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Research

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

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In a rapidly changing world, it is important to understand how environmental modifications by humans affect species behavior. This is not a simple task, since we need to deal with a multitude of species and the different external contexts that affect their behavior. Here, we investigate how interpatch short-distance movements of 73 common forest bird species can be predicted by forest cover and forest isolation. We modeled bird movement as a function of environmental covariates, species traits – body mass and feeding habit – and phylogenetic relationships using Joint Species Movement Models. We used field data collected in forest edges and open pastures of six 600×600 m plots in the Atlantic Forest biodiversity hotspot. We found that birds fly larger distances and visit more forest patches and remnant trees with decreasing forest cover. Increasing landscape isolation results in larger flight distances, and it increases the use of trees as stepping-stones for most species. Our results show that birds can adjust their behavior as a response to spatial modification in resource distribution and landscape connectivity. These adjusted behaviors can potentially contribute to ecosystem responses to habitat modification.

Keywords: bayesian model, frugivory, landscape connectivity, seed dispersal, spill over, stepping-stones

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 in behavior (Kremen et al. 2007, Martin and Fahrig 2018, Tucker et al. 2018).

Although subtle, changes in movement behavior are widespread responses to environmental alterations, mostly due to behavioral plasticity (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 (Weimerskirch et al. 2007, Roshier et al. 2008, Sih et al. 2011, Da Silveira et al. 2016). These behavioral responses, and their intensities, are related to species traits (Sih et al. 2011, Spiegel et al. 2017, Martin and Fahrig 2018). 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 fruit availability is ephemeral and spatially unpredictable, which requires 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. In the context of landscape fragmentation, the movement of animals in the matrix is particularly important, considering that it directly affects the maintenance of species populations (Uezu and Metzger 2011, Neuschulz et al. 2013), and the flow of ecosystem functions and services (Kremen et al. 2007, Mitchell et al. 2015). Assessing community-wide changes in the movement behavior requires overcoming field methods and statistical limitations, since we need to deal with a multitude of species, and the different external contexts that affect their behavior. To describe variation in movement characteristics among species, previous researchers have used a two-step approach, where movement parameters are estimated separately for each species, or included species as random effects (Morales et al. 2013, Neuschulz et al. 2013, Tucker et al. 2018). However, these methods do not allow incorporation of shared traits between species and, thus, are not efficient for community-level datasets, which are often sparse with a large number of rare-species.

Here, we present a community-based study to investigate how the movement behavior of common forest birds in landscape matrix and forest edges depends on landscape structure. Considering that movement is intrinsically related to allometric relationships and particular species needs, we use a Joint Species Movement Model (Ovaskainen et al. 2019), 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 how bird movement parameters (mean flight distance, mean perching time and movement bias toward forest and trees in pasture) depend on landscape structure. For this we collected short-distance movement data of birds in six fragmented landscapes in the Atlantic Forest biodiversity hotspot, 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 (Weimerskirch et al. 2007, Da Silveira et al. 2016); 2) the movement bias toward 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 – frugivores and large bodied birds (Buchmann et al. 2012).

Material and 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 area still harbors many forest patches, the landscape is a mosaic mainly composed of cattle pasture, forestry, agriculture, and urban areas. We selected five square plots of 600 × 600 m, located at least 3 km from each other (Fig. 1c). Areas of this size in the study region encompass the heterogeneity of vegetation types, are not too large to hinder data surveys, and hold a relatively large number of bird species (Pizo and dos Santos 2011, Barros et al. 2019). The criteria for selecting the plots were: 1) the presence of a hilly relief to make the observation of bird movements possible (see below); 2) the predominance of cattle pasture as non-forest habitat; and 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). We classified areas within the plots 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
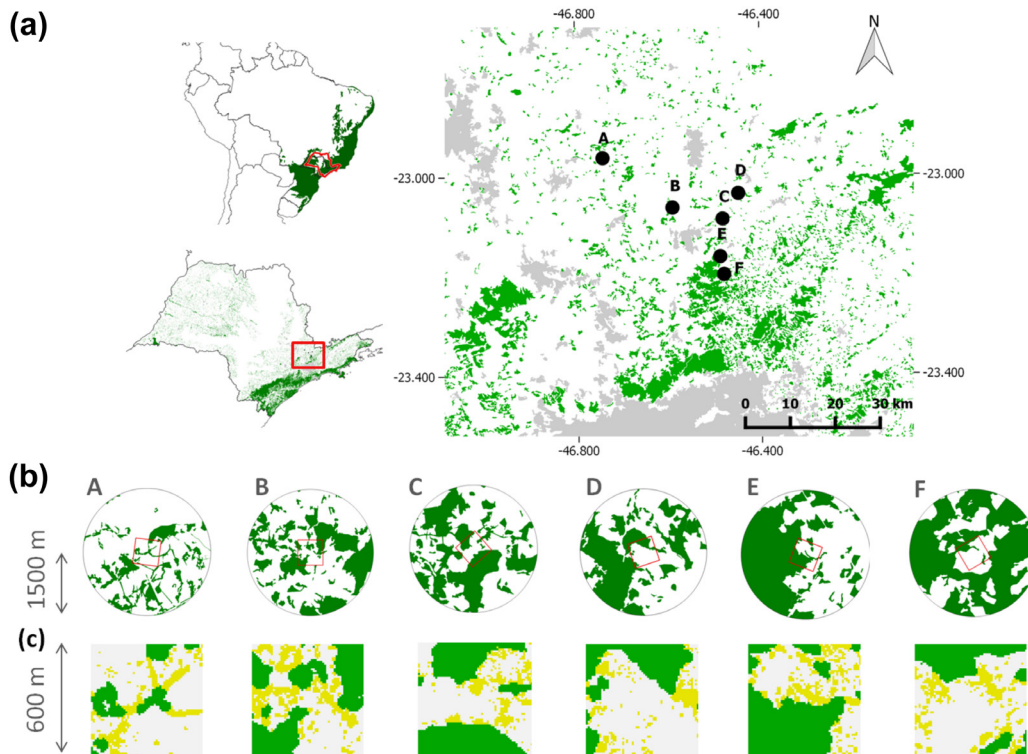
Figure 1. The Cantareira–Mantiqueira Corridor region (a) with the location of studied plots (dots A–F). The studied plots were 600 × 600 m squares (c), for which we show the surrounding circular landscape (A–F) used to calculate the forest cover percentage (b). Green represents forest in (a) and (b) while gray represents urban areas. In (c), green and yellow distinguish forest patches and remnant trees (respectively) while gray represents pasture.

forest patches because birds can make an unequal use of these landscape elements, as reported by previous studies in the region (Pizo 2004, Pizo and dos Santos 2011). Only patches wider than 40 m were classified as forest. 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 due to edge effect and the incursion of cattle, since most of them were not fenced. We classified the vegetation cover types using manual digitalization and visual interpretation of high resolution satellite images (Open Layers Plugin Google Satellite at Quantum Gis 1.8) at the 1:2000 scale, followed by field validation.

As landscape structure variables, we calculated forest cover (%) and mean isolation (see the metrics values for each plot in Supplementary material Appendix 1 Table A1). Forest cover was quantified within a 1500 m radius buffer around the centroid of each plot (Fig. 1b), and ranged from 20% to 70%. We used manual digitalization and visual interpretation of high resolution satellite images (Open Layers Plugin Google Satellite at Quantum Gis 1.8) at the 1:5000 scale, followed by field validation, to quantify the amount of forest in each buffer. Home range sizes vary greatly among bird species, so we set this buffer 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 Fortin and Dale (2005) by Ribeiro et al. (2009). Since forest birds usually avoid perching on open pasture, mean isolation represents how much of open habitat birds need to cross to reach other perches. Thus, we measured isolation at the plots level to be representative of the observed movements scale. The forest cover of the buffer and the plot mean isolation are not correlated in this study (adjusted $r^2 = -0.25$; $p > 0.05$).

Bird movement survey

We monitored short-distance movement of forest-dependent bird species in each landscape from September to December 2014 and September to December 2015, totaling 72 h of observation per landscape. Although this period corresponds to the breeding season of most birds (Supplementary material Appendix 1), we avoided recording repetitive movements, such as flights to or from nests, and protection of small areas – typical of tyrants, to avoid movement bias. We assume that most movements correspond to foraging activity. To collect data, we adapted the methods described by Morales et al. (2013), which allow surveying a large number of species and a high level of observation detail. Each landscape was divided into a grid of 10 × 10 m, i.e. 3600 cells.

We distributed vantage points on the plots from which we had a broad view of the landscape, allowing us to have a homogeneous survey of all landscape cells at the end of data collection. At sunrise, two observers started looking for birds from two different vantage points for four and a half hours, with the help of 10×42 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 left the study plot or was lost. We considered as movement steps the discrete movement of an individual from one location where it had been stationary to another location, and as tracks the consecutive sequence of steps. To record the sequence of cells, we used a printed high resolution (0.5×0.5 m) satellite image of each plot (Supplementary material Appendix 1 Fig. A1). To control for variation in weather conditions, we didn't survey bird movements in rainy or windy days. This method does not enable identification of individuals. So, we assumed that all tracks were independent. This method does not allow the quantification of long flights. Thus, we recorded only short movements (up to 300 m).

Modeling bird movements: integrating landscape structure and species traits

We analyzed the movement data using the Joint Species Movement Modeling (JSMM) framework proposed by Ovaskainen et al. (2019). The JSMM framework enables the simultaneous estimation of species- and community-level movement parameters by modeling movement activity and habitat affinities as a function of species traits and their phylogenetic relationships. In Ovaskainen et al. (2019), the authors 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 bird movements correlate with landscape covariates.

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. As bird traits, we used the log-transformed body mass and the feeding habit, obtained from Wilman et al. (2014). Feeding habit was described by three continuous variables, from 0 to 1, describing the proportion of 1) insects, 2) fruits, and 3) seeds in bird diet. We chose to use continuous variables instead of a discrete classification since most birds feed on different resources, mixed in different proportions. We built a phylogenetic correlation matrix with the package ape 4.0 (Paradis et al. 2004) from 100 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 (see below) will model movements in a landscape with average values of landscape covariates. We divided the data analysis into two components: 1) spatial aspects, describing the typical flight distance and the movement bias to remnant trees and forest patches; and 2)

temporal aspects, describing the perching time. The movement bias measures the preference of birds to a particular vegetation cover type – remnant trees or forest patches – given their availability in the landscapes. We fitted separate models to the spatial and temporal aspects of the data.

To estimate the spatial aspects of movement, we adapted the frugivory and seed dispersal model described by Morales and Carlo (2006) which is a biased random walk model and can also be considered a spatio-temporal point process model (Johnson and Stinchcombe 2007, Hooten et al. 2017). Assuming that an individual of species $s = 1, \ldots, n_s$ is currently at grid cell $i = 1, \ldots, 3600$ of landscape $l = 1, \ldots, n_l$, we model the probability p_{slji} that it will next move to grid cell j by

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

where d_{ij} is the Euclidean 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 $\left(h_{lj}^{(1)} = 1\right)$ or not $\left(h_{lj}^{(1)} = 0\right)$ 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 $\left(h_{lj}^{(2)} = 1\right)$ or not $\left(h_{lj}^{(2)} = 0\right)$, 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 likelihood of the data was computed as the product of the movement probabilities over all the steps observed in the data.

The three ($n_p = 3$) parameters α_{sl}, $\beta_{sl}^{(1)}$ and $\beta_{sl}^{(2)}$ describe the spatial aspects of 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 and landscape covariates. To do so in a simplified notation, we denote the movement parameters by ϑ_{slp}, where $p = 1, \ldots, n_p$ is an index of the movement parameter: $\vartheta_{sl1} = \log(\alpha_{sl})$, $\vartheta_{sl2} = \beta_{sl}^{(1)}$, and $\vartheta_{sl3} = \beta_{sl}^{(2)}$. We model the movement parameters ϑ_{slp} with the help of the regression model

$$\vartheta_{slp} = \sum_{c=1}^{n_c} B_{lc} \theta_{scp} + \epsilon_{slp}$$

where B_{lc} denotes the covariate $c = 1, \ldots, n_c$ ($n_c = 3$) for landscape l, and the parameter θ_{scp} measures how the landscape covariate c influences the movement parameter p of species s. The landscape covariates are the percentage of forest cover

($c = 2$) and the mean isolation ($c = 3$). To include the intercept in the model, we set $B_{l1} = 1$ for all landscapes. We model the residuals ϵ_{slp} with a multivariate normal distribution with covariance structure

$$\text{Cov}\left(\epsilon_{slp}, \epsilon_{s'l'p'}\right) = \delta_{ss'}\delta_{ll'}V_{pp'}$$

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

$$\theta_{scp} = \sum_{t=1}^{n_t} T_{st}\zeta_{tcp} + \varepsilon_{scp}$$

where T_{st} includes the $n_t = 5$ traits for species s: the log-transformed body mass (T_{s2}) and the proportion of insects (T_{s3}), fruits (T_{s4}), and seeds (T_{s5}) in bird diet, in addition to which we set $T_{s1} = 1$ to include the intercept in the model. 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

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

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 Σ 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 in the Bayesian framework, we developed a Markov chain Monte Carlo (MCMC) sampling scheme (see Supplementary material Appendix 1 for details).

Modeling 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

$$\log\left(P_{slq}\right) \sim N\left(\beta_{sl}, \sigma_{sl}^2\right)$$

where β_{sl} is the average log-transformed perching time for bird species s in landscape l.

The species- and landscape-specific perching time models involve $n_p = 2$ parameters, which we denote by ϑ_{slp}. The first parameter is the regression parameter, $\vartheta_{sl1} = \beta_{sl}$, and the additional parameter is the variance parameter, $\vartheta_{sl2} = \log\left(\sigma_{sl}^2\right)$. While in the movement model the parameter ϑ_{slp} models a specific movement behavior parameter p of species s in landscape l, in the perching time model ϑ_{slp} models a specific perching time parameter p of species s in landscape l. We used the same hierarchical structure of the movement model to estimate the perching time parameters as a function of landscape covariates and species traits.

We acknowledge that both the spatial and temporal models are very simplistic, and they omit many processes such as territoriality, inter-individual interactions, home range area, memory, resource density. We made these simplifications to enable a unified model to be fitted for all species, and because our focus was to understand the influence of landscape structure on bird behavior rather than to build a precise description of bird movement. The data and the R-code used to analyze it are freely available under GLP2 at the following Github repository: <https://github.com/leeclab/MultipleLandscapes_JSMM>. The description of the posterior data analysis is in the Supplementary material Appendix 1.

Results

We recorded flight sequences of 1–9 steps (on average 1.6 steps with 0.6 of variance by track, and 44.8 steps with 11 604.2 of variance by species). We also recorded 1–713 perching times for each species (on average 44.3 perching times with 5546.0 of variance by species). In total, we collected flight sequences of 68 species and perching time data of 73 species. Sixteen species were observed in all landscapes and were responsible for 77% of the flight data and 75% of the perching time data. The most frequently observed species were *Tangara sayaca* and *Dacnis cayana* (Thraupidae), *Turdus leucomelas* and *Turdus rufiventris* (Turdidae), and *Patagioenas picazuro* (Columbidae), responsible for 50% of the collected data. See Supplementary material Appendix 1 for details on quantity of data recorded by landscape, posterior values of the parameters and marginal posterior means convergence.

We found no evidence of phylogenetic signal in the movement parameters. The mean estimate of the parameter ρ was 0.02, with (0.00, 0.06) as 95% credible interval for the spatial components of movement, and 0.03, with (0.00, 0.08) as 95% credible interval for the temporal components of movement, while the prior distribution was uniform in the range from 0 to 1.

Movement of birds in an average landscape

We found evidence that bird traits were associated with certain movement behaviors. Large birds tended to fly longer

distances ($\text{Pr}(\zeta_{tcp} > 0) = 0.82$), to show less movement bias to remnant trees and forest ($\text{Pr}(\zeta_{tcp} < 0) > 0.90$), and to perch longer than small birds ($\text{Pr}(\zeta_{tcp} > 0) = 0.99$), where t corresponds to body size, p corresponds to the focal movement parameter and c corresponds to the intercept of the landscape covariates (Fig. 2). Flight distance and movement bias to remnant trees and forest were larger for birds feeding mostly on fruits than feeding mostly on insects ($\text{Pr} > 0.90$), while birds feeding mostly on seeds perched longer than species feeding mostly on fruits ($\text{Pr} > 0.90$) (Fig. 2), where Pr is the posterior probability of differences between the estimated parameters. The diet of the birds was more important than their body mass to explain the variability in posteriors mean values of flight distance and movement bias to forest (Fig. 2). In turn, bird body mass was more important to explain the variability in posteriors mean values of movement bias to remnant trees and perching time.

Effects of landscape on species-specific movement parameters

We found evidence of correlation between forest cover and mean isolation on the species- and landscape-specific parameters of most bird species. While landscape covariates, by their own, were responsible for a small fraction of the variation in landscape- and species-specific movement parameters (1–8%), the landscape covariates and bird traits together were the main component explaining the variation in movement parameters (32–50%) (Fig. 3). Mean landscape isolation was more important than forest cover to explain variation in movement parameters. Bird traits explained 21–36% of variation, and 25–35% of variation was not explained by traits nor landscape variables (Fig. 3).

With increasing forest cover, birds tended to fly shorter distances, and to have a smaller movement bias to remnant trees and forest, and, consequently, to visit more pasture areas (Fig. 2). During data collection, we could see individuals landing on pasture, mainly near to remnant trees and forest edges, or on scattered bushes. We observed a weak effect of bird traits on how movement parameters depended on forest cover. In turn, the effect of mean landscape isolation was different for species with different diet preferences. Flight distance tended to increase with increasing landscape isolation, except for birds feeding mostly on seeds, which flew shorter distances with increasing isolation (Fig. 2). Movement bias to remnant trees and to forest increased with increasing landscape isolation and preference for fruits, and decreased with increasing landscape isolation and increasing preference for insects and seeds. Differently from expected, we found little evidence of correlation between body mass and the effect size of environmental covariates on movement parameters (posterior probability for a negative or positive effect was < 0.9 in all cases; Fig. 2). The largest effect of species traits was movement bias to forest increasing with body mass in isolated landscapes ($\text{Pr} = 0.83$). Then, despite their preference for seeds, large pigeons (*Patagioenas picazuro* and *Patagioenas cayennensis*) showed a larger movement bias to forest with increasing landscape isolation (Fig. 2). We found no consistent changes in perching time caused by landscape covariates.

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, Martin and Fahrig 2018). In this study, we showed evidence that birds change their movement in matrix and forest edges in response to landscape structure. To our knowledge, this is the first empirical community-based report about effects of human landscape modifications on bird movement. Such effects were related to the species traits, especially bird diet, while phylogenetic relationships were not good predictors of movement changes. Our results suggest that the amount and spatial distribution of resources, allometry and short spatio-temporal decisions can shape the response of birds to landscape change.

We found support to the hypothesis that birds move faster in hostile environments, flying longer distances and perching for shorter time intervals, and use more remnant trees as stepping-stones within the open vegetation. Our results are consistent with previous empirical studies done in either small scales (Bélisle and Desrochers 2002, Weimerskirch et al. 2007, Awade and Metzger 2008) or large scales, using long movement tracks (Weimerskirch et al. 2007, Roshier et al. 2008, Da Silveira et al. 2016, Martin and Fahrig 2018, Tucker et al. 2018). Based on this findings, three potential mechanisms can explain the observed movement changes: 1) birds surpass the hostile or less adequate habitats (Bélisle and Desrochers 2002, Hodgson et al. 2007, Awade and Metzger 2008, Neuschulz et al. 2013, Biz et al. 2017, Kennedy et al. 2017, Martin and Fahrig 2018), like the pasture in this study; 2) birds move more in environments with fewer resources (Weimerskirch et al. 2007, Hansbauer et al. 2008, Roshier et al. 2008, de Jager et al. 2011, Tucker et al. 2018), represented here by forest cover and isolation, to meet their energetic requirements; and 3) birds can benefit from new foraging opportunities created by landscape modification (Roshier et al. 2008, Pizo and dos Santos 2011, Da Silveira et al. 2016, Tucker et al. 2018). With this understanding, we can infer that increases in landscape isolation and decreases in forest cover motivated birds to move faster and to fly larger distances to reach other patches, and to use more remnant trees as stepping-stones and protection in open areas (Fig. 4d). At this point, it is important to highlight that each species responds differently to landscape change, as our results also show. Forest specialists, for example, will hardly cross open habitats or use resources out of the forest, and can be more susceptible to extinction (Kennedy et al. 2017).

Regardless the importance of external factors shaping movement, the sum of species traits and landscape structure was the main source of variation in species-specific parameters. Unlike our hypothesis, we could not see a clear general relation between the mobility of the species and the
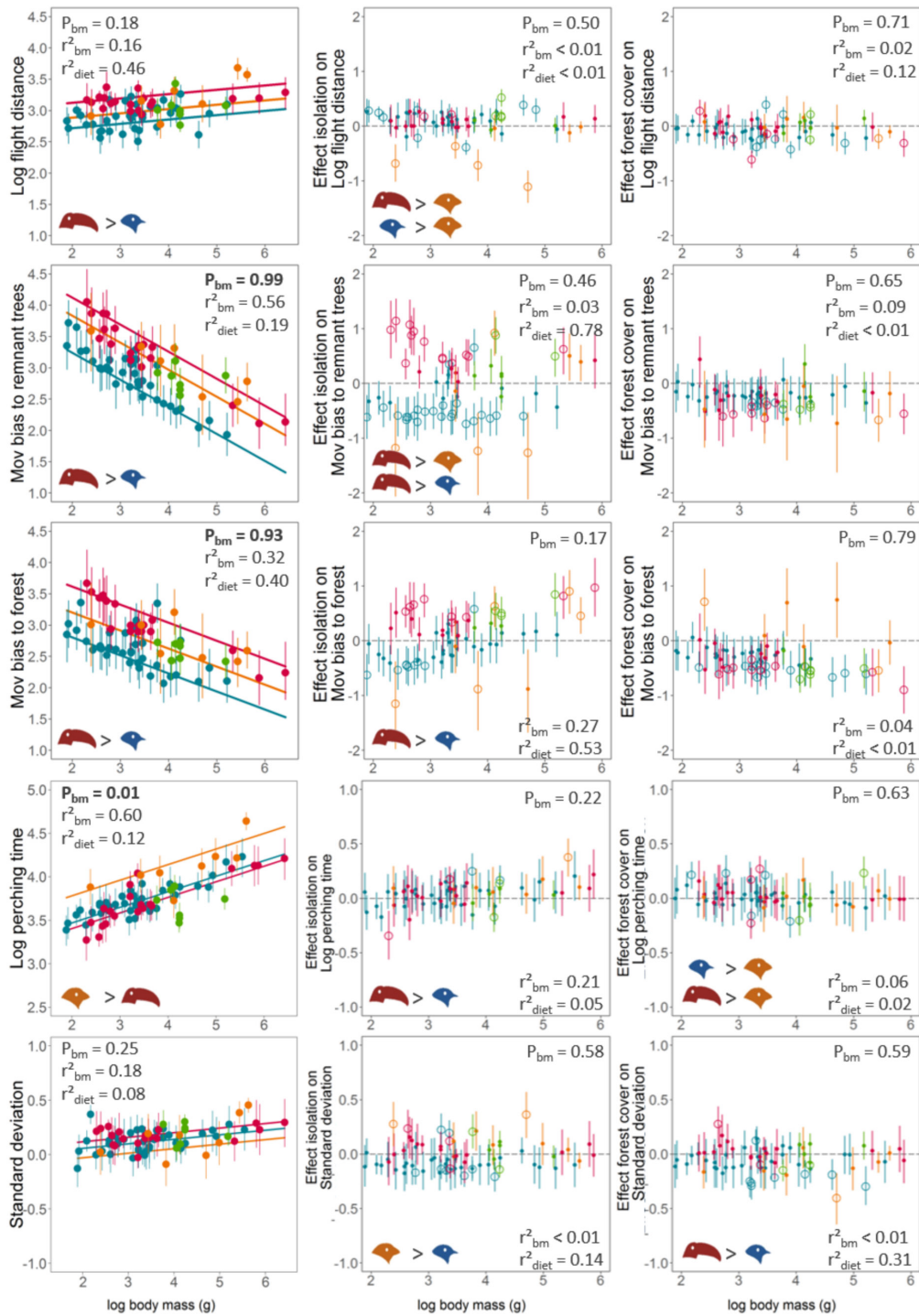
Figure 2. The influence of species traits and landscape structure on species-specific movement parameters. The left panels show the movement parameters in an average landscape, the middle panels show the influence of landscape mean isolation on movement parameters, and the right panels show the influence on forest cover on movement parameters. Dots represent the posterior mean values for each species, and the bars show the 25% and the 75% quantiles. The large circles highlight the parameters that are either positive or negative with at least 80% posterior probability. Colors represent the most common resource in the species diet: fruits (red: 🐦), insects (blue: 🐦), seeds (orange: 🐦), or similar proportions for more than one resource (green). The pairs of images inside the panels indicate statistical support for a difference between each pair of ζ_{tcp} parameters, considering the traits t correspondent to the proportions of fruits, seeds or insects in diet, and the same movement parameter p and landscape covariate c for each pair, with at least 90% posterior probability. The lines show the posterior mean prediction based on species body size and food resource proportion in diet. We show the variability explained by the traits (r^2_{bm} for body mass and r^2_{diet} for diet traits) and the posterior support for a negative effect of body mass ($p_{bm} = \Pr(\zeta_{tcp} < 0)$, where t corresponds to body mass, p corresponds to the slope parameters and c are the landscape covariates).
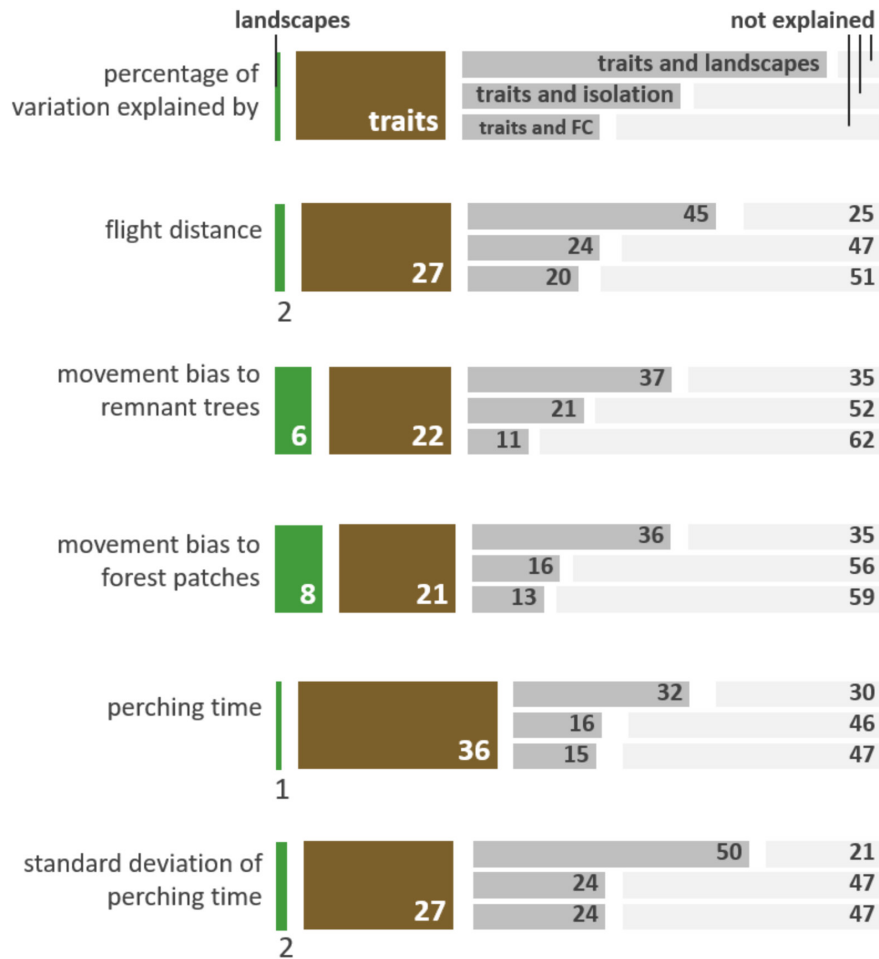
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Figure 3. Percentage of variation in movement parameters explained by landscape covariates, bird traits, traits and landscape covariates together, or not explained by the analyzed factors. 'FC' means 'percentage of forest cover', and 'landscapes' means 'landscape covariates', i.e. mean isolation and percentage of forest cover.

intensity of the response to landscape structure. We show, however, that the response of specific-movement parameters depends on the body mass and diet of bird species, probably as a reflection of the effect of movement capacity and energetic needs on bird behavior. First, the smaller the organism, the higher the mass-specific metabolic rate, i.e. more energy is spent per unit of mass (Brown et al. 2004). Secondly, the larger the organism, the greater its movement capacity (Neuschulz et al. 2013). Finally, lack of spatial predictability of resources usually induces birds to move more frequently (Levey and Stiles 1992). For instance, researchers describe that frugivores have larger home ranges than other species 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). Our results are consistent with such patterns: large birds flew longer distances and perched for longer times, and birds feeding mostly on fruits flew larger distances and perched for shorter times than other

species, since fruit production in unpredictable in space (van Schaik et al. 1993). In addition, small species showed a greater bias toward remnant trees and forest, probably because they are more vulnerable to predators (Wheelwright 1991), and can shelter in trees, and because they have less movement capacity and can benefit from remnant trees acting as stepping-stones between forest patches. Likewise, birds preferring seeds or insects probably benefited from the pasture as a source of resources, and increase the use of open-areas with increasing landscape isolation.

We highlight that our results are suggestive rather than conclusive, and they should be generalized with caution. The main reason for this is that our data originate from six landscapes only, and thus we have a limited data to infer how bird movements correlates with landscape structure. While we would have ideally included some tens of landscapes, in the present study we did not have the resources of conducting such a large-scale research program. Besides, we found a dominance of only five species out of 72, which was expected, since this general pattern was previously reported for the
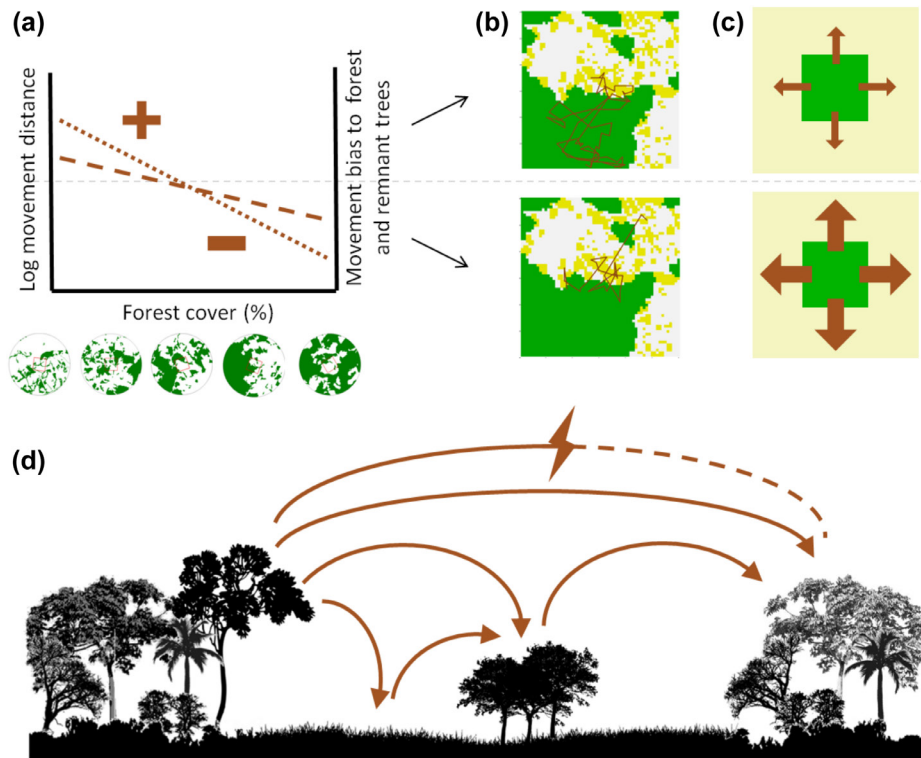
Figure 4. Effects of changing movement behavior on landscape-level movements. (a) The movement bias to forest and remnant trees and the typical flight distance decrease with increasing forest cover, causing (b) smaller displacement, and (c) more movements between remnant trees or from forest to pasture. (d) Increasing typical flight distance and the use of remnant trees can conserve landscape functional connectivity with increasing landscape isolation. Dashed and dotted brown lines in (a) represent the decrease in movement distance and bias to forest and remnant trees with increasing forest cover. The arrows in (d) represent the possible movements of birds between forest patches, including landing on pasture, use of remnant trees as stepping-stones, direct flight from one patch to another, and the absence of movement due to forest isolation (half dashed line).

studied area and other altered landscapes of the Atlantic Forest (Pizo 2007, Pizo and dos Santos 2011, Barros et al. 2019). So, we suppose that the community-level parameters were estimated with a higher accuracy than the species-level parameters, considering that the hierarchical structure of the JSMM enables an accurate estimation of the former with data on many species (Ovaskainen et al. 2019), while the specific-level parameters are more accurate for the species with more data. In this study, we could not distinguish the individuals, and thus we assumed that movement parameters are a species-level rather than individual-level feature. If the identity of the individuals could have been recorded, the model should have included the individual as a random effect, thus quantifying variation among individuals within a species. Further, our results are conservative because we did not model explicitly observation error, likely reducing signal-noise ratio. While our results are not conclusive, especially for more diverse communities, we note that they are consistent with the expectations based on earlier studies and the ecological knowledge on the species. We hope that our approach and results motivate the initiation of large-scale research program that would make it possible to examine the dependency of movements at the community level more conclusively in the future.

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 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). Therefore, we address the implications of the observed bird movement changes for ecosystem functioning by expanding the movement variation to the landscape level (Fig. 4).

One of the most obvious implications of movement variation in the matrix and forest edges 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 (Martensen et al. 2012) and, thus, a logical bridge between movement and landscape ecology has been built. In this study, we observed only short sequences of movements in forest edges and landscape matrix, and we were not able to survey bird dispersal. However, by interacting with plants and carrying seeds and pollen, birds can

connect plant populations in fragmented landscapes, even within short scale movements (González-Varo et al. 2017). Besides, their behavior can change the spatial provision of ecosystem services, such as pest control (Kremen et al. 2007). 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 use to refer to processes involving different patches of forest.

The parameters most correlated with 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, 4a). With shorter mean distances, birds would 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 usually increases with forest cover in real landscapes (Ribeiro et al. 2009), and could off-set the shorter movement distances. At the same time, birds would be more prompt to use pasture, and to cross forest edges, which can improve spillover (Fig. 4c). The increasing mean isolation mainly increased the flight distances for birds preferring fruits or insects, and the movement bias to forest patches and remnant trees of birds eating mostly fruits (Fig. 4d). In turn, increasing isolation decreased the flight distance of birds eating mostly seeds, and the movement bias to forest patches and remnant trees of birds eating mostly seeds or insects.

Changes in movement caused by increase of landscape isolation can be important mechanisms of landscape resilience, since birds can overcome the decrease in structural connectivity (Giubbina et al. 2018) by using stepping-stones, using more pasture or moving farther (Fig. 4d). 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 (Spiegel and Nathan 2007, Bello et al. 2015). Likewise, environmental variation can directly influence movement, regardless behavioral rules (Cosgrove et al. 2017). Their relative importance in shaping movement should be investigated for a correct diagnostic of movement impediments and for effectiveness of biodiversity management.

Concluding remarks

We detected an interaction between species particular needs and limitations – intrinsic factors – and landscape limitations and opportunities – external factors – shaping the movement of birds in forest edges and landscape matrix. Our results also support the importance of remnant trees within human-use areas, likely used as shelter, stepping-stones and source of resources, to the movement of birds. By assessing bird movement with a high level of observational detail, our results contribute to fill the lack of information about the exact mechanisms of the ecosystem responses to fragmentation, given the fundamental importance of movement, and can potentially contribute to the improvement of models that evaluate landscape connectivity, species loss, function loss and other questions of conservation science. Further studies should deal with the challenge of linking animal movement to empirical data on ecosystem services provision and ecosystem functioning variation.

Data availability statement

The data and the R-code used to analyze it are freely available under GLP2 at the following Github repository: <https://github.com/leeclab/MultipleLandscapes_JSMM>.

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Supplementary material (available online as Appendix ecog-04888 at <www.ecography.org/appendix/ecog-04888>). Appendix 1.