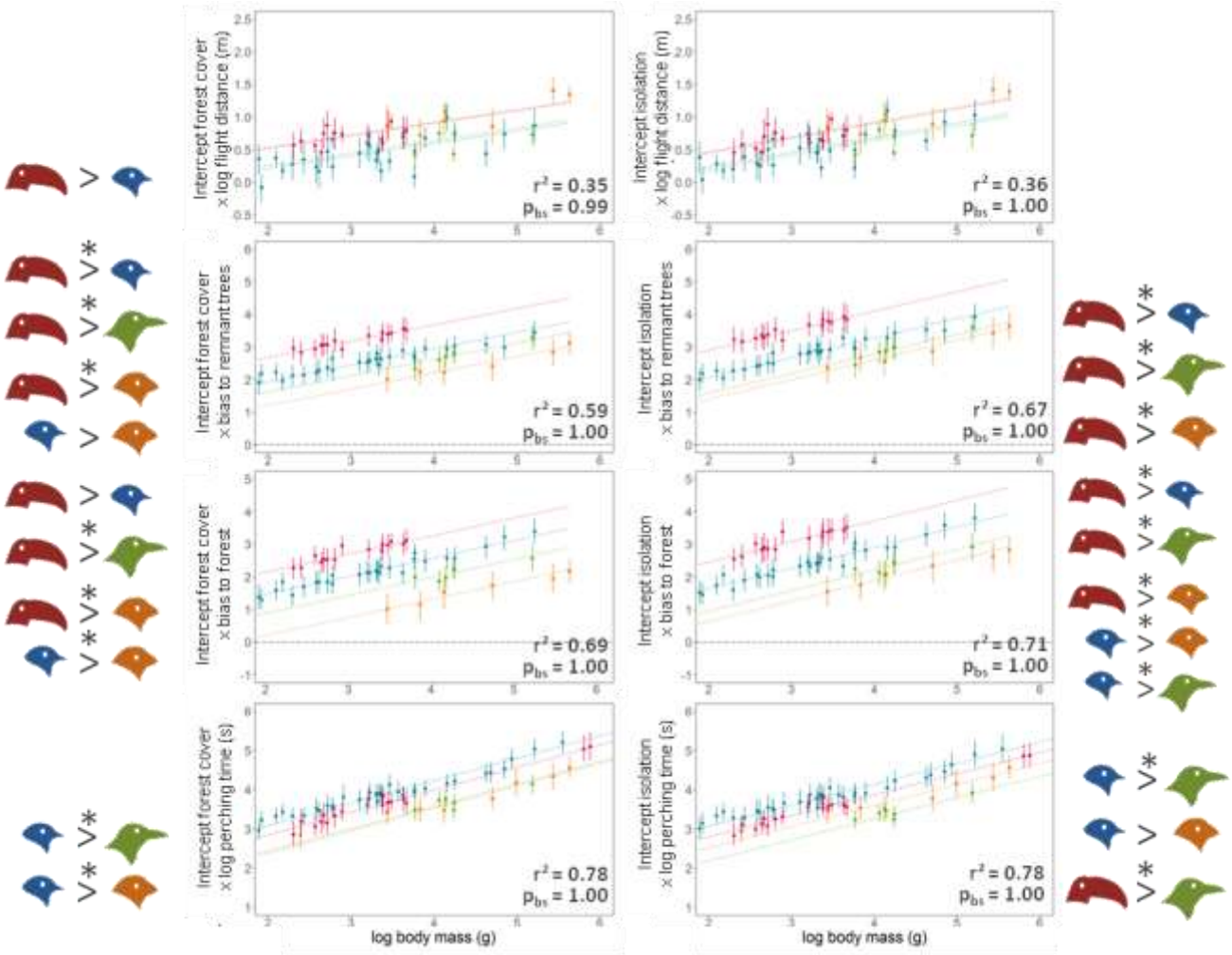


Figure 3. The intercept of the landscape- and species-specific movement parameters in relation with the environmental covariates – forest cover and mean isolation, as a function of bird functional traits. The dots represent the mean posterior values for each species, and the bars are the 25% and the 75% quantiles. The colors represent the diet groups: frugivores (red:), insectivores (blue:), granivores (orange:), and omnivores (green:). The pairs of images beside the panels indicate statistical support for a difference between each pair of feeding classes ($p > 0.9$). The colors represent the same diet groups described above, and the asterisks (*) indicate difference probability of at least 0.95. The dashed lines show the posterior mean prediction of expected intercepts based on

species body size, for each diet group. For all intercepts we also show the variability explained by the traits (r^2), and the posterior support for the positive correlation between intercept and body size ($p_{bs} = \Pr(\zeta_{tcp} > 0)$, where t corresponds to body size, p corresponds to the intercept parameters, and c are the landscape covariates).

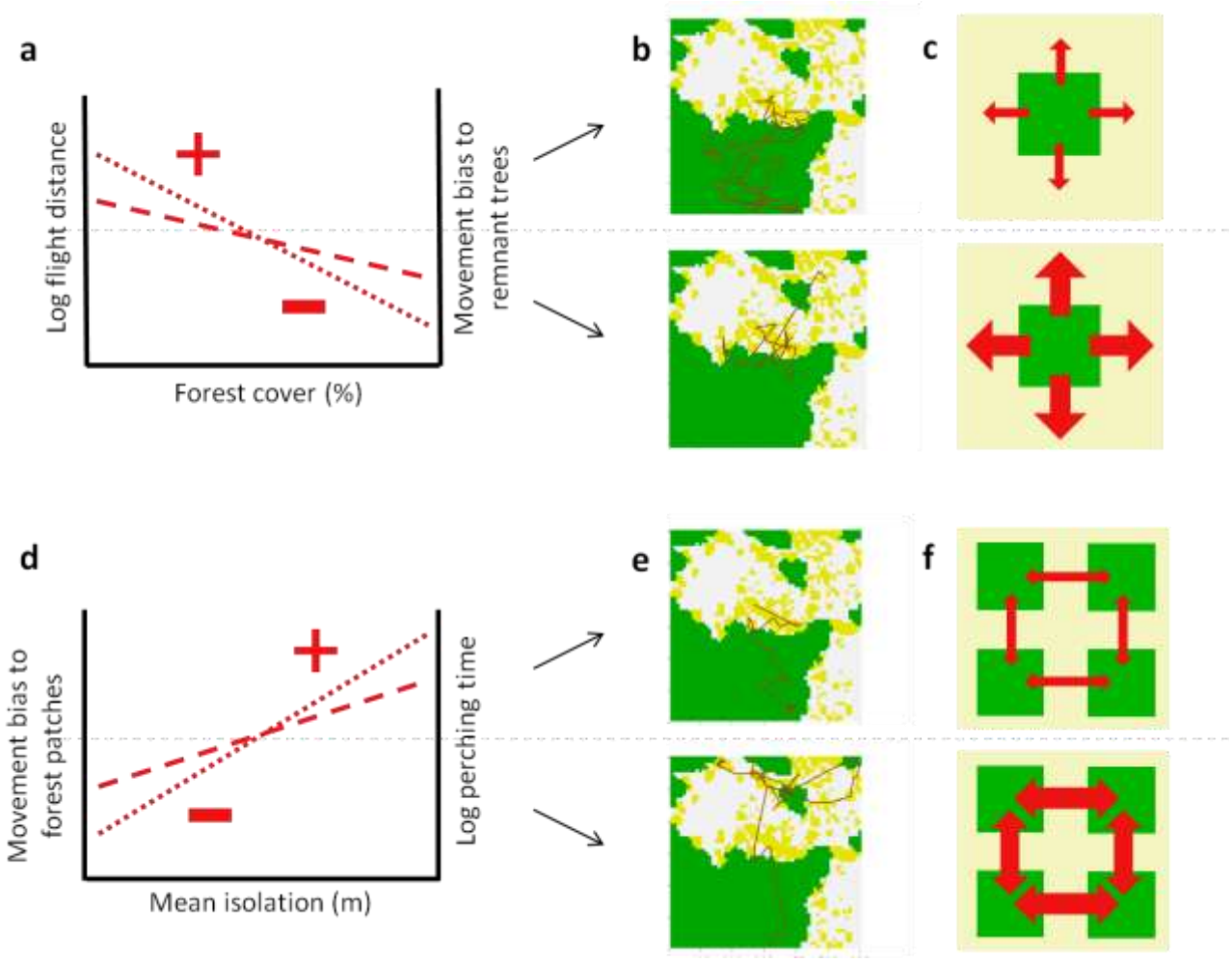


Figure 4. Conceptual framework of the effects of changing movement behavior on landscape-level movements of birds. (a) The movement bias to remnant trees and the typical flight distance decrease with increasing forest cover, causing (b) smaller displacement, and (c) more time spent in pasture. In turn, (d) increasing mean isolation causes an increase in perching time and in movement bias to remnant trees and forest patches. As a consequence, (e) the movement tracks are shorter and (f) the number of patches used and forest edges crossed are larger.

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Supporting Information

Vegetation structure sampling

To describe the vegetation structure we systematically arranged circular plots of 2.5 m radius in the studied landscapes. We split the landscape into a grid of 900 cells with 20 x 20 m each, and positioned the circular plots in the center of intercalated cells. For each plot we (1) counted the number of adult trees with diameter at breast height (DBH) in the following size categories: < 3 cm, 3 - 10 cm, 10 - 30 cm, and > 30 cm, (2) measured the canopy closure using a spherical densitometer, and (3) recorded the presence or absence of understory, predominance of grass cover, lianas, and cattle activity. All vegetation samplings were made by the same observer at the same day of bird movement surveys. We performed a Principal Components Analysis (PCA) to transform all vegetation variables described above into principal components (PCs). The first three PCs corresponded to 33.17%, 15.82%, and 14.79% of the data variation (total of 63.77%). The forest cover and the landscape isolation explained less than 20% of the variation in the PCs values for forest and remnant trees habitat. Therefore, we considered vegetation structure as no correlated with forest cover and landscape isolation.

Bird community sampling

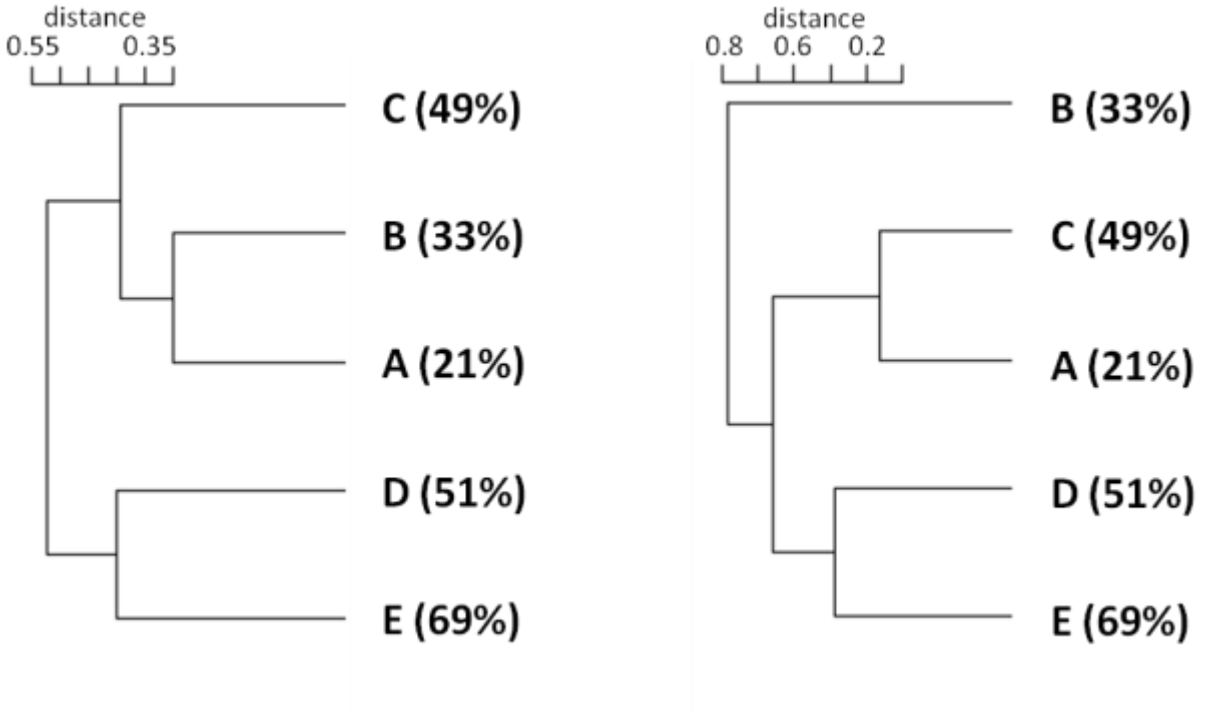
We sampled bird community in all studied landscapes by paired point counts (10 min, each one) within forests and pastures, both located 70-100 m away from the forest boundary. All birds seen or heard were recorded by one trained observed (FMB) for three different days along two bird breeding seasons (2014-2015) when they are usually more

detectable. We estimated the similarity between the bird communities of the five studied landscapes using the Morisita-Horn quantitative index, based on species relative abundances (Magurran 2004). We later performed a cluster analysis with the similarity results and the Ward method (Ward 1963). The analyses were made separately for recorded data from forest edges and pasture. The similarities between communities ranged from 0.30 to 0.49 when sampled in forest edges and from 0.37 to 0.78 when sampled in pasture. The cluster analysis grouped the bird communities according to the forest cover of the landscapes (Supporting Figure 1), which is an evidence of dependence between these two variables.

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Supporting Figure 1. Grouping of plots according to bird community similarity using data collected in forest edges (left) and in pasture (right). The letters A-E correspond to the plots and the values in parenthesis are the respective percentages of forest cover.

Supporting Table 1. Percentage of forest cover, mean isolation and number of species recorded with point count methods for each studied plot.

Plot	Forest Cover (%)	Mean Isolation (m)	N. Species in Forest Edge	N. Species in Pasture
A	21	34.8	41	40
B	33	20.9	35	16
C	49	34.4	43	36
D	51	17.7	43	26
E	69	32.7	60	21

MCMC sampling scheme

Prior distributions

The parameters for which prior distributions need to be defined are $\mathbf{z}$, $\mathbf{\Sigma}$, $\mathbf{V}$ and ρ, where $\mathbf{z}$ is the vectorized version of the $n_t \times n_c n_p$ matrix $\mathbf{Z}$ containing the ζ_{tcp} parameters.

- For the vector $\mathbf{z}$**,** we assumed the multivariate normal prior $\mathbf{z} \sim \mathrm{N}(\boldsymbol{\mu}_z, \mathbf{\Sigma}_z)$, where we set the mean $\boldsymbol{\mu}_z$ to a zero vector and the variance-covariance matrix $\mathbf{\Sigma}_z$ to an identity matrix.
- For $\mathbf{\Sigma}$ we assumed an Inverse-Wishart prior $\mathrm{W}^{-1}(\mathbf{\Psi}_{\mathbf{\Sigma}}, \nu_{\mathbf{\Sigma}})$, where we set the degrees of freedom parameter to the number of parameters ($\nu_{\mathbf{\Sigma}} = n_c n_p$) and the scale matrix $\mathbf{\Psi}_{\mathbf{\Sigma}}$ to the identity matrix.
- For $\mathbf{V}$ we assumed an Inverse-Wishart prior $\mathrm{W}^{-1}(\mathbf{\Psi}_{\mathbf{V}}, \nu_{\mathbf{V}})$, where we set the degrees of freedom parameter to the number of parameters ($\nu_{\mathbf{V}} = n_p$) and the scale matrix $\mathbf{\Psi}_{\mathbf{V}}$ to the identity matrix.
- For the phylogenetic signal parameter ρ, we assumed a discrete prior, which assigned the probability of 0.5 for $\rho = 0$ (corresponding to independence among species), and the remaining probability of 0.5 uniformly to the range (0,1], discretized to 100 values.

Posterior sampling by MCMC

To fit the model to the data, we developed a Markov chain Monte Carlo (MCMC) sampling scheme in which we updated each of the following parameters in turn: $\boldsymbol{\theta}$, $\widehat{\boldsymbol{\theta}}$, $\mathbf{z}$, $\mathbf{\Sigma}$, $\mathbf{V}$ and ρ.

- The species- and landscape specific parameters $\widehat{\boldsymbol{\theta}}$ were sampled using a Metropolis-Hastings step in which the proposal distribution was adapted during the burn-in to reach an optimal acceptance ratio.

- The parameter $\boldsymbol{\theta}$ was sampled directly from its full conditional which is $\boldsymbol{\theta}\sim\mathrm{N}(\boldsymbol{\mu}_{\boldsymbol{\theta}*}, \boldsymbol{\Sigma}_{\boldsymbol{\theta}*})$, where

$$\boldsymbol{\Sigma}_{\boldsymbol{\theta}*} = \left((\mathbf{W}\otimes\boldsymbol{\Sigma})^{-1} + \mathbf{B}^{\mathrm{T}}(\mathbf{V}\otimes\mathbf{I}_{n_l}\otimes\mathbf{I}_{n_s})^{-1}\mathbf{B}\right)^{-1},$$

$$\boldsymbol{\mu}_{\boldsymbol{\theta}*} = \boldsymbol{\Sigma}_{\boldsymbol{\theta}*}\left((\mathbf{W}\otimes\boldsymbol{\Sigma})^{-1}\mathbf{Q}\mathbf{z} + \mathbf{B}^{\mathrm{T}}\left(\mathbf{V}\otimes\mathbf{I}_{n_l}\otimes\mathbf{I}_{n_s}\right)^{-1}\widehat{\boldsymbol{\theta}}\right).$$

- The parameter ρ was sampled directly from its full conditional by using a discrete grid sampler, with pre-computed the determinants and inverses of the variance-covariance matrices $\mathbf{W} = [\rho\mathbf{C} + (1-\rho)\mathbf{I}]$ for all ρ values included in the discrete grid prior. To increase computational speed, in the beginning of the MCMC approach, we pre-computed the determinants and inverses of the variance-covariance matrices 1 for all values included in the discrete grid prior (see above).

- The parameter $\mathbf{z}$ was sampled directly from its full conditional which is $\mathbf{z}\sim\mathrm{N}(\boldsymbol{\mu}_{\mathrm{z}*}, \boldsymbol{\Sigma}_{z*})$, where

$$\boldsymbol{\Sigma}_{z*} = (\boldsymbol{\Sigma}_z^{-1} + \mathbf{Q}^{\mathrm{T}}(\mathbf{W}\otimes\boldsymbol{\Sigma})^{-1}\mathbf{Q})^{-1},$$

$$\boldsymbol{\mu}_{\mathrm{z}*} = \boldsymbol{\Sigma}_{z*}(\boldsymbol{\Sigma}_z^{-1}\boldsymbol{\mu}_{\mathrm{z}} + \mathbf{Q}^{\mathrm{T}}(\mathbf{W}\otimes\boldsymbol{\Sigma})^{-1}\boldsymbol{\theta}).$$

- The parameter $\boldsymbol{\Sigma}$ was sampled directly from its full conditional $W^{-1}(\boldsymbol{\Psi}_*, \nu_*)$, where

$$\nu_* = \nu_{\mathbf{\Sigma}} + n_s,$$

$$\mathbf{\Psi}_* = \mathbf{\Psi}_{\mathbf{\Sigma}} + \mathbf{A},$$

$$\mathbf{A} = \mathbf{E}^{\mathbf{T}}\mathbf{W}^{-1}\mathbf{E},$$

$$\boldsymbol{\theta} - \mathbf{Qz} = \mathrm{v}(\mathbf{E}^{\mathbf{T}}).$$

- The parameter **V** was sampled directly from its full conditional $W^{-1}(\mathbf{\Psi}_*, \nu_*)$, where

$$\nu_* = \nu_{\mathbf{V}} + n_l n_s,$$

$$\mathbf{\Psi}_* = \mathbf{\Psi}_{\mathbf{V}} + \mathbf{A},$$

$$\mathbf{A} = \mathbf{E}^{\mathbf{T}}(\mathbf{I}_{n_l} \otimes \mathbf{I}_{n_s})^{-1}\mathbf{E},$$

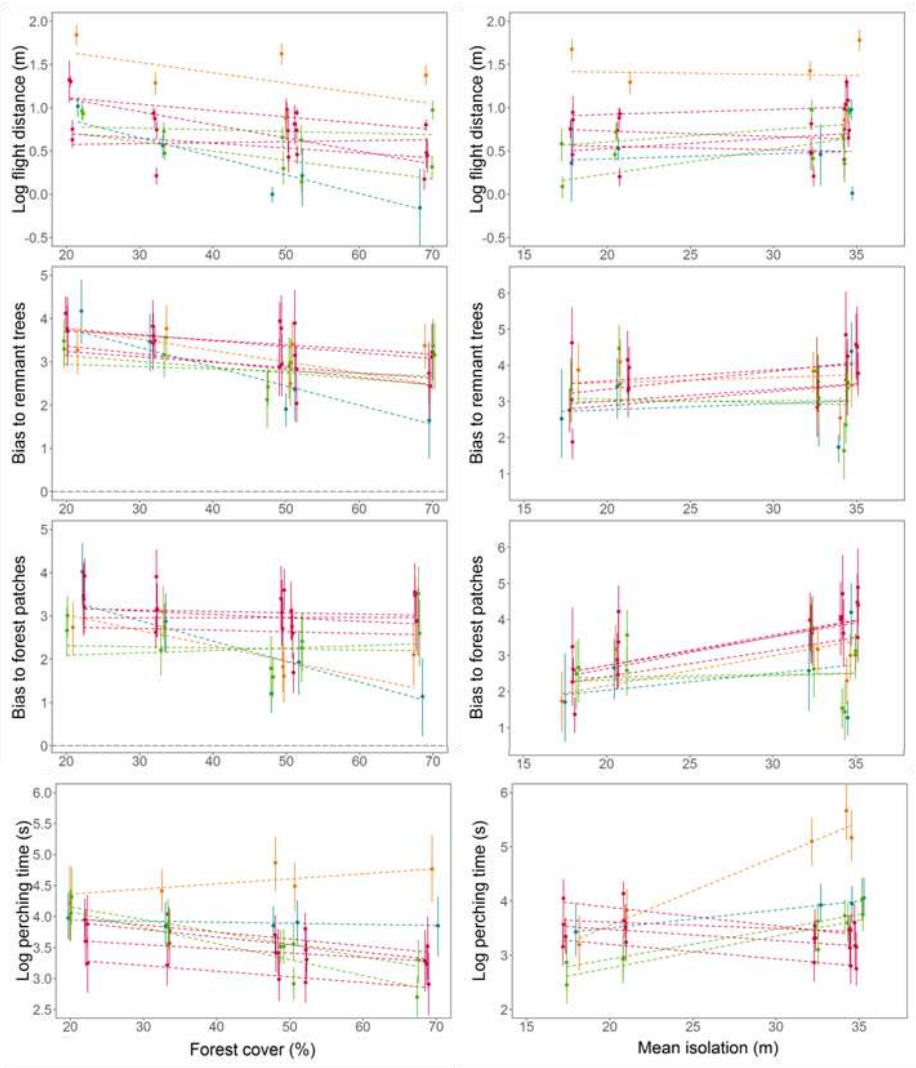
$$\widehat{\boldsymbol{\theta}} - \mathbf{B}\boldsymbol{\theta} = \mathrm{v}(\mathbf{E}).$$

We ran a total of 10,000 iterations, with a 2,000 burn-in period and thinning interval of 10, for each of the four models: (1) one model to estimate the spatial components of the movement as function of forest cover; (2) one model to estimate the spatial components of the movement as function of mean isolation; (3) one model to estimate the temporal components of the movement as function of forest cover; (4) one model to estimate the temporal components of the movement as function of isolation. We ran three chains for each model and checked the convergence of the posteriors using the Gelman-Rubin convergence statistic (Gelman and Rubin, 1992), with the package CODA (Plummer et al., 2006). The convergence results and the posterior values can be found at the Github repository https://github.com/LEEClab/MultipleLandscapes_JSMM .

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Supporting Figure 3. Effect of forest cover and mean isolation on the landscape- and specific-parameters of the eight most abundant species. The colors represent birds diets: red are frugivores (*Tangara sayaca*, *Dacnis cayana*, *Tangara cayana*, and*Tachyphonus coronatus*), blue is insectivore (*Empidonomus varius*), green are omnivores (*Turdus leucomelas*, and *Turdus rufiventris*), and orange is gramnivore (*Patagioenas picazuro*). The dots represent the mean posterior values for each species at each study plot, and the bars are the 25% and the 75% quantiles. The dashed lines show the posterior mean prediction of expected movement parameters based on landscapes covariates and species traits.

Supporting Table 2. Observed forest birds, their respective traits (diet class and body size), and number of recorded flight distances and perching times by studied plot. The species are ordered by increasing body mass.

Scientific Name	Diet Class	Body Mass (g)	N. Observed Flights/Plot						N. Observed Perching Times/Plot					
			A	B	C	D	E	TOTAL	A	B	C	D	E	TOTAL
Serpophaga subcristata	Insectivore	6.6	0	0	1	0	0	1	0	1	2	1	0	4
Parula pitiayumi	Insectivore	6.8	0	0	0	19	0	19	0	0	0	13	0	13
Camptostoma obsoletum	Insectivore	8.1	7	3	29	12	9	60	5	2	17	9	10	43
Conirostrum speciosum	Insectivore	8.8	19	5	5	13	8	50	10	4	9	10	16	49
Myiophobus fasciatus	Insectivore	9.9	0	0	0	0	19	19	4	0	0	1	14	19
Coereba flaveola	Frugivore	10.0	3	0	0	0	1	4	3	0	0	0	2	5
Sporophila caerulescens	Granivore	10.9	0	0	0	0	0	0	3	0	0	1	2	6
Euphonia chlorotica	Frugivore	11.0	0	5	0	1	0	6	0	2	0	1	0	3
Lathrotriccus euleri	Insectivore	11.3	1	0	0	0	0	1	1	0	0	0	0	1
Dacnis cayana	Frugivore	13.0	39	27	9	25	13	113	26	26	17	39	16	124
Basileuterus flaveolus	Insectivore	13.2	0	1	0	0	0	1	0	1	0	0	0	1
Cnemotriccus fuscatus	Insectivore	13.6	0	1	0	0	0	1	0	2	0	0	0	2
Euphonia cyanocephala	Frugivore	14.0	0	3	0	0	1	4	0	3	0	0	2	5
Euphonia pectoralis	Frugivore	14.4	0	0	0	3	0	3	0	0	0	2	0	2
Euphonia violacea	Frugivore	15.0	0	1	0	0	0	1	0	1	0	0	1	2
Basileuterus leucoblepharus	Insectivore	15.1	1	0	0	0	0	1	1	0	0	0	0	1
Nemosia pileata	Insectivore	16.0	5	12	7	8	1	33	2	10	3	13	1	29
Vireo chivi	Insectivore	16.1	0	5	7	0	0	12	1	4	4	1	0	10
Tangara cyanoventris	Frugivore	16.5	0	0	0	0	3	3	0	0	0	0	2	2
Tangara cayana	Frugivore	18.0	3	37	1	36	28	105	4	22	5	36	29	96
Colonia colonus	Insectivore	18.3	0	0	0	0	0	0	0	1	0	0	0	1
Legatus leucophaius	Insectivore	22.2	3	0	0	0	0	3	2	0	0	0	0	2

Conopias trivirgatus	Insectivore	24.4	6	0	0	0	0	6	5	0	2	0	0	7
Elaenia flavogaster	Frugivore	24.8	5	0	9	0	5	19	3	1	9	3	7	23
Myiarchus swainsoni	Insectivore	25.1	1	0	0	0	0	1	1	0	0	4	0	5
Empidonomus varius	Insectivore	27.1	33	19	43	0	0	95	23	16	39	0	0	78
Myiarchus ferox	Insectivore	27.5	1	1	11	3	6	22	2	3	9	4	6	24
Myiozetetes similis	Insectivore	28.0	11	1	0	0	0	12	10	0	0	3	0	13
Cyclarhis gujanensis	Insectivore	28.8	3	12	9	0	2	26	5	10	6	2	11	34
Tersina viridis	Frugivore	29.0	25	5	16	7	2	55	25	6	14	21	6	72
Tachyphonus coronatus	Frugivore	29.3	45	34	1	2	10	92	37	23	3	5	27	95
Lepidocolaptes angustirostris	Insectivore	29.6	0	0	0	0	0	0	0	0	2	0	0	2
Forpus xanthopterygius	Granivore	31.0	0	3	0	0	0	3	0	4	0	0	0	4
Schistochlamys ruficapillus	Frugivore	31.2	5	0	0	0	1	6	3	0	0	0	6	9
Tyrannus savana	Insectivore	31.9	7	0	0	0	8	15	3	0	0	1	6	10
Tangara sayaca	Frugivore	32.5	149	109	77	213	114	662	129	99	80	200	125	633
Myiarchus tyrannulus	Insectivore	35.5	0	0	0	0	0	0	0	0	1	0	0	1
Tyrannus melancholicus	Insectivore	37.4	31	7	13	1	0	52	21	3	15	5	3	47
Piranga flava	Frugivore	37.7	0	0	0	0	5	5	0	0	0	0	3	3
Tangara palmarum	Frugivore	39.0	0	0	0	3	0	3	0	0	0	5	0	5
Pachyramphus validus	Insectivore	43.0	3	6	3	0	23	35	5	4	3	0	26	38
Myiodynastes maculatus	Insectivore	43.2	21	11	10	7	3	52	16	10	7	15	7	55
Saltator similis	Omnivore	43.3	1	1	0	0	7	9	3	1	0	0	8	12
Columbina talpacoti	Granivore	46.0	0	5	0	0	0	5	2	4	3	0	0	9
Xolmis velatus	Insectivore	49.1	1	9	0	0	6	16	1	4	0	0	12	17
Turdus amaurochalinus	Omnivore	57.9	0	5	25	9	18	57	1	3	16	11	21	52
Brotogeris chiriri	Granivore	61.6	0	5	0	0	0	5	0	4	0	0	0	4
Pitangus sulphuratus	Omnivore	62.9	25	7	7	7	1	47	18	3	9	7	2	39
Mimus saturninus	Insectivore	63.7	0	1	1	0	13	15	0	2	3	1	9	15
Turdus leucomelas	Omnivore	69.1	80	65	9	24	25	203	59	41	9	43	28	180

Turdus rufiventris	Omnivore	69.4	46	35	19	12	30	142	30	29	20	11	24	114
Megarynchus pitangua	Insectivore	69.9	3	15	5	10	0	33	5	12	4	11	0	32
Piaya cayana	Insectivore	102.0	13	13	0	0	0	26	7	9	0	3	0	19
Zenaida auriculata	Granivore	110.2	0	0	1	0	1	2	0	1	2	1	3	7
Colaptes melanochloros	Insectivore	127.3	1	1	1	0	0	3	1	0	1	0	0	2
Celeus flavescens	Insectivore	139.0	0	0	0	0	0	0	1	0	0	0	0	1
Leptotila verreauxi	Granivore	146.9	0	0	0	0	0	0	1	0	0	0	0	1
Cyanocorax cristatellus	Omnivore	178.0	9	5	3	0	3	20	4	8	6	7	3	28
Dryocopus lineatus	Insectivore	183.2	0	1	0	0	0	1	0	1	0	1	0	2
Patagioenas cayennensis	Granivore	229.0	3	0	1	9	1	14	8	1	1	7	6	23
Campephilus melanoleucos	Insectivore	256.0	0	0	0	0	0	0	0	0	0	0	1	1
Patagioenas picazuro	Granivore	279.0	34	20	36	33	42	165	41	33	40	31	63	208
Ramphastos dicolorus	Frugivore	331.0	0	0	0	0	0	0	0	0	0	1	0	1
Pyroderus scutatus	Frugivore	357.0	0	0	0	0	0	0	0	0	0	0	1	1
Ramphastos toco	Frugivore	618.0	0	0	0	0	0	0	0	1	0	0	0	1

CAPÍTULO 3

Effects of bird movement on simulated seed dispersal patterns in degraded areas

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Abstract

Predicting seed dispersal patterns is crucial for the management of degraded landscapes and to define conservation strategies, particularly in areas originally covered by forests. Here, we disentangle the effects of fruit availability, bird abundance, and matrix structure on seed rain density and seed dispersal distance into the open matrix of landscapes. Using observed movement data from three common seed-dispersing birds and gut passage times, we fitted a mechanistic model to simulate seed dispersal in virtual landscapes. We show that seed dispersal to pasture cells was negligible beyond 200 m from forest edge, while perches concentrated a high density of seed rain. The presence of perches also increased more than two times the average seed dispersal distance from forest edge into matrix. Abundance of birds was the main factor influencing seed density in landscape matrix. Although many studies advocate on the importance of habitat amount, our study highlights that stepping-stones also play an important role within matrix, promoting connectivity and maintaining the resilience, which increases the chance of landscape natural regeneration.

Introduction

Seed dispersal has direct impacts on biodiversity, since it constitutes the template for subsequent recruitment and ecological processes that influence population and community structure (Nathan and Muller-Landau 2000). By carrying seeds, dispersal agents promote gene flow between populations, improve genetic structure, and enable species persistence (Jeltsch et al. 2013). Seed dispersal also makes possible the colonization of degraded areas by native species, accelerating plant regeneration and providing a free help to restoration activities (Holl and Aide 2011). Therefore, in the actual context of increasing habitat loss and fragmentation, it is critical to enhance plant species flow by the management of seed dispersal.

Researchers have long tried to predict seed dispersal into vacant sites and between habitat patches (Duncan and Chapman 1999, Bertoncini and Rodrigues 2008, Pizo and dos Santos 2011). This has been a hard task, since numerous factors can act at different spatial scales to shape seed dispersal spatial patterns. Examples of such factors are seed availability, the morphological traits and behavior of seed dispersers, and the availability of adequate microsites for seed deposition (Nathan and Muller-Landau 2000, Morales et al. 2013). Carlo and Morales (2016), for example, did not find a clear correlation between local fruit availability and the number of dispersed seeds. They also observed an abundant bird-generated seed rain under perches within pasture. In field studies, it is not possible to control all factors to properly disentangle their effects on seed dispersal. Furthermore, most previous works fitted phenomenological models to seed density data (e.g. Bertoncini & Rodrigues 2008; Cubiña & Aide 2001). This approach does not evaluate the elements that directly produce seed dispersal patterns, i.e. the characteristics of plants and their dispersal agents (Nathan and Muller-Landau

2000), and does not produce results that can be used for generalizations to other systems.

There is a need to resolve these uncertainties and knowledge gaps to predict vegetation changes in degraded landscapes. Advances in movement ecology research (Nathan et al. 2008) enabled new insight into seed dispersal spatial patterns. Mechanistic models now combine movement of dispersal agents with the gut-passage time of seeds, enabling us to test hypothesis defined a priori about seed dispersal spatial patterns (Nathan and Muller-Landau 2000, Morales et al. 2013). Here, we simulate seed rain in virtual landscapes, with the aim of disentangling the effects of forest patch features—fruit availability and bird abundance—and matrix structure on seed arrival density and seed dispersal distance in degraded areas. For this, we simulated the movement of the three most abundant seed-dispersing birds in Atlantic Forest biome, using field collected movement data. We hypothesized that seed density and seed dispersal distance would be positively correlated with the presence of perches, fruit availability and bird abundance in the virtual landscape. Ours results can potentially be used for identification of priority areas for conservation and reduce costs of forest restoration.

Material and methods

Bird species and study system

We chose as a basis for the simulations a common situation of the Atlantic Forest biome in São Paulo State (Brazil): landscapes with patches of semi-deciduous forest mostly immersed in a matrix of cattle pasture containing remnant trees, with around 10% of forest cover (Ribeiro et al. 2009). Fleshy-fruited, small-seeded trees, mainly

Casearia sylvestris, *Erythroxylum deciduum*, and *Myrsine* spp. are very common in this type of environment (Pizo and dos Santos 2011).

We used field data of three taxonomic groups of birds to parameterize seed dispersal simulations: sayaca tanagers (*Tangara sayaca*), thrushes (*Turdus leucomelas*, *T. rufiventris*, and *T. amaurochalinus*), and pigeons (*Patagioenas picazuro*, and *P. cayenensis*). They are among the most common birds, and the main seed dispersers in highly fragmented landscapes in the Atlantic Forest (Pizo 2007, Pizo and dos Santos 2011). Although these birds are habitat generalists, their morphology, feeding habit and behavior differ. Sayaca tanagers are small (32.5 g) canopy birds, and roughly half of their diet consists of fruits (Wilman et al. 2014).Thrushes are ground and understory-dwelling birds and may depend more on forests than sayaca tanagers (Silva 1995). Their average weight is 69.1 g and 30% to 60% of their diet is composed of fruits (Wilman et al. 2014). Of the studied birds, pigeons are the largest in the region (254 g) and the most common in open areas (Silva 1995, Wilman et al. 2014).Though pigeons are regarded as seed-eating birds, up to 70% of their diet can be composed of fruits, whose seeds may be found intact in feces (Wilman et al. 2014; see Supporting Information). Both the diet and habitat use of generalist bird species have been identified as critical for seed dispersal and early plant regeneration in degraded areas (Pizo and dos Santos 2011, Carlo and Morales 2016).

Simulated landscapes

We built a 1200 m x 1200 m square virtual landscape divided into 3600 equal-sized cells of 20 m x 20 m (Fig. 1). The center of the landscape was occupied by a squared forest patch of 400 m x 400 m. The surrounding matrix of virtual landscapes

represented open productive vegetation, from now on referred as pasture. Some of the 20 m x 20 m cells in the matrix were assigned as perches, which represent remnant trees in pasture (Fig. 1). We assigned to each cell the value of the total area of the arboreal vegetation it contained: 16 ha for cells in the forest patch, 0.04 ha for cells with perches, and zero for cells with pasture.

Movement model

We used a spatially explicit, event-driven, stochastic mechanistic model developed by Morales & Carlo (2006) and adapted by Morales et al. (2013). The model simulated birds' foraging activity and kept track of their defecation events. Bird movements started in a random cell i within the forest patch, and were the result of a spatial component – sequence of grid cells and the flight distances between consecutive cells – and a temporal component – cumulative sum of the sequence of perching intervals and flight intervals. We considered as positions the centroids of the grid cells. Once perching time expired, the individual decided where to move—within the same cell i or to another cell j—until it completed 90 hours of movement. We assumed that two factors affected the individual's choice to move to a particular cell: the distance from its current location and the total area of the perch or the forest patch (Morales et al. 2013). For matrix cells, we considered only the effect of distance from forest cells (Eq. 3).To calculate the probability of moving to the j-th cell, we first computed the effects of the Euclidean distance from the current location ($\delta_{ij,}$, the flight distance), and the total area of the destination patch or perch ($area_j$) as

$$d_{ji} = 1 - \tanh\left(\left(\delta_{ij}/a_d\right)^{b_d}\right) \qquad \text{(Eq. 1)}$$

$$ar_{ji} = \tanh(area_j / a_{ar}). \quad \text{(Eq. 2)}$$

Each equation calculates a vector of relative probabilities of length 3600 (one value for each landscape cell). The coefficients a_d and a_{ar} are scale parameters, and b_d is a shape parameter of the sigmoid function $\tanh(x)$.

If j-th cell is matrix,

$$k_{ji} = d_{ji}. \quad \text{(Eq. 3)}$$

If j-th cell is forest or perch and has a positive area value,

$$k_{ji} = d_{ji} ar_{ji} . \quad \text{(Eq. 4)}$$

The resultant vector k is standardized into a vector $p_{ji}$of probabilities for each cell in the landscape:

$$p_{ji} = \frac{k_{ji}}{\sum(k_{ji})} . \quad \text{(Eq. 5)}$$

Once a bird was perched, it could decide to eat or not one seed if the current location had fruits. We limited bird consumption to only one seed because our aim in this study was to understand the effects of forest patch features and matrix structure on seed dispersal patterns, rather than simulate a realistic seed rain. When gut passage time expired after a series of steps, one defecation event occurred and the corresponding cell was recorded.

Bird data

To parameterize the model, we collected bird movement data in field surveys during two breeding seasons (October 2014 to January 2015; September to December 2015). Data were collected in a landscape of 20% forest cover in the Atlantic Forest

biome where forest patches were in a matrix of pasture with remnant trees and live fences. We distributed vantage points in hilltops within the landscape from which we could track the movement of birds, with the help of binoculars and a printed high resolution map of the landscape (Sup. Fig. 1; see methods details in Supporting Information). For each observed track, we recorded the perching time, the sequence of used perches, and the flight time. To estimate parameters from observed movement data, we first used equations 1-5 to build likelihood functions (Sup. Table 2, Sup. Fig. 2). For each species we then fitted the functions to the observed tracks using a Markov chain Monte Carlo (MCMC) sampling scheme with 2000 iterations. We used for this calculation the observed tracks, replacing δ_{ij} and $area_j$ by the observed values of flight distance (Euclidean distance between consecutive perches) and total area of the destination patch or perch, respectively. The Gelman-Rubin convergence statistic (Gelman and Rubin 1992) was approximately equal to 1 for all models, indicating posteriors convergence. At each track simulation, we sorted the movement parameters from the joint posterior distributions (last 1,000 iterations of the MCMC sampling scheme), to add variability to the data.

The residence time was sorted from a gamma distribution fitted to the observed perching time for each bird species (Sup. Fig. 2). We used the average flight speeds observed in the field for each species: sayaca tanagers flew at a constant speed of 640 m/s, thrushes at 779 m/s, and pigeons at 453 m/s for pigeon (see Supporting Information for speed calculation methods).

The probability of eating fruits was independent from the residence time. It was obtained from the percentage of times each bird species was seen foraging in a pool of instantaneous field observations of the bird species activities (M. A. Pizo, unpublished

data). Every time the observers found a bird during walks through the study area, they recorded its activity (for example calling, foraging, moving, resting). If foraging, they recorded the food item (as arthropod, fruit, nectar). Only one record was made for each bird, after which they resume walking. Observations were made throughout the year. Gut passage times were sorted from gamma distributions, which were fitted for the studied bird groups (Sup. Fig. 2) using time data collected during feeding trials of captive birds with seeds of common fleshy-fruited plants (methods described in Supporting Information).

Bird species were represented in the simulated community according to their relative abundance, as recorded by F. M. Barros (see Supporting Information of Chapter 1) at the same real landscape where bird movements were monitored. For this, bird species were sampled by point counts in forest habitat and in pasture close to forest patches.

Experimental design

To understand the effect of landscape on seed rain patterns, we used a factorial design that combined various proportions of fruit and perch availability within matrix: 50%, 67% and 90% probability of the presence of fruit in forest cells; and 0, 10, and 100 matrix cells with the presence of perches. For each combination, we also varied the number of simulated seed-disperser birds: 10, 20 or 40 individuals. We had a total of 27 combinations of factors, and ran 30 replicates for each one.

The proportions of fruit availability were determined after a phenological survey in the real Atlantic Forest landscape at the same time of movement data collection. We

recorded the availability of fruits within grid cells in different types of habitats, and the probability of fruit presence, which ranged from 50% to almost 100% for habitats as forest hedges on humid areas.

Data analysis

We analyzed simulated seed arrival in the matrix up to 400 m from the forest edge, composing a homogeneous buffer around the forest patch. For pasture cells, we used a three-way ANOVA model with fixed effects, and we calculated eta-squared values as a measure of the effect size of factors on average seed distances from forest edge and average seed density. For perch cells, we used a similar analysis, but with two factors—fruit availability and number of birds—for each landscape with perches.

Results

The averages and variances of seed dispersal distance and density for the different factors combinations stabilized through simulations repetitions (Sup. Fig. 3 and 4). Seed dispersal decreased quickly with increasing distance from forest edge in all simulations, except seed rain under perches (Fig. 2). Average seed dispersal distance under perches was almost three times higher than in pasture cells for the landscape with 10 perches, and two times higher for the landscape with 100 perches (Figs. 3 and 4). Seed arrival at perches for simulations with 100 perches was almost uniform with increasing distance from forest edge, suggesting a higher probability of long-distance dispersal events; meanwhile, the probability of seed dispersal to pasture cells was negligible at distances greater than 200 m from forest edge. Seed dispersal kernel for

perch cells was less leptokurtic than for pasture cells (Fig. 2). Therefore, finding seeds within the matrix depended more on the presence of perches at distances greater than 150 m from forest edge. For simulations with 10 perches, for example, the number of seeds per cell at 150 m from forest edge could vary by a factor of 50 or more. In contrast, the number of seeds per cell at distances shorter than 100 m from forest edges was reduced by the increasing number of perches within matrix (Fig. 2). For the simulations with the highest amount of fruits and birds, for example, the mean seed density in pasture was 142, 130, and 86 seeds x $cell^{-1}$ for the simulations with 0, 10, and 100 perches, respectively. For perch cells the difference was even higher, 875 and 340 seeds x $cell^{-1}$ for the simulations with 10 and 100 perches, respectively.

Average dispersal distance in pasture cells was strongly affected by the number of perches within the matrix (Fig. 3). As indicated by the variation partition of factorial ANOVA, 82.2% (ss = 0.279; F =1903.0) of average dispersal distance increase was explained by the number of perches. In contrast, less than 1% of variation occurred due to changes in fruit availability or bird abundance. Only 7.6% to 36.6% of cells with pasture (for combinations with 10 birds and 40 birds, respectively) received seeds. Most of the pasture cells received no seeds and average seed density was zero for all simulations.

The probability of birds to use the matrix was higher in the landscape with 100 perches, and the flight distances were smaller, due to the higher proximity between perches and between them and the central patch. At the same time, the movement bias towards perches was more evenly distributed between the cells, and the probability of using each particular perch was smaller. Consequently, average seed dispersal distance and average seed density under perches were lower in simulations for landscapes with

100 perches, when compared to landscapes with 10 perches (Fig. 4). Higher fruit availability and bird abundance caused an increase in average seed density under perches. Bird abundance had a stronger effect on average seed density than fruit availability, and explained 67.5% (ss = 46.438; F = 462.9) of variability in landscapes with 10 perches, and 75.4% (ss = 8.199; F = 1476.4) in landscapes with 100 perches. Fruit availability explained 9.7% (ss = 6.664; F = 66.4) of variability in landscapes with 10 perches, and 13.4% (ss = 1.458; F = 262.6) in landscapes with 100 perches. There were no relevant effects of fruit availability and bird abundance on average seed dispersal distances in perch cells.

Discussion

Movement ecology has grown in importance for conservation projects due to the recognition of the key influence of organisms movement on biodiversity maintenance and structure, and the recent advances in collection and analysis of movement data (Nathan et al. 2008, Morales et al. 2010, Jeltsch et al. 2013). Predicting seed dispersal, for instance, is crucial for improving landscape planning and identification of priority areas for conservation and low-cost forest restoration (García et al. 2010, Holl and Aide 2011, Niebuhr et al. in prep.). However, the best way to predict seed dispersal by animals is to integrate plant and disperser characteristics, including movement behavior, into mechanistic models (Nathan and Muller-Landau 2000). Here, we used observed movement data and gut passage time to simulate seed dispersal in virtual landscapes. We showed that seed dispersal kernels within the matrix are closely connected to the movement of birds and matrix structure. Other features related to habitat, such as fruit availability and bird abundance, can potentially increase the number of seeds dispersed into the matrix.

The number of perches in the matrix was the only factor affecting seed dispersal distance from the forest edge. Other studies have suggested that a matrix with perches—isolated trees and live fences—can facilitate the movements of frugivorous birds, enhancing the frequency of long-distance seed dispersal events (Herrera and García 2009, Pizo and dos Santos 2011, Sasal and Morales 2013). In the present study, the presence of perches also increased dispersal distances in their vicinity, due to bird movement biased toward arboreal structures. Despite often using open areas, birds usually prefer resting on perches rather than on the ground (Carrière et al. 2002, Pizo and dos Santos 2011). When perches are present, bird activity in the matrix increases and, consequently, seed dispersal kernels have fatter tails.

Besides increased seed dispersal distance, seed density in cells with perches was higher than in pasture cells. Indeed, directed seed dispersal to remnant trees and isolated perches in open areas has been described in various studies (Duncan and Chapman 1999, Galindo-González et al. 2000, Bertoncini and Rodrigues 2008, Herrera and García 2009).However, it is noteworthy that seed density decayed faster in pasture with increasing distance from forest edge, in sharp contrast to situation under perches. Seed density in pasture cells at distances larger than 200 m was minimal, while average seed dispersal distances for cells with perches were between 200 m and 250 m, and perch cells received almost 50 times more seeds than pasture cells beyond 150 m from forest edge. Previous empirical works reported similar patterns in open areas (Cubiña and Aide 2001, Bertoncini and Rodrigues 2008). Bertoncini and Rodrigues (2008) rarely found animal-dispersed seeds in an abandoned pasture located more than 50 m from a forest patch, and a sharp reduction of plant regeneration capacity beyond 200 m.

Most of the studies that relate seed dispersal to degraded areas and distance from forest edges considered variables associated with seed sources and the community of seed dispersers (Chazdon 2003). However, our results revealed that fruit availability has minor effects on seed dispersal patterns in deforested landscapes. Many studies have reported that fleshy-fruited plants attract birds (Calviño-Cancela, 2002; Morales et al., 2013; Pizo and dos Santos, 2011); however, we did not include bird movement bias toward fleshy-fruited plants in our simulation model. Additionally, we did not consider that birds have spatial memory and may prefer using predictable food sources (Westcott and Graham 2000). These factors could further reduce the importance of fruit availability for seed dispersal patterns in nature; nevertheless, the present study did not account for fruit diversity. Plant or disperser communities with high species richness may promote richer seed rain and a faster regeneration of degraded areas (García and Martínez 2012).

Our results have several implications for biodiversity conservation and policy. First, we emphasize the need for environmental laws to stimulate the use of wildlife-friendly practices, as pointed out by other researchers (e.g. Athayde et al., 2015; Chazdon, 2003; Chazdon et al., 2009). The presence of arboreal elements in the matrix by itself, such as remnant trees, live fences, and riparian corridors, increases the functional and phylogenetic diversity in agricultural landscapes (Athayde et al. 2015). The use of these perches by the fauna can potentially increase seed dispersal distance from forest patches, and, consequently, ameliorate the connectivity and resilience of populations. Our results can also help to improve restoration projects, to which it is fundamental to predict forest regeneration capacity and landscape regenerability (*sensu* Niebuhr et al. in prep.). After disturbance, degraded areas usually have no sources of

regeneration, such as soil seed bank and resprouting, and offer few incentives for the visit of frugivores (Duncan and Chapman 1999, Chazdon 2003). As we showed in this study, remnant trees can enhance seed dispersal from forest patches to matrix and could be a low-cost help for forest restoration actions. Our results also point out, however, a negative effect of perches for seed density close to forest edges. Therefore, it is important to consider the aim of the restoration project to determine the role of matrix perches. If, for example, increasing patch sizes by natural regeneration is one important goal, managers should avoid high density of remnant trees. These contradictory roles of perches within matrix should be further investigated.

Successful conservation and landscape regeneration of highly degraded forests, such as the Atlantic Forest (Ribeiro et al. 2009, Tambosi et al. 2014, Niebuhr et al. in prep.), is contingent upon a holistic view of ecosystems, which should include anthropic land use. We showed that matrix characteristics are the main factors shaping bird movement and seed dispersal patterns, though fruit availability and bird abundance may have positive effects on seed species diversity. We suggest that similar studies involving simulated data, complex landscapes, and empirical data are needed to improve our understanding of the roles of matrix and remnant vegetation in landscape connectivity, seed rain, and landscape regenerability of degraded areas.

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Figures

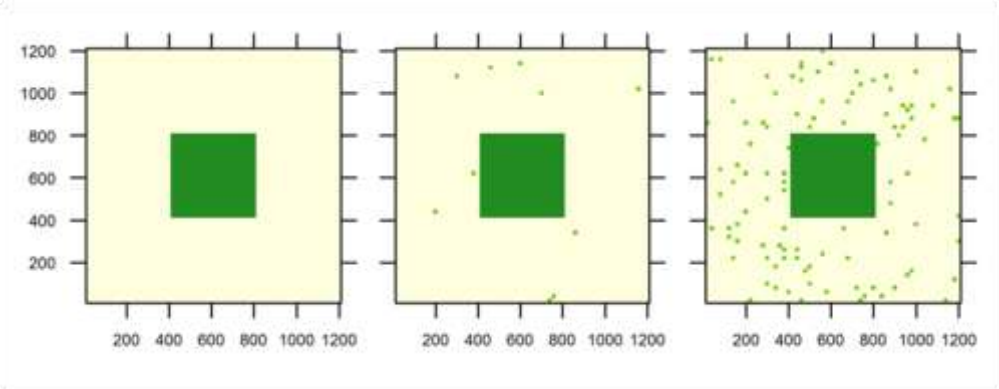


Figure 1. Virtual landscapes built for movement simulations with no perches (left), 10 perches (center), and 100 perches (right). Each landscape is 1200 m x x1200 m and has a central forest patch of 400 m x 400 m (dark green central square). Perches (light green squares) are randomly positioned within pasture (yellow).

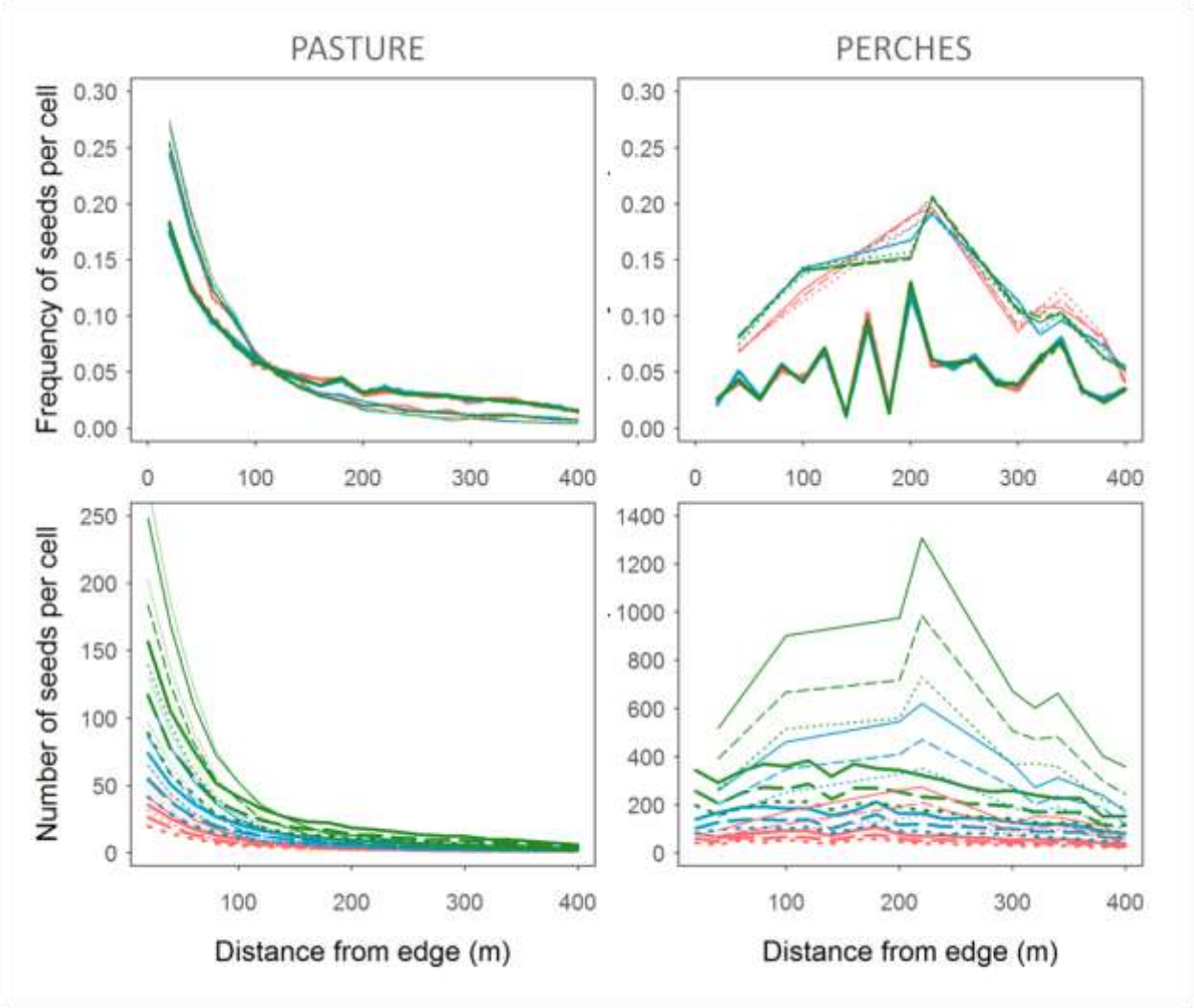


Figure 2. Observed mean frequencies of seeds moving to increasing distances from forest edge, and observed number of seeds per cell for pasture (left column) and perches (right column). Red, blue and green lines represent simulations with 10, 20 and 40 birds, respectively. Solid, dashed and dotted lines represent 90%, 67% and 50% probability of presence of fruits in forest cells, respectively. Thin, medium width and thick lines represent simulations for the landscape with 0, 10 perches and 100 perches, respectively.

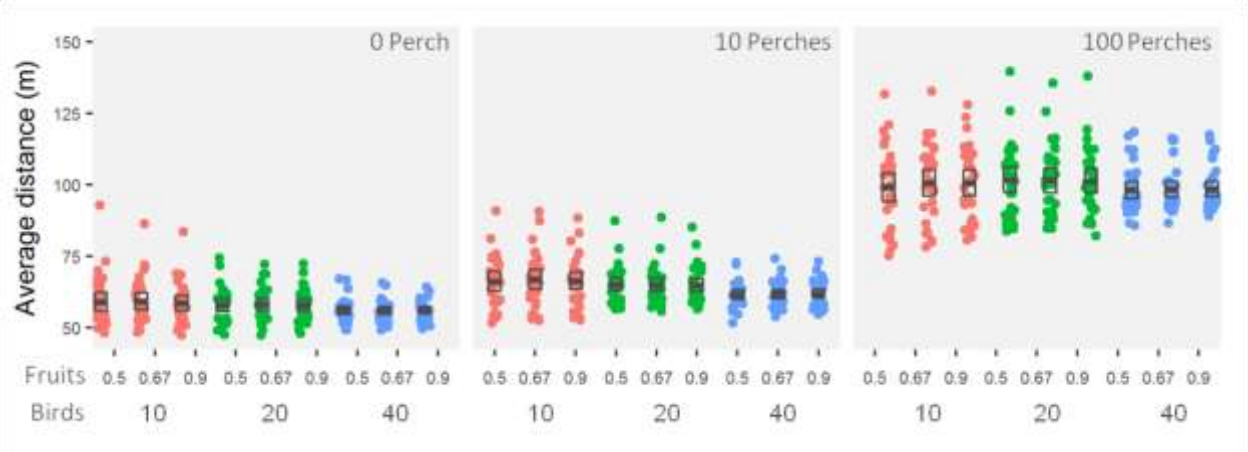


Figure 3. Average dispersal distance from forest edge in pasture cells. Points represent average values for each of the 30 simulation replicates. Boxes show the averages and 95% confidence interval limits for each combination of factors, calculated with nonparametric bootstrap. Average seed density in pasture cells was zero for all simulations and is not shown. Red, green and blue lines represent simulations with 10, 20 and 40 birds, respectively.

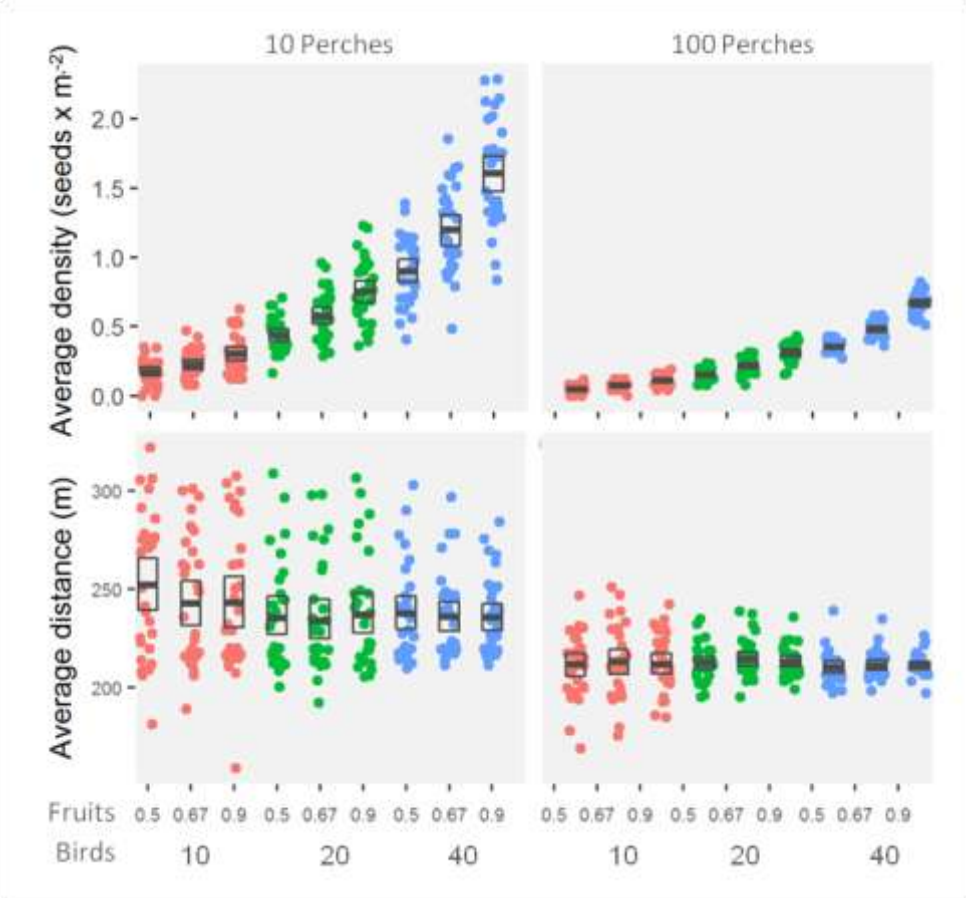


Figure 4. Average dispersal distance from forest edge and average seed density in cells with perches. Points represent average values for each of the 30 simulation replicates. Boxes show the averages and 95% confidence interval limits for each combination of factors, calculated with nonparametric bootstrap. Red, green and blue lines represent simulations with 10, 20 and 40 birds, respectively.

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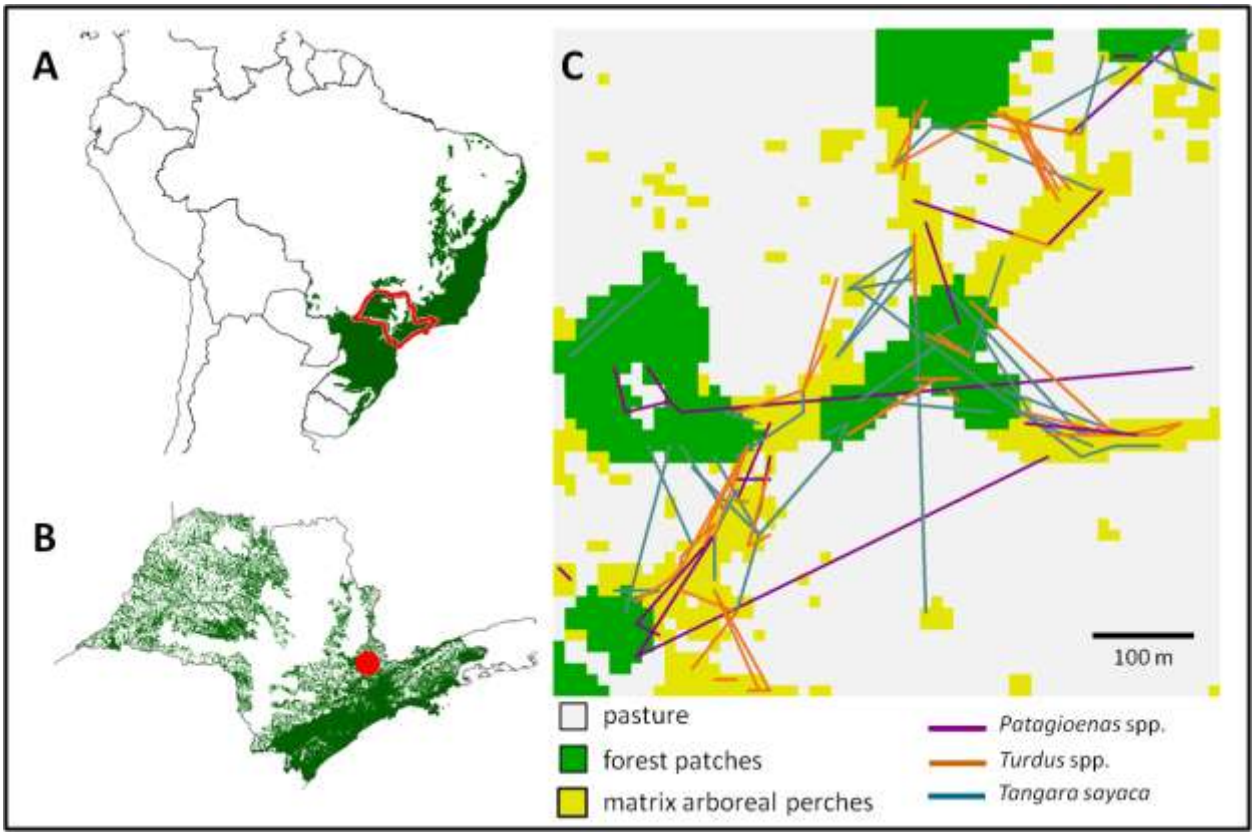
Supporting Information

Field movement observations

Data was collected in a 600 m x 600 m landscape regularly divided into 10 m x 10 m cells (total of 3600 cells) (Sup. Fig. 1). The landscape was a mosaic of forest patches, live fences, small groups of trees and remnant trees within cattle pasture. To sample bird movements, we adapted the methods described by Morales et al. (2013). We distributed vantage points in hilltops within the landscape from which we could track bird movement with the help of binoculars and a printed high resolution map of the landscape. We sampled birds from each vantage point during four and a half consecutive hours, for one morning (from 6:00 a.m. to 10:30 a.m.). We did not sampled birds on windy or rainy days, to control for climate variation. Once a bird was located, we recorded the species, the sequence of grid cells used for perching, and the perch and flight time intervals, until the bird was lost from sight. The perching time (in seconds) was the time lapse between two consecutive flights, while the bird used close branches of a perch. We calculated the flight distance of each step as the Euclidean distance between the used grid cells' centroids. The division of the flight distances by the flight time interval resulted in flight speeds for each step. We then calculated the average flight speed for each bird species.

We did not identified bird individuals. However, we assume that we sampled data from several individuals because: (1) we sampled in a large temporal scale (during two wet seasons); (2) we looked for hints to identify the individuals and to avoid sampling them several times, *e.g.* size of the flocks, perches used, behavior; (3) the species observed have a large home range, and likely did not limit their activities to our field of

view. We sampled 85, 79 and 32 steps for *T. sayaca*, *Turdus* spp. and *Patagioenas* spp., respectively, in 72 observation hours (Sup. Fig. 1C).



Supporting Figure 1. Movement tracks of the studied bird species observed in the study landscape. A: Brazil, São Paulo State (red) and the Brazilian portion of the Atlantic Forest bioma (green). B: São Paulo State, remnant patches of the Atlantic Forest (green), and location of the study landscape (red dot). C: Study landscape and observed movement tracks of the three groups of studied birds.

Gut-passage time experiments

To assess gut-passage time, we used captive individuals of the studied bird species: 5 *Tangara sayaca*, 4 *Patagioenas picazuro*, and 2 *Turdus leucomelas*. The birds were kept in individual 50 cm x 50 cm x 50 cm cages, where they had access to water and food *ad libitum*, including fruits and commercial food. During feeding trials, birds were kept without food for at least four hours and then fed with a mixture of banana and seeds, for *T. sayaca* and *T. leucomelas*, or commercial food and seeds, for *P. picazuro*, for 10 minutes. Following this feeding, we removed all remaining seeds and then, using cameras, monitored the time of each defecation for four hours or until no seeds could be found in the faeces. We inspected all faeces to collect and count the seeds. The seeds used in the feeding trials were from native plant species, which we chose according to the size of the seeds, composing 3 size classes (Sup. Table 1). We recorded a total of 670 intact defecated seeds for *T. sayaca*, 229 for *T. leucomelas*, and 313 for *P. picazuro*.

Supporting Table 1. Seed species and sizes used for feeding trials of captive birds.

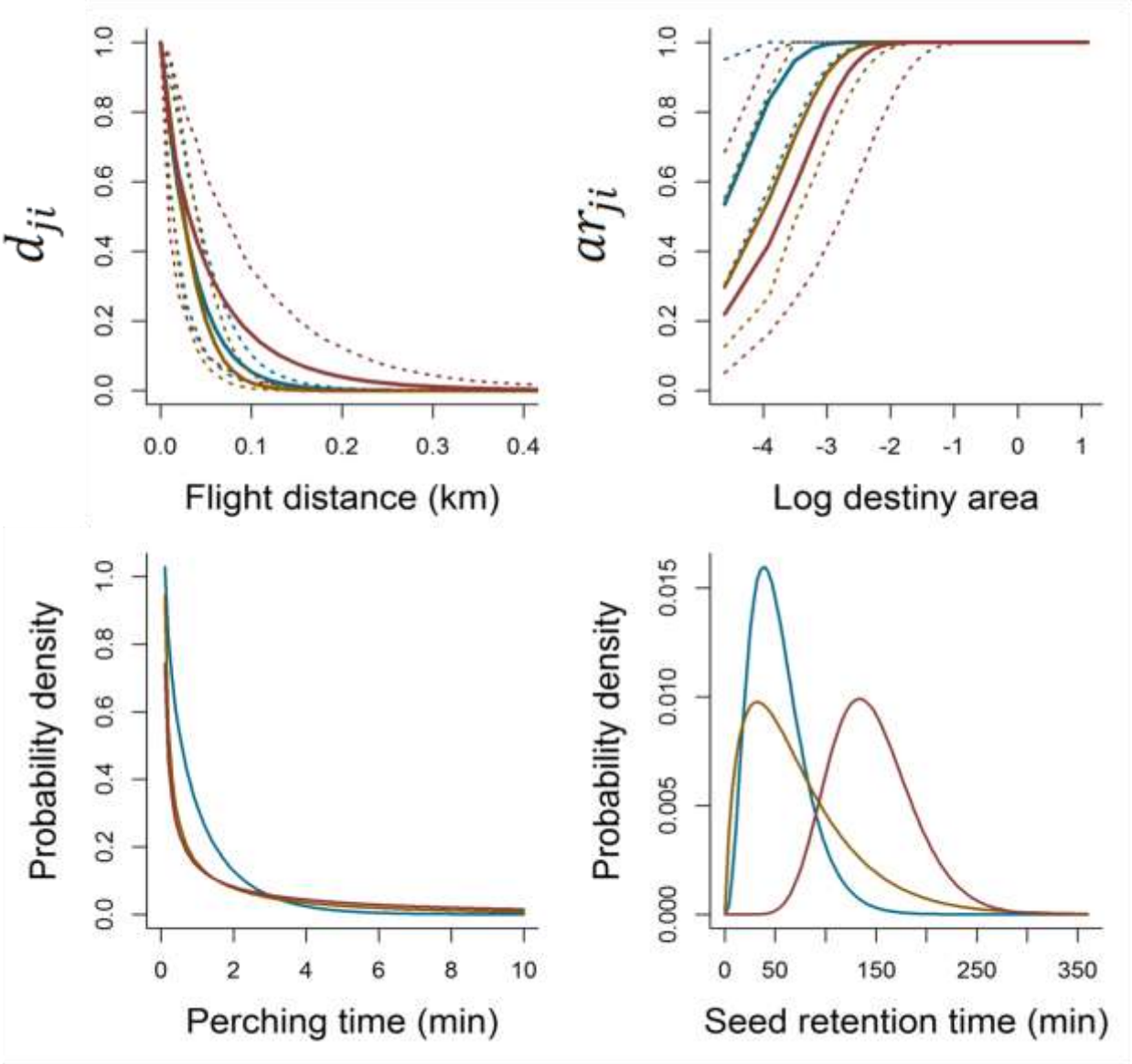
Species	Size (mm)
Ficus luschnathiana	1-2
Solanum erianthum	1-2
Zanthoxylum rhoifolium	4-5
Psidium guajava	4-5
Psidium cattleianum	5-6
Cytharexyllum myrianthum	5-7

Movement model parameters

Supporting Table 2. Parameter values used to simulate seed dispersal by birds. The parameters are specific for each group of species (thrushes, sayaca tanagers and pigeons). The scale and shape parameters of the effects distributions of distance and area of the destination on movement (d_{ji} and ar_{ji}) were computed fitting the likelihood function (equations 1-5; main text) to the observed tracks with MCMC sampling scheme. We show in this table the mean (first quartile; third quartile) of the posteriors (1000 iterations).

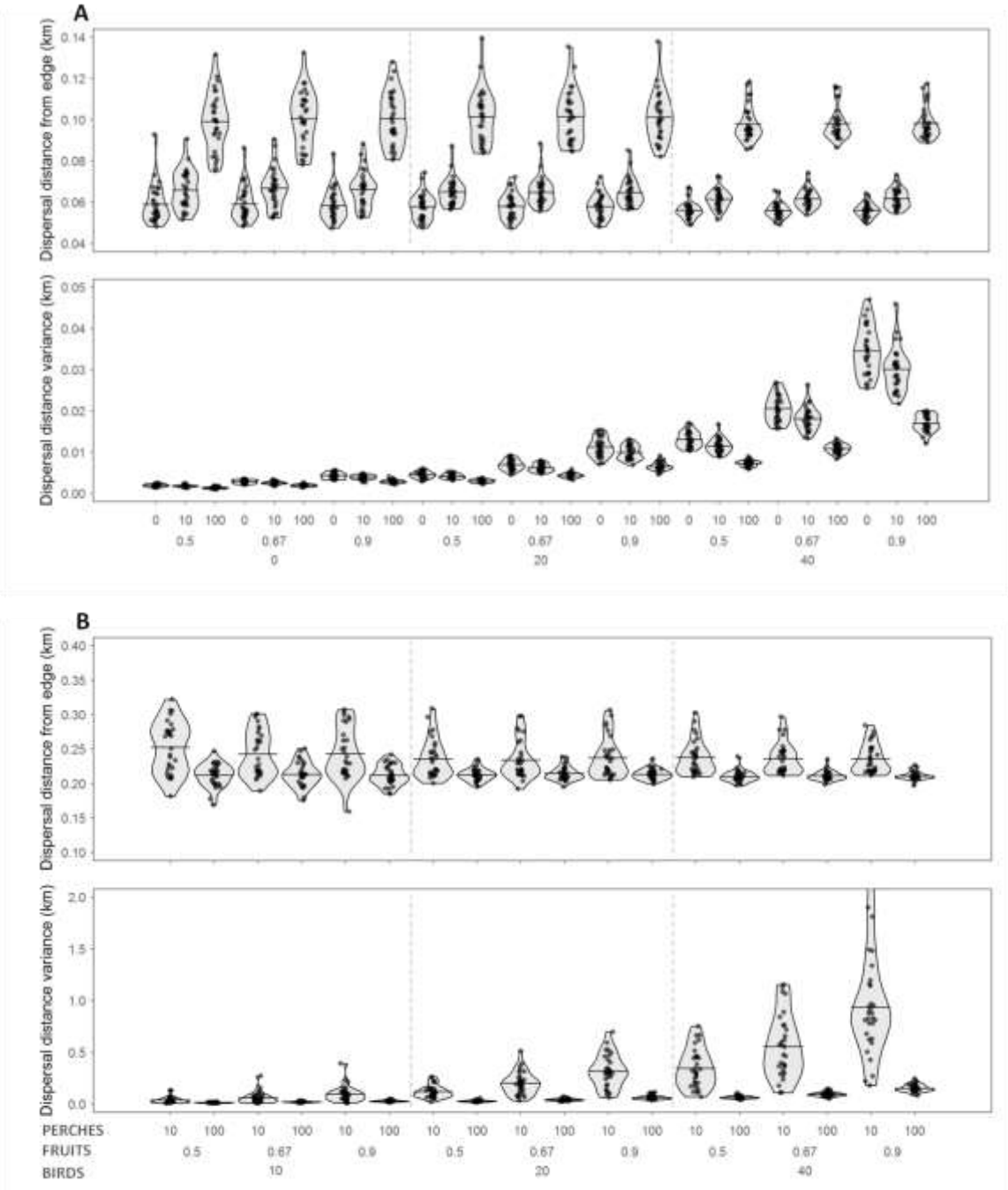
	Parameter	**Value**		
		Thrushes	**Tanagers**	**Pigeons**
Distance effect on movement (d_{ji})	Scale parameter a_d	0.046 (0.038; 0.052)	0.050 (0.041; 0.058)	0.075 (0.051; 0.097)
	Shape parameter b_d	1.023 (0.880; 1.147)	0.844 (0.745; 0.930)	0.685 (0.575; 0.782)
Effect of the area of the destination patch or perch on movement (ar_{ji})	Scale parameter a_{ar}	0.033 (0.023; 0.039)	0.017 (0.011; 0.020)	0.045 (0.026; 0.055)
Probability of eating fruits		0.283	0.224	0.041
Gamma distribution of the perching time	Scale parameter	6.9	1.3	13.7
	Shape parameter	0.26	0.79	0.32

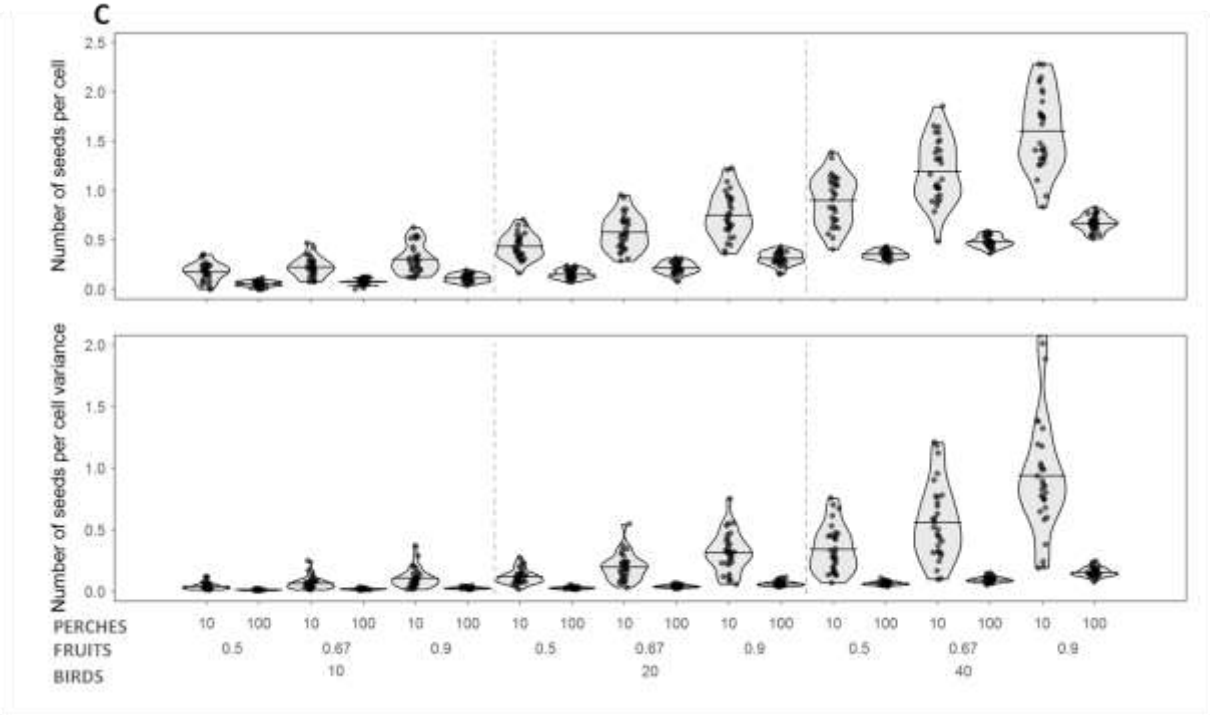
Gamma distribution of the gut retention	Scale parameter	42.2	15.1	11.9
time	Shape parameter	1.8	3.5	12.2
Flight speed		778.5 m/s	639.7 m/s	452.8 m/s



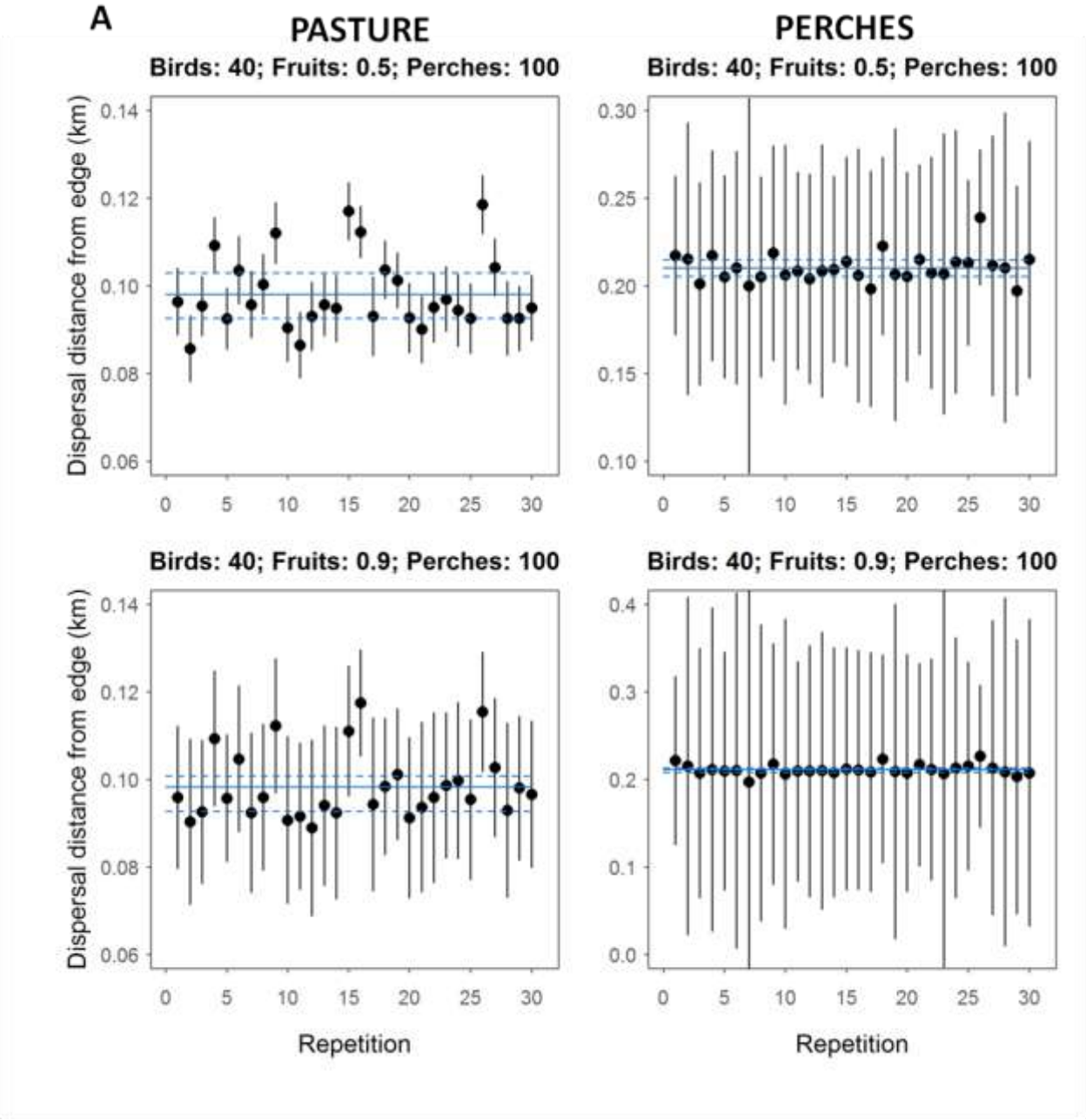
Supporting Figure 2. Distribution models fitted to observed data of studies species (solid lines). The dashed lines represent the confidence interval of the posteriors. The blue, brown, and red lines are the distribution models for sayaca tanagers, thrushes, and pigeons, respectively. Perching time and seed retention time are gamma distributed.

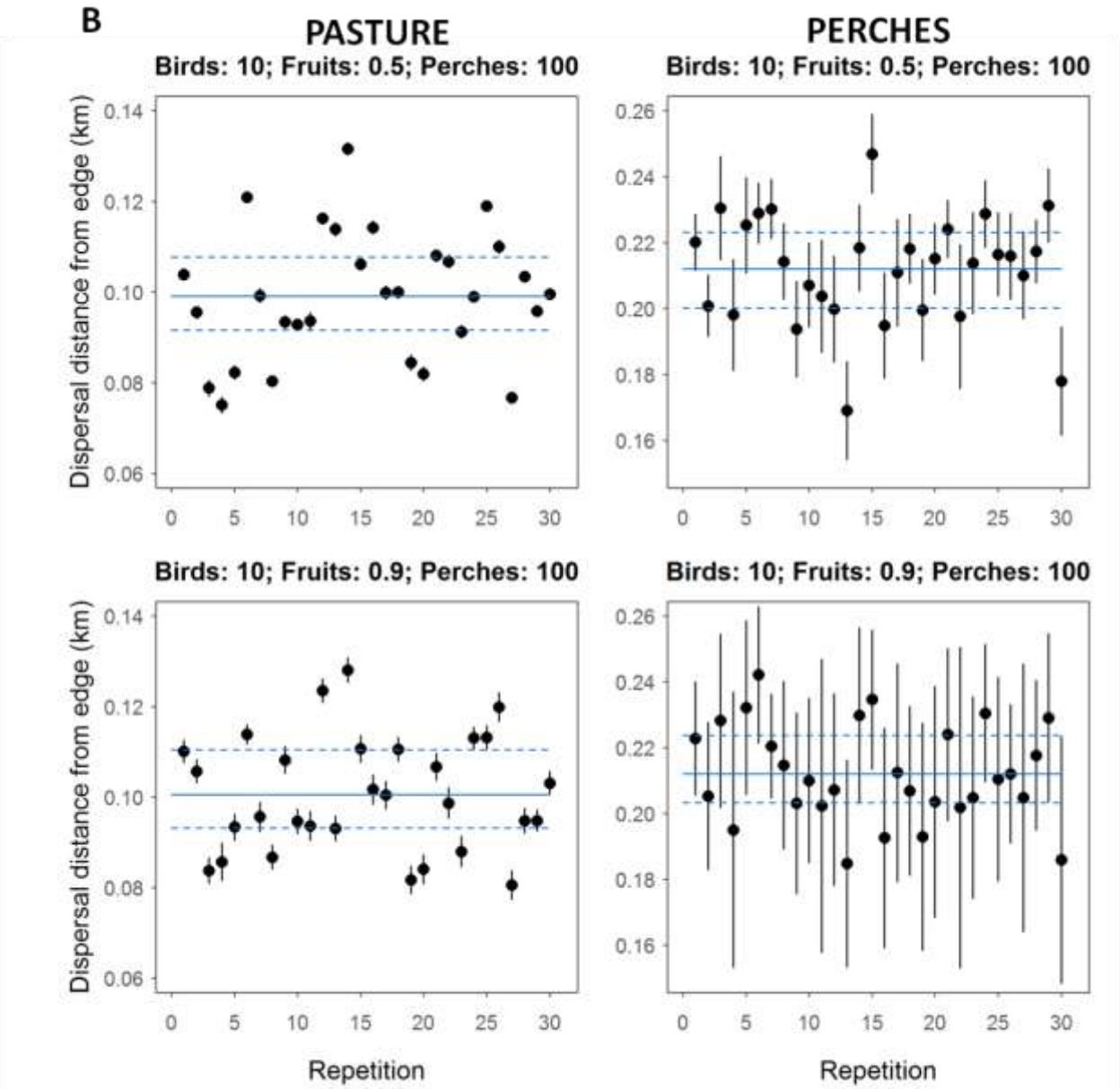
Simulations repetitions results

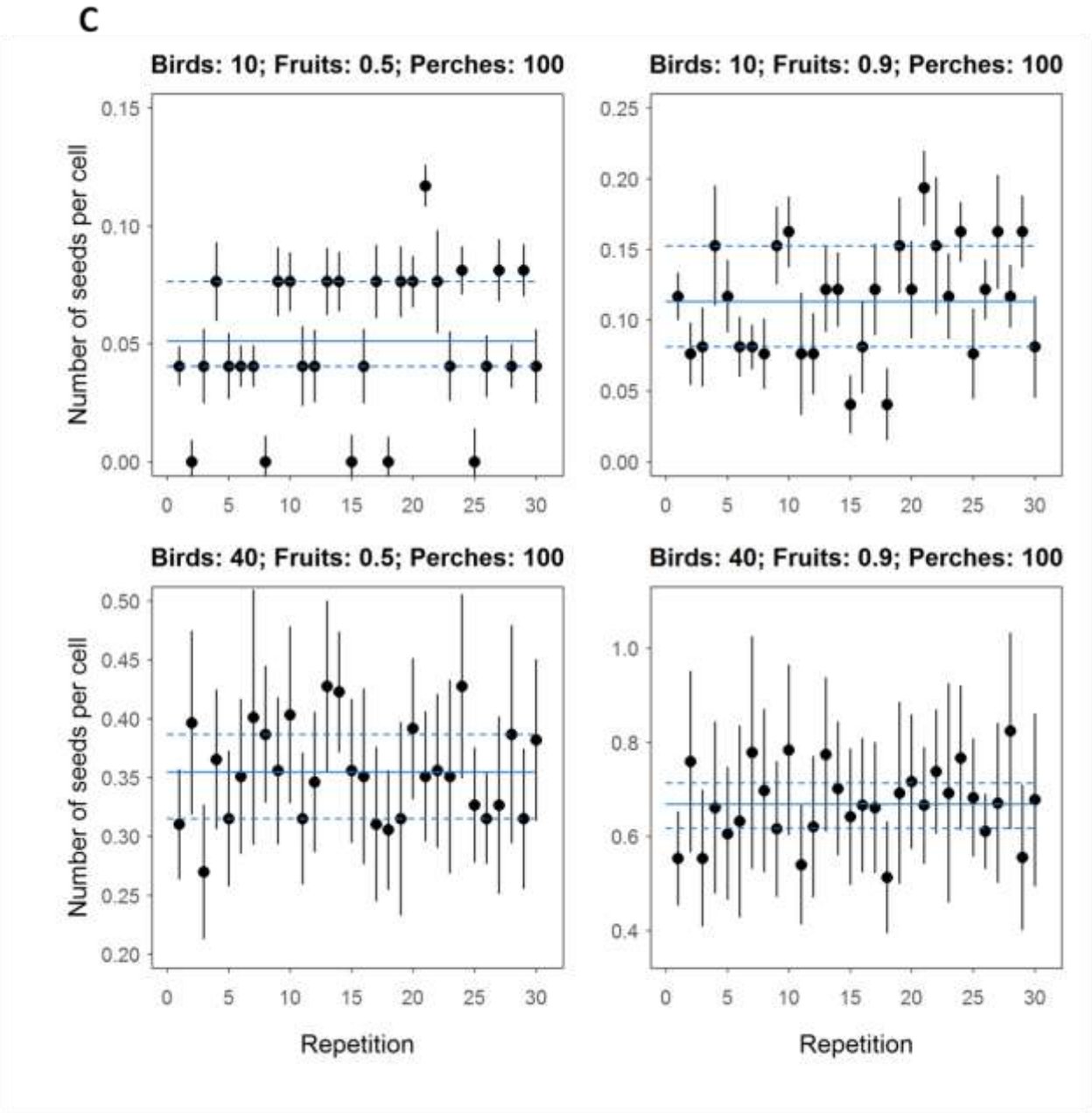




Supporting Figure 3. Average dispersal distances from patch edge, seeds densities and variances resultant from each simulation repetition for each combination of predictor factors. The dots represent average values of the repetition (30 for each factors combination), the bean is the smoothed density of results for the combination of factors, and the vertical bars are central tendencies. A: Average dispersal distances and dispersal distance variance for pasture cells. B: Average dispersal distances and dispersal distance variance for perch cells. C: Average number of seeds per cell and number of seeds per cell variance for perch cells.


A
PASTURE
PERCHES
Birds: 40; Fruits: 0.5; Perches: 100
Birds: 40; Fruits: 0.5; Perches: 100
Birds: 40; Fruits: 0.9; Perches: 100
Birds: 40; Fruits: 0.9; Perches: 100
Dispersal distance from edge (km)
Dispersal distance from edge (km)
Repetition
Repetition


B
PASTURE
PERCHES
Birds: 10; Fruits: 0.5; Perches: 100
Birds: 10; Fruits: 0.5; Perches: 100
Birds: 10; Fruits: 0.9; Perches: 100
Birds: 10; Fruits: 0.9; Perches: 100
Dispersal distance from edge (km)
Repetition



Supporting Figure 4. Means (dots) and variances (vertical lines) of seed dispersal distance from patch edge (A and B) and density of seeds per cell (C) for pasture and grid landscape cells, for each simulation repetition. The solid blue lines are the mean values for all repetitions, and the dashed blue lines are the first and third quantiles for all repetitions.

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Morales, J.M., García, D., Martínez, D., Rodriguez-Pérez, J., Herrera, J.M., 2013. Frugivore behavioural details matter for seed dispersal: a multi-species model for cantabrian thrushes and trees. PLoS One 8, e65216. doi:10.1371/journal.pone.0065216

CONSIDERAÇÕES FINAIS

Nesta tese de doutorado, buscamos descrever diversos preditores e consequências do movimento de aves florestais abundantes da Mata Atlântica (Fig. 1). Iniciamos descrevendo como atributos funcionais – peso e dieta – e correlações filogenéticas podem ser usados de forma eficiente para estimar parâmetros de movimento espécie-específicos, em uma abordagem inovadora baseada em comunidades e conjunta para espécies (*Joint-Species Movement Model*, Capítulo 1). Aprofundamo-nos no desenvolvimento dessa abordagem expandindo-a a modelos multi-paisagens (Capítulo 2), o que nos permitiu verificar que aspectos estruturais de paisagens fragmentadas afetam o movimento de aves florestais. Mostramos em nossos resultados que a distância de voo de aves e o uso de manchas arbóreas têm uma relação negativa com a cobertura florestal, enquanto que intervalos de pouso e o uso de manchas florestais aumentam com o aumento do isolamento da paisagem. Por fim, apresentamos as consequências das diferenças de comportamento de movimento, devido a variações em atributos funcionais ou a alterações causadas pelo ambiente, sobre serviços ecossistêmicos baseados em aves: polinização, controle de pragas e dispersão de sementes (Capítulos 2 e 3). Mostramos que o fluxo de aves para a matriz aumenta com a cobertura florestal, o que pode ampliar a dispersão de sementes para áreas degradadas e o controle de pragas. Usando simulações de movimentos de aves e sementes, encontramos evidência da importância da abundância de aves para o aumento da dispersão de sementes desde fragmentos fonte para áreas degradadas. Por sua vez, a conectividade de fragmentos de florestas aumenta com a redução do isolamento da matriz, promovida pela presença de poleiros na matriz de pasto

(*stepping-stones*). Em nossas simulações, a distância de dispersão de sementes foi alterada positivamente apenas pela presença de *stepping-stones*.

Os resultados apresentados nesta tese convergem ao demonstrar a importância de aves comuns em paisagens fragmentadas no fluxo de recursos e espécies nestas paisagens. As espécies de aves observadas neste trabalho, embora florestais, frequentam áreas com predomínio de atividades humanas, promovendo serviços ecossistêmicos entre os diferentes habitat. Trabalhos anteriores sobre o movimento de aves em paisagens tropicais degradadas abordaram um número reduzido de espécies ou aves florestais que, em geral, restringem suas atividades ao interior de fragmentos (por exemplo, Graham 2001, Hansbauer et al. 2008, Uriarte et al. 2011). Essas aves florestais cruzam pequenas distâncias em áreas abertas para alcançar recursos em outros fragmentos e novas áreas de colonização (Boscolo et al. 2008, Awade and Metzger 2008). Apesar desse tipo de estudo ter implicações importantes para o entendimento de dinâmica de populações e para a conservação da biodiversidade, ele limita a compreensão dos mecanismos responsáveis pelas mudanças ecossistêmicas observadas devido às atividades antrópicas. Somado a isso, cada vez mais pesquisadores têm apontado o papel de espécies generalistas na resiliência de florestas tropicais (Carlo and Morales 2016, Da Silveira et al. 2016, Emer et al. 2018) e na estabilidade da provisão de serviços ecossistêmicos (Winfree et al. 2015, Genung et al. 2017).

Destacamos também o papel chave da presença de poleiros na matriz como catalisadora da conectividade de habitat, não só entre fragmentos de floresta como na interface entre habitat distintos. Seja em pequenos agrupamentos ou isoladas, árvores remanescentes na matriz oferecem proteção e recursos para a fauna (Herrera and García 2009, Pizo and dos Santos 2011), são núcleos de biodiversidade (Prevedello et al. 2017) e facilitadoras do estabelecimento de espécies nativas (Manning et al. 2006). A

presença de árvores remanescentes também é benéfica para a criação de gado, já que proporcionam sombreamento e um abrigo microclimático para os animais (Hartel et al. 2017). Apesar de sua importância, árvores em áreas produtivas não são protegidas pela legislação ambiental brasileira, e sua manutenção pode ser evitada por produtores rurais devido a limitações técnicas ou econômicas e falta de incentivos governamentais (Murgueitio et al. 2010, Athayde et al. 2015). Nosso estudo ajuda a entender em quais situações de estrutura de paisagem o movimento de aves pode ser mais beneficiado pela manutenção de árvores na matriz, com potencial para uso na redução dos custos da conservação da biodiversidade e serviços ecossistêmicos, e planejamento de legislação adequada para o manejo de paisagens. Além disso, nossos resultados indicam uma importância relativamente maior de árvores remanescentes para aves que precisam de maiores áreas de vida, especialmente frugívoros e espécies grandes. Nesse contexto, esta tese ressalta que diferentes estratégias de conservação podem afetar de modo distinto as diversas espécies, serviços e funções ecossistêmicos. Nossos resultados também evidenciam a falta de informação quanto aos efeitos da distribuição espacial de *stepping-stones* na matriz para a efetividade de sua função de conexão de habitats. Essas estruturas podem assumir diversos formatos estruturais, desde árvores isoladas, até pequenos capões, cercas-vivas e corredores de mata ripária, e podem estar em maiores ou menores densidades em paisagens rurais, a diferentes distâncias de fragmentos florestais. Todas essas características têm potencial para limitar ou facilitar o uso de *stepping-stones* pela fauna (Cole et al. 2010, Pizo and dos Santos 2011). Além disso, ainda é debatida a hipótese de que o aumento de recursos na matriz pode causar escoamento de diversidade e serviços na paisagem, com efeitos inversos aos buscados na conservação. Pérez-Hernández et al. (2015), por exemplo, encontraram uma menor conectividade funcional para árvores de *Persea lingue* em paisagens com corredores.

Assim, mais estudos são necessários para entendermos as implicações da interação do movimento de aves com a estrutura da paisagem para a provisão de serviços ecossistêmicos e para o manejo da biodiversidade.

Embora com uma abordagem baseada em comunidades, não apresentamos dados de movimento de espécies especialistas de floresta, em geral mais sensíveis a alterações ambientais. Para a conservação das populações dessas aves, o aumento de habitat adequado é mais importante do que melhorar a permeabilidade da matriz (Phalan et al. 2011). Além disso, não se sabe ainda a importância relativa de espécies sensíveis às atividades humanas ou raras para a provisão de serviços ecossistêmicos. Como espécies generalistas de habitat são abundantes em áreas antrópicas, onde a demanda por serviços ecossistêmicos é maior, seu papel ambiental torna-se mais evidente. No entanto, a perda de espécies mais vulneráveis reduz a integridade de processos ecológicos (Leitão et al. 2016), com efeitos, por exemplo, em dinâmicas evolutivas (Galetti et al. 2013) e no estoque de carbono (Bello et al. 2015).

Acreditamos que este trabalho oferece uma base consistente para uma mudança de escala em estudos de movimento – de abordagens baseadas em espécie para as baseadas em comunidades – e para o entendimento dos mecanismos de geração de funções ecológicas e provisão de serviços ecossistêmicos, particularmente em áreas tropicais (Fig. 1). Esse tema será potencialmente beneficiado pelo aumento de dados empíricos em situações que abranjam a heterogeneidade de paisagens fragmentadas, permitindo o aprimoramento da conservação da biodiversidade.



Figura 1. Resumo dos principais fatores estudados nesta tese de doutorado. Características intrínsecas às aves interagem com fatores ambientais para moldar seus comportamentos de voo. A sequência de voos compõe trajetórias na paisagem em função da permeabilidade das coberturas de solo, que podem facilitar o movimento (como pela presença de poleiros), ou dificultá-lo. As características das trajetórias das aves determinam o fluxo de serviços e funções ecossistêmicas, cuja intensidade é modulada pela comunidade de aves e plantas no ambiente. As variáveis abordadas nesse estudo foram: (1) Aves - tamanho, dieta e características filogenéticas; (2) Ambiente - (cobertura florestal e isolamento médio; (3) Comportamento de voo -

distância de voo, preferência por habitat e tempo de pouso; (4) barreiras da paisagem – presença e quantidade de poleiros; (5) Comunidade de aves e plantas – abundância de aves e frutos; (6) Funções e serviços ecossistêmicos – distância e densidade de dispersão de sementes simulada.

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