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The role of environmental heterogeneity for the maintenance of distinct bird communities in fragmented forests

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ABSTRACT

If a forest fragment maintains original heterogeneous habitat conditions after deforestation and fragmentation of the landscape, is it possible that distinct communities can still remain within the forest remnant as they once occurred in the continuous forest landscape? In the present study, we assessed whether a single forest fragment could harbour different bird communities and the potential factors driving this distinction. Bird abundance and composition were compared between two distinct regions within a single large forest fragment, which differ in topography and vegetation physiognomy. The forest fragment was located in southern Brazil and consisted of pristine semi-deciduous forest. Our analysis indicates the occurrence of two different bird communities within the interior area of a single forest fragment. Variation partitioning also indicated that environmental features, particularly bamboo cover and humidity, were the main factors explaining bird species occurrence. We suggest that habitat heterogeneity is important for the maintenance of these bird communities and it leads to: (1) high levels of bird species diversity, and (2) maintenance of important ecological mechanisms (e.g. species sorting) within the forest fragment. Understanding the ecological processes involved in habitat distribution inside single forest fragments is important, yet usually not properly evaluated in forest fragmentation studies. Our results suggest that considering forest fragments as single ecological units can be misleading. We highlight the need to critically evaluate individual features of forest fragments, beside other landscape metrics, in order to identify important forest fragments for biodiversity conservation.

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Bird communities; forest fragmentation; environmental heterogeneity; bamboo bird species; forest humidity; conservation

Introduction

Forest fragmentation is a process that involves the dismantling of a continuous forest landscape into one or more fragments (Bierregaard *et al.* 1992; Ewers and Didham 2006). Economic development generally leads to an increase in forest fragmentation by means of: deforestation (i.e., habitat loss); the breakdown of a single forest into several smaller forest fragments (i.e., habitat fragmentation); and the conversion of forest vegetation into different forms of land use (i.e., landscape modification) (Bennett and Saunders 2010). Because of the increase of these anthropogenic constraints, the selection of appropriate forest fragments for conservation is a tremendous challenge (Valente and Vettorazzi 2008). Landscape features, such as habitat connectivity and matrix permeability, have been widely studied and are recognised as crucial components in the maintenance of biodiversity at the landscape level (Martensen *et al.* 2008; Thompson *et al.* 2017). However, less attention has been given to how internal features of forest fragments could be important for conservation purposes in fragmented landscapes.

Although it is well established that larger forest fragments will have higher levels of biodiversity (Martensen *et al.* 2008; Prugh *et al.* 2008), the understanding of the ecological processes involved in the distribution of species inside forest fragments is still an understudied topic. This is partly due to the poor knowledge on the factors that explain the distribution of species, even for large continuous forest areas. The idea that temperate and tropical forests are made up of a mosaic of different habitats is quite old in the literature (Holmes 1990; Karr 1990). However, the factors associated with the determination of habitat boundaries (i.e., the limits between the mosaics) are still poorly understood. This is an important issue in the study of forest fragmentation, because if in a single forest fragment two or more well-defined habitat mosaics persist, then the forest fragment should have greater species beta-diversity. Studies at the landscape level usually do not consider beta-diversity inside a single forest fragment and assume that forest fragments are single ecological units. In fact, studies in

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 Supplemental data for this article can be accessed [here](#).

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forest fragments have demonstrated only that species composition differs between the edge and the interior (core area) due to variation in habitat features (Murcia 1995; Harper *et al.* 2005), or that the selection of microhabitats by a small group/guild of species affect their distributions in the fragment's interior (Lopes *et al.* 2006; Kosicki *et al.* 2015). Studies have not evaluated if the availability of different habitats in the interior area of a single forest fragment could result in distinct communities. Understanding the boundaries of different habitats in a single forest fragment is therefore an important issue at the community level.

Here we evaluated if the presence of distinct habitats can affect the distribution of species, allowing the forging of distinct bird communities inside a single forest fragment. In other words, if after the deforestation of the surrounding landscape different habitat conditions still remain within a forest fragment, the maintenance of distinct communities could be preserved as it once was prior to the deforestation process of the continuous landscape (Haddad *et al.* 2017). For example, a forest fragment may contain an elevation gradient, which will affect vegetation structure and can lead to changes in species composition (Lee and Marsden 2008; Kosicki 2017). Also, the presence of rivers could potentially create an ecological gradient that affects plant species composition, and consequently different animal communities (see Naiman and Decamps 1997; Richardson *et al.* 2007). Thus, a forest fragment that extends over a hill (i.e. a sloped area) and contains streams and small rivers, should comprise of a vegetation mosaic (i.e., a mosaic of different habitats) capable of supporting different bird communities.

To illustrate how the presence of different habitats can increase the possibility of a single forest fragment harbouring distinct communities, three hypothetical scenarios are provided in Figure 1. The first scenario is of a small forest fragment that consists only of forest edge (Figure 1(a)). The second scenario is of a large pristine forest fragment comprised by a relatively homogeneous habitat in its interior (Figure 1(b)). The third scenario is

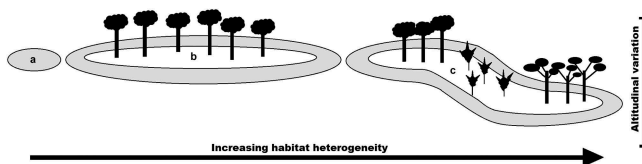


Figure 1. Three hypothetical scenarios illustrating forest fragment complexity. (a) a small forest fragment comprised only of edge (grey) habitat; (b) a large pristine forest fragment comprised of homogenous habitat conditions and edge habitat; (c) a large pristine forest fragment comprised of a complex vegetation mosaic due to an altitudinal gradient.

a large pristine forest fragment that has different vegetation types, as a result of variation in altitude, which leads to the presence of different habitat conditions in its interior (Figure 1(c)). The latter scenario should be considered as a conservation priority, because it could harbour different communities and hence higher species diversity. In this study, we test if a single forest fragment located along an elevation gradient harbours different bird communities (i.e., Figure 1(c)). This has important implications for conservation because conservation strategies at both local and broad spatial scales (e.g. Melo *et al.* 2013) seek to identify important forest fragments for conservation (Valente and Vettorazzi 2008; Brancalion *et al.* 2013). Therefore, to recognize if a single forest fragment consists of a single forest community, or whether a single forest fragment can harbour several communities, is an important task for conservation.

The goals of this study were to: (1) investigate whether a single large forest fragment (which is commonly seen in the literature as harbouring a single community) is capable of supporting different bird communities and (2) identify potential factors driving this distinction. For this, we evaluate whether a forest fragment can be considered as a single unit of measurement in community studies through the use of a statistical approach (*sensu* Morin 2011). Birds are an interesting study system because they are highly mobile organisms (Neuschulz *et al.* 2013) and at the same time have high levels of habitat specialisation (Jankowski *et al.* 2009). This high level of specialisation could lead to species being strongly associated with particular habitats within the forest fragment, and variation in habitat conditions may result in changes in bird species distribution, leading to the detection of different bird communities. However, as habitats are highly connected within the forest fragment, dispersal capability could homogenise species distribution (Presley *et al.* 2012) and, in this case, only a single bird community will be detected. Also, if habitats are not clustered within the forest fragment but dispersed in a mosaic manner, then a single community should be detected. We suggest that forest fragments that harbour two or more bird communities should be considered as having high conservation value.

Methods

Study area

The study was conducted in Mata dos Godoy State Park (23°26'S; 51°15'W, hereafter MGSP, Figure 2), municipality of Londrina, Paraná state, southern Brazil. MGSP covers 656 ha and consists of seasonal semi-deciduous forest, a forest type of the Atlantic

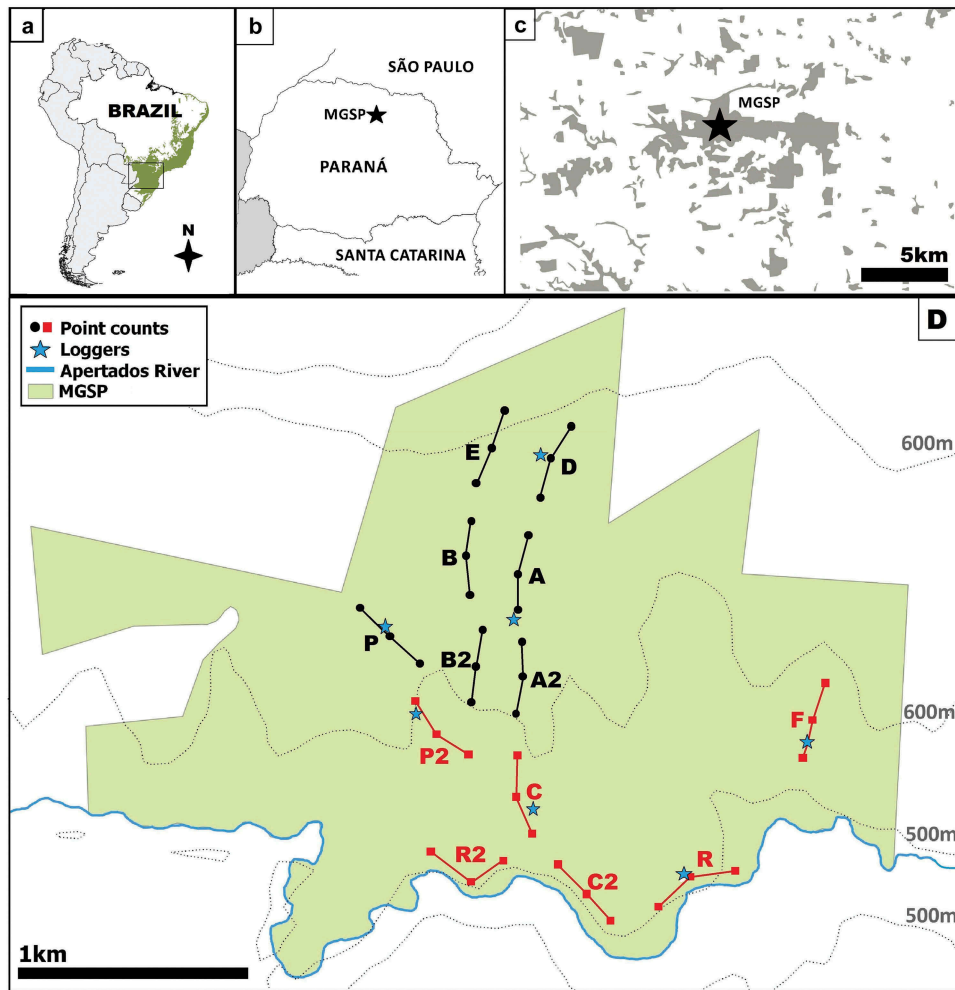


Figure 2. Mata dos Godoy State Park (MGSP, 23°26'S, 51°15'W), Londrina municipality, north of Paraná State, south of Brazil. (a) The original forest cover of the Atlantic Forest Biome. (b) Location of the study area in the Paraná State, southern Brazil. (c) Fragmented landscape surrounding MGSP (forest fragments in grey). (d) MGSP: trails (sample units) correspond to a set of three point counts (black circles or red squares). Trails of the northern region (black/black circles): A, A2, B, B2, D, E and P. Trails of the southern region (red/red squares): C, C2, R, R2, P2 and F. Stars correspond to data logger locations.

rainforest biome. In Brazil, the Atlantic rainforest originally covered the coast, with more inland areas occurring mainly in the south and southeast areas of the country (Figure 2). After a strong deforestation process, this biome became a landscape composed of a myriad of forest fragments with different sizes and degrees of connectivity, with 80% of forest fragments being smaller than 50 ha (Ribeiro *et al.* 2009). The landscape surrounding MGSP (500 km²) is no different, with only 17 forest fragments being larger than 100 ha, 133 between 10–99 ha, and 1,187 smaller than 10 ha (Torezan 2003). MGSP is one of the last largest pristine forest fragments in the north Paraná region (Anjos *et al.* 2007). This forest fragment has a natural topographic variation that consists of a plateau in its northern portion, where altitudes range around 600 m, and a hillside in its southern portion with altitudes that

vary from 600 to 470 m, which is limited by the Apertados river (Figure 2). This topographic variation is responsible for changes in vegetation physiognomy and in the richness of arboreal plant species (Silveira 2006). The northern region presents a dense and uniform canopy with an open understory, while the southern region has scattered trees, rarefied canopy and widespread occurrence of bamboo in the understory (Silveira 2006). Moreover, small streams (tributaries of the Apertados river) are present only in the hillside.

To test the hypothesis that this forest fragment harbours distinct bird communities, we considered the differences in vegetation physiognomy between the northern and southern regions and divided the MGSP in two distinct regions: north (plateau, at 600 m a.s.l.) and south (hillside, ranging from 600 to 470 m a.s.l.). In these two regions, 600 m trails were established for

bird sampling and environmental characterisation (described below). Trails were at least 100 m away from forest edges. Seven trails were distributed in the northern region (A, A2, B, B2, E, D and P in [Figure 2](#)), while six were positioned in the southern region (C, C2, P2, R, R2 and F in [Figure 2](#)), giving a total of 13 sampling trails.

Bird sampling

We used point counts for sampling birds (Bibby *et al.* 1992). Three point counts with 200 m intervals were established in each of the 13 trails, giving a total of 39 point counts (13×3) for the entire study area ([Figure 2](#)). Each point count was sampled four times between September and December 2014 (spring season), resulting in 12-sampled point counts per trail (3×4) and 156-sampled point counts for the entire study area (39×4). Only a single trail was sampled during a sampling day (between 05:40 to 08:00 a.m.), and we alternated the sampling point sequence during trail replications. Each point count was sampled for 15 min as recommended by Cavarzere *et al.* (2013). A single observer (GW) was responsible for sampling, and bird species were recorded using observations with the aid of a binocular (10×42) or vocalizations with the aid of a recorder (Sony PCM-M10) and the number of individuals were counted. Individuals that were detected flying were not considered in this study because no precise association could be made with habitat characteristics. The radius for detecting birds in each point count was 50 m, and was chosen to avoid the overlap of detection radius between points, ensuring that the same individual was not counted in different point counts. Moreover, the chosen radius eliminates bird records in peripheral habitats and maintains an association between birds and the measured habitat characteristics of a point (Lee and Marsden 2008).

Based on the number of observations per species in the sampling points, we first calculated the Index of Point Abundance (IPA) of each species at each of the 39 point counts (Bibby *et al.* 1992). The IPA was calculated by dividing the number of observations of the species at a specific point by the number of times the point was sampled (i.e. by 4). Then, we summed the IPA values from the three point counts of each trail, in order to obtain the relative abundance of each bird species per trail. These abundance values per trail were used in all analyses.

Environmental variables

To verify the influence of environmental variables on bird species abundance and composition, 10×5 m plots were

used to characterise the vegetation of each point count. Plots were positioned one meter from the centre of the point count (main trail), and placed on its right or left side (determined by the flip of a coin). The selected environmental variables are commonly used in the literature to describe the microhabitat of Atlantic rainforest birds (e.g., Lopes *et al.* 2006; Lee and Marsden 2008). Moreover, the environmental variables were selected because they are associated with several groups (different guilds) of birds (Lee and Marsden 2008). In each plot, the following vegetation characteristics were measured: (1) large trees (number of woody stems with >80 cm girth at breast height (gbh)); (2) medium trees (number of woody stems with 20–80 cm gbh); (3) small trees (number of woody stems with <20 cm gbh); (4) palms (number of palm stems ≥ 2 m height); (5) dead trunks (number of dead trunks); (6) herbaceous cover (visual estimate of the percentage of non-woody vegetation less than 2 m height covering the plot, with the exception of bamboo and ferns); (7) bamboo (visual estimate of the percentage of bamboo covering the plot); (8) ferns (visual estimate of the percentage of ferns covering the plot); (9) open understory (visual estimate of understory that is free from ferns, bamboo and shrubs); (10) vines and lianas (visual estimate of the percentage of vines and lianas in the plot). Plots were divided in four quadrants to facilitate visual estimates. For lianas and vines, we estimated the volume occupied in the plot, since they can occur from the understory to the canopy. Additionally, at each point, the percentage of canopy cover was measured using a photographic method (Suganuma *et al.* 2008). Altitude was also used as an environmental variable.

We also measured temperature and humidity during bird sampling using seven data loggers (NOVUS model LOG BOX-RHT-LCD) installed in the study area ([Figure 2](#)). The data loggers were configured to record temperature and humidity every two hours, resulting in 12 daily measurements. The following variables were obtained for each trail: (1) maximum temperature; (2) minimum temperature; (3) average temperature; (4) average of maximum temperatures; (5) average of minimum temperatures; (6) maximum daily temperature range; (7) average of daily temperature range; (8) maximum humidity; (9) minimum humidity; (10) average humidity; (11) average maximum humidity; (12) average minimum humidity; (13) maximum daily humidity range; (14) average of daily humidity range. As the number of trails was higher than the number of available data loggers, temperature and humidity data of each trail was obtained from the data logger located closest to the trail. For each environmental variable, we calculated the mean for each trail considering the three sampled points.

Spatial variables

Spatial relationship among sampling sites (trails) was also verified through the inclusion of spatial variables in the variation partitioning analysis (see below). To obtain the spatial variables, we used the geographic coordinate of the central point of the trails and the Principal Coordinates of Neighbour Matrices (PCNM) method as described by Borcard and Legendre (2002). The method consists of the following steps: (1) construct an Euclidian distance matrix between the sampled sites (trails) using the geographical coordinates; (2) truncate this distance matrix to retain only the distances among neighbouring sampling sites; (3) compute a Principal Coordinate Analysis (PCoA) on the truncate matrix to extract eigenvectors (Borcard and Legendre 2002; Borcard *et al.* 2011). Only eigenvectors associated with positive eigenvalues can be used as spatial variables (Borcard and Legendre 2002). The analysis was conducted in R version 3.1.1 (R Core Team 2014) with the *PCNM* package (Legendre *et al.* 2013).

Statistical analyses

Non-Metric Multidimensional Scaling (NMDS) with a Bray-Curtis distance matrix (Borcard *et al.* 2011) was used to verify differences in species abundance and composition between the northern and southern regions of MGSP. A stress value equal or lower than 20 was considered as the minimum threshold to evaluate if the generated NMDS adequately summarised the relationships between sample units (McCune and Grace 2002). For this analysis, abundance data of birds were square root transformed to reduce the effect of observations with very high values (Leps and Smilauer 2003; Borcard *et al.* 2011). Permutational Multivariate Analysis of Variance (PERMANOVA) with 9999 permutations was also used to test if the two regions of the forest fragment were significantly different ($\alpha = 0.05$) regarding bird abundance and composition. Both NMDS and PERMANOVA were conducted in R version 3.1.1 (R Core Team 2014) using packages *vegan* (Oksanen *et al.* 2018), *MASS* (Venables and Ripley 2002) and *BiodiversityR* (Kindt and Coe 2005).

Before conducting the variation partitioning (see below), forward selection of the explanatory variables was used as described by Blanchet *et al.* (2008). The purpose of this procedure was to pre-select a subset of significant predictor variables that explain the same amount of variance as the global model (i.e., model with all explanatory variables) (Blanchet *et al.* 2008). In addition, the forward selection seeks to avoid overestimation of the explained variance in bird species data (Blanchet *et al.* 2008), as well

as to reduce linear correlations between explanatory variables (Borcard *et al.* 2011). This selection of variables was applied separately to environmental and spatial variables using the package *packfor* (Dray 2013) in R version 3.1.1 (R Core Team 2014).

Finally, variation partitioning using partial Redundancy Analysis (pRDA) was conducted to evaluate the contribution of each group of explanatory variables (environmental and spatial) to the variation in bird communities (Borcard *et al.* 1992). This analysis quantifies the percentage of variance explained by the different sets of predictor variables controlling for the effect of one over the other (Borcard *et al.* 2011) resulting in the following components: (a) pure environmental effects; (b) shared effects of environment and space (spatially structured environmental variables); (c) pure spatial effects and; (d) unexplained variance (Borcard *et al.* 1992; Peres-Neto and Legendre 2010). The percentage of variance explained by the predictors is provided by adjusted R^2 (Peres-Neto *et al.* 2006) and significance was tested using ANOVA with 10000 permutations. For pRDA, bird species abundance was Hellinger-transformed as recommended by Borcard *et al.* (2011). The analysis was conducted in R version 3.1.1 (R Core Team 2014) using the *vegan* package (Oksanen *et al.* 2018).

Results

A total of 3,118 observations were obtained from 115 bird species throughout the entire study area. We obtained 1,517 observations from 97 species in the northern region and 1,551 observations from 101 species in the southern region of MGSP. Fourteen species were exclusive to the northern region while 18 were exclusive to the southern region. NMDS (Figure 3; stress 9.34) and PERMANOVA ($F = 6.417$, $R^2 = 0.368$, $P = 0.0001$) indicate that bird species abundance and composition are different for the northern and southern regions of MGSP.

Forward selection procedure of explanatory variables selected only two of the 26 environmental variables: bamboo (BB, $R^2_{adj} = 0.239$, $P = 0.001$) and average minimum humidity (U.medmin., $R^2_{adj} = 0.052$, $P = 0.003$). PCNM generated seven spatial descriptors (PCNM1 to PCNM7) and only PCNM1 was selected ($R^2_{adj} = 0.217$, $P = 0.001$).

Variation partitioning using only the pre-selected variables showed that environmental variables explained 29.2% ($R^2_{adj} = 0.292$, $P = 0.001$) of the variation in species abundance and composition, while spatial descriptors explained 21.6% ($R^2_{adj} = 0.217$, $P = 0.001$). The shared effects of environmental and spatial variables were 21.1% ($R^2_{adj} = 0.211$), which indicates that environmental and spatial variables were correlated and also

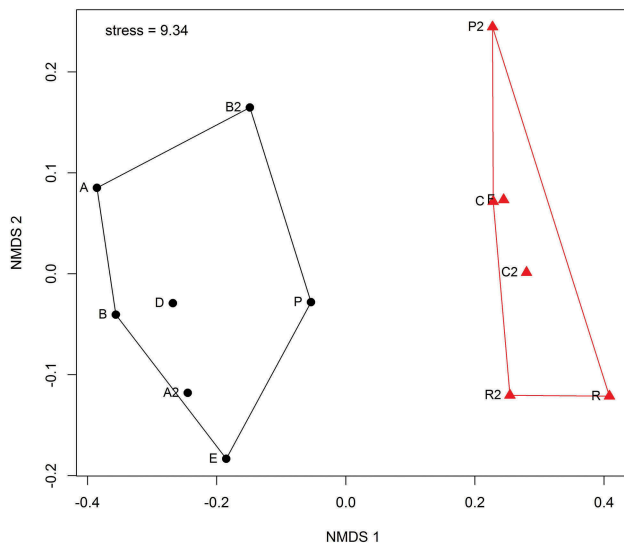


Figure 3. Non-Metric Multidimensional Scaling (NMDS) based on bird abundance in 13 trails (sample units) in Mata dos Godoy State Park, Londrina, north of Paraná State, southern Brazil. Trails of the northern region (black circles): A, A2, B, B2, D, E and P. Trails of the southern region (red triangles): C, C2, R, R2, P2 and F. Final stress: 9.34.

that environmental variables were spatially structured. When the effects of predictor variables were controlled for, only environmental variables explained a significant part of the variation (8%, $R^2_{adj} = 0.081$, $P = 0.006$), while spatial variables alone did not ($>1\%$, $R^2_{adj} = 0.006$, $P = 0.376$). Unexplained variance was 70% ($R^2_{adj} = 0.701$).

The RDA biplot based on samples sites (trails) and environmental variables (Figure 4) indicates that trails in the southern and northern regions of MGSP were separated mainly by the first RDA axis (21.7% of total variation explained), which was associated with bamboo cover. The second axis (7.5% of total variation explained) was associated with the average of the minimum humidity (Figure 4). The RDA biplot based on species abundance and environmental descriptors (Figure S1, supplementary material) also show that some bamboo specialist species (according to Parker III *et al.* 1996) were more abundant in the southern region.

Discussion

Our study revealed that a single forest fragment was capable of harbouring two distinct bird communities, and that natural environmental differences were responsible for determining bird species abundance and composition. This is important because the diversity of birds within the interior area of a single forest fragment could be associated to the fragment's internal

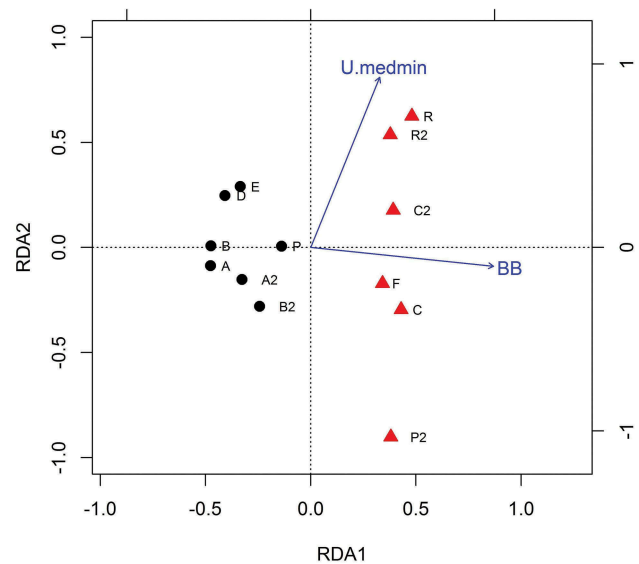


Figure 4. Biplot of pRDA representing the relationship between sample units and environmental variables in Mata dos Godoy State Park, Londrina, Paraná, south of Brazil. Arrows represent environmental variables: BB = bamboo cover; U.medmin = average of the minimum humidity. Trails of the northern region (black circles): A, A2, B, B2, D, E and P. Trails of the southern region (red triangles): C, C2, R, R2, P2 and F.

features, which suggests that natural habitat diversity can be just as important as other metrics, like fragment size, matrix composition and fragment connectivity.

Our results have important implications for the conservation of biodiversity in fragmented landscapes because it demonstrates an ecological process inside a single large forest fragment, which is yet to be properly considered in future studies on forest fragmentation. The results suggest that considering forest fragments as single ecological units can be misleading. In fact, forest fragments may have more than one main habitat, which can result in a higher contribution of a single forest fragment to the overall species richness of a fragmented landscape because of the increase in beta-diversity between the main habitats. The relevance of size and isolation of forest fragments as important determinants of species richness at the landscape level have been recently contested (see Fahrig 2017). Indeed, it was suggested that a set of several small forest fragments can support a higher number of species when compared to a set of larger fragments (Fahrig 2017; Fahrig *et al.* 2019). It has been argued that a set of small forest fragments would manage to encompass a greater diversity of habitats, and hence support species with different ecological requirements leading to higher beta diversity across the landscape (see Fahrig 2017; Fahrig *et al.* 2019; but see Fletcher *et al.* 2018). This highlights the importance of small forest fragments for the conservation of biodiversity. Our data suggest caution with such an approach. A forest fragment,

independent of its size, tends to harbour a single bird community if it presents homogeneous habitat features (Figure 1(a,b)), which should result in a lower number of species. However, if a large forest fragment contains heterogeneous habitat (e.g. different habitat types due to topographical variation; Figure 1(c)) it tends to harbour more than one bird community and, therefore, higher number of species, which would increase the overall beta-diversity in a given fragmented landscape. Moreover, in a continuous heterogeneous forest landscape, different communities are expected to occur and interact in complex ways (Haddad *et al.* 2017). Therefore, fragments that have high internal environmental variation could also maintain the coexistence mechanisms (e.g. Leibold *et al.* 2004) responsible for the maintenance of biodiversity in a landscape over time. For example, the preservation of species sorting dynamics, which preserve species richness, ecosystem functioning and stability, can be lost after the fragmentation process (Thompson *et al.* 2017). We argue that habitat diversity within and between forest fragments need to be adequately investigated before prioritizing which forest fragments should be conserved in a landscape.

We also found evidence that bamboo cover (*Chusquea* sp.) played an important role in driving the two interconnected but different bird communities in our studied forest fragment. It is known that bamboo tangles provide a distinct set of microhabitats and several bird species are specialised in exploiting resources associated with bamboo (Reid *et al.* 2004; Santana and Anjos 2010; Areta and Cockle 2012). For example, bamboo tangles can support a large variety of arthropods or produce large amounts of seeds that are food resources for insectivorous and granivorous birds (Areta and Cockle 2012). Also, non-specialist birds can benefit from the vegetation structure promoted by bamboo tangles, which are similar to other habitats like forest edges or vine tangles (Santana and Anjos 2010; Socolar *et al.* 2013). However, our study indicates that bamboo cover could affect the occurrence of numerous bird species to the point of differentiating bird communities within a single forest fragment and should be considered as a distinct habitat within the studied forest fragment. Because bamboo species are widespread across the tropical and subtropical regions, like Americas, Asia, Africa and Oceania (Areta and Cockle 2012), it is possible that bamboo tangles can be an important driver of bird community composition of forest fragments worldwide. Indeed, bamboo seems to be an important environmental factor driving the distribution of bird species particularly in the Neotropical region (Cockle and Areta 2013), such as in the Atlantic Forest (e.g. Santana and Anjos 2010) and Amazonia (e.g. Kratter 1997), as well as in temperate zones in South America (e.g. Reid *et al.* 2004). However, it is poorly documented

in other tropical and subtropical regions worldwide, and more studies are needed in other locations such as Asia.

Average minimum humidity, which was slightly higher and more variable in the southern region of the forest fragment, was also associated with species compositional change. This fact could be related to the presence of the Apertados River and its tributaries, which could maintain high levels of humidity. Also, proximity to rivers is a factor that can explain the higher diversity of riparian forest when compared to upland forests (Smith *et al.* 2007; Ewert *et al.* 2011). However, it is important to highlight that valley bottoms could have temporary water flows as a result of heavy tropical rain, which could help maintain high humidity levels. Effects of rivers and streams on birds are known in riparian zones from both tropical (Anjos *et al.* 2007; Mitchell *et al.* 2018) and temperate (Staufer and Best 1980; Glass and Floyd 2015) regions, mainly due to changes in floristic composition (Glass and Floyd 2015) and food availability (Petit *et al.* 1985; Smith *et al.* 2007; Ewert *et al.* 2011; Xiang *et al.* 2016). Therefore, differences in humidity may result in habitat differences, giving more evidence that measuring the amount of habitat using forest cover in fragmented landscapes can be misleading.

Other environmental factors could also affect bird species distribution. Plant species composition, for example, could be important drivers of bird species composition in tropical forests (Lee and Marsden 2008). Also, competitive interactions (Segre *et al.* 2014) and the presence of predators (Ellingsen *et al.* 2015) could help shape communities. However, these factors were not measured in our study, which could help explain the large amount of unexplained variance (70%). We recommend that future studies should try to assess these factors within forest fragments.

It is important to mention that our study did not correct species' abundance according to the detection probability of each bird species (i.e. occupancy models; *sensu* Mackenzie *et al.* 2005). The reason for not using detection probabilities was due to the low rates of occurrences for most of the bird species in our study area, which reduces the precision of detection probabilities. Considering our data set, only 30% of the species had contact numbers high enough to allow the proper use of occupancy models (Mackenzie *et al.* 2005). We believe that this would not be representative of the bird communities. It is actually very challenging to use this method in tropical birds communities in general because tropical species are usually rare and will have low rates of occurrence (as opposed to low rates of detection). Nevertheless, we adopted some procedures to reduce the effects of species detectability

variation in space and time. First, we chose a detection radius of 50 m in the point counts. A recent study has shown that the probability of detection is very high (close to 1) for several species (i.e., different acoustic signals) when the radius of detection is up to 50 m (MacLaren *et al.* 2018). We also concentrated the sampling period in one season (approx. 2 months), reducing possible biases in detectability due to species' temporal aspects. Moreover, each point count was sampled 4 times (alternating the hour of sampling; see methods) during the season to reduce the non-detection of some bird species according to the time (hour) of sampling and birds' acoustic behavior. Therefore, the field methods used are solid enough to test for the presence of different communities, despite not properly evaluating detectability.

Previous studies have already suggested the role of environmental differences in distinguishing interconnected communities. In the Andean region, Herzog *et al.* (2005) found different but connected bird communities along a sharp altitudinal gradient over short distances. Also, habitat heterogeneity associated with riparian zones is known to influence species distribution (Anjos *et al.* 2007; Xiang *et al.* 2016; Mitchell *et al.* 2018) allowing the maintenance of interconnected communities. Moreover, Gianuca *et al.* (2013) found a strong effect of environmental heterogeneity (e.g. vegetation height, sand cover) on species distribution among connected bird communities in a coastal ecosystem. However, to our knowledge, this is the first study that demonstrates the co-occurrence of two interconnected bird communities within the interior area of a single forest fragment. This indicates that some bird species could be dependent on the presence of particular environmental features within forest fragments, and that different habitats can be present in a single forest fragment, which in turn could increase species richness in a single forest fragment.

We conclude that forest fragments that have different natural habitats may present distinct bird communities within the fragment, and hence higher levels of biodiversity and ecosystem services and also complex interactions, which in turn should have high conservation value. Forest fragments harbouring interconnected but different communities may be passing undetected in fragmented landscapes. Therefore, we suggest that higher attention should be dedicated to understanding their individualities in order to properly conserve biodiversity in fragmented landscapes worldwide.

Geolocation information

Coordinates of the study area: 23°26'33.0"S 51°15'10.8"W.

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