JOSÉ CLEMENSOU DOS REIS JÚNIOR

PARTICIONANDO A DIVERSIDADE EM PAISAGENS AGRÍCOLAS: O VALOR DAS FLORESTAS E DAS AGROFLORESTAS DE CACAU NA CONSERVAÇÃO DE AVES

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Dissertação apresentada ao programa de Pós-graduação em Ecologia e Conservação da Biodiversidade da Universidade estadual de Santa Cruz, para obtenção do título de Mestre em Ecologia e Conservação.

Orientadora: Dra. Deborah Maria de Faria

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The value of cacao agroforest and native forests to the maintenance of bird diversity in anthropogenic landscapes in the Atlantic Forest

RESUMO GERAL

A pressão humana sobre as florestas tropicais tem resultado em paisagens nas quais os remanescentes florestais estão cada vez mais reduzidos e isolados por ambientes modificados (*i.e*. matrizes). Entre as matrizes mais amigáveis para a biodiversidade estão as agroflorestas, principalmente de café (*Coffea arabica* L.) e cacau (*Theobroma cacao* L.). No Brasil, a região do sul da Bahia é conhecida por ser uma das maiores regiões produtoras de cacau no mundo, nessa região encontram-se sistemas tradicionais de agroflorestas de cacau são conhecidas como cabrucas. Junto com as florestas nativas, estas agroflorestas de cacau compõem a cobertura florestal da região, além de contribuir com a manutenção da diversidade e endemismo de espécies da fauna e flora. O presente estudo teve como objetivo compreender a contribuição dos ambientes florestais e das agroflorestas para a manutenção da diversidade regional de aves (gama) em paisagens antrópicas da região do sul da Bahia, levando em conta a diversidade local (alfa) e a diferença na composição de espécies (diversidade beta). Além disso, avaliamos a influência de diferentes contextos de paisagem na determinação destes padrões, em especial, em agroflorestas e florestas inseridas em paisagens com grande cobertura florestal, mas variando na representatividade de cada um dos dois tipos de habitat, e em paisagens mais desmatadas com extensas áreas abertas, portanto, analisando a influência destes diferentes contextos de paisagem na determinação destes padrões e na manutenção da diversidade gama. Para tanto, foram amostrados seis fragmentos florestais e seis agroflorestas em três paisagens com diferentes contextos de matriz, totalizando 36 sítios. Para responder nossos objetivos utilizamos como ferramenta de análise a partição da diversidade taxonômica (alfa, beta e gama). As aves foram amostradas através do método de ponto de contagem, com quatro pontos no interior de cada sitio amostral, evitando 100m de borda, considerando a detecção dos espécimes num raio de 30m e, com distância mínima de 150m entre os pontos, com permanência de 15min do observador. Um total de 7001 espécimes de aves pertencentes a 17 ordens, 42 famílias, 141 gêneros e 183 espécies foram registrados nos 36 sítios amostrais. Destas, noventa e cinco espécies pertencem ao grupo de especialistas florestais enquanto que oitenta e cinco foram classificadas como generalistas. A proporção de especialistas florestais e generalistas varia de acordo com o contexto de paisagem e o habitat amostrado. No geral, florestas apresentaram mais espécies especialistas enquanto que os generalistas foram mais ricos em agroflorestas de cacau. Como esperado, a diversidade alfa foi sempre maior em sítios de floresta do que em agroflorestas de cacau em todas as regiões. Especialistas florestais apresentaram o mesmo padrão. Já os generalistas tiveram maior riqueza em agroflorestas de cacau. O componente beta variou entre paisagens e habitat, sendo que agroflorestas apresentaram beta maior para o grupo de especialistas florestais enquanto que as aves generalistas tiveram a maior beta em florestas. Destacamos que a diversidade regional de cada um dos três contextos foi mantida de formas diferentes. Sendo que a paisagem desmatada com áreas abertas manteve sua diversidade gama através de uma beta alta, enquanto que a paisagem com alta cobertura agroflorestal manteve através do componente alfa. Neste sentido, paisagens com alta cobertura agroflorestal se mostram melhores se comparados com paisagens com baixa cobertura florestal na conservação de aves, em especial das especialistas florestais, bem como na persistência das comunidades a longo prazo.

Palavras-chave: beta-diversidade; aves; agroflorestas de cacau; cabrucas, floresta tropical

ABSTRACT

Human pressure on tropical forests have been resulting in landscapes in which forest remnants are increasingly reduced and isolated by modified environments (*i.e.* matrices). Among the most biodiverse friendly matrices are agroforests, mainly coffee (*Coffea arabica* L.) and cocoa (*Theobroma cacao* L.) agroforests. In Brazil, the south of Bahia region is known as one of the largest cocoa producing regions in the world, in this region are located traditional systems of cocoa agroforest known as cabrucas. Along with native forests, those cocoa agroforests increase the forest cover of the region, and contribute to the maintenance of diversity and endemism of the flora and fauna species. The present study aimed to understand the contribution of forest and agroforest environments to the maintaining of the regional bird diversity (gamma) in human-altered landscapes of the southern region of Bahia, and a local diversity (alpha) and the difference in species composition (beta diversity). In addition, we evaluated the influence of different landscape contexts on these abovementioned patterns, especially in agroforest and forests inserted in landscapes with large forest cover, but varying in representativeness of each of the two types of habitat, and in more deforested landscapes with extensive open areas, then, analyzing the effect of different landscape contexts in determining these patterns and on maintaining gamma diversity. Therefore, six forest fragments were sampled six agroforest landscapes with three different contexts matrix, totaling 36 locations. In order to answer our objectives, we used the partition diversity (alpha, beta and gamma) as a tool for analyzing taxonomic diversity. Birds were sampled using the point-count method, with four points inside each sampling site, 100m from the edge, considering a sample detection within a radius of 30m and with a minimum distance of 150m between the points, with a permanence of 15min the observer. A total of 7001 specimens of birds belonging to 17 orders, 42 families, 141 genera and 183 species were recorded along 36 sample sites. Ninety-five species belong to forest-specialist group, while eighty-five were classified as generalist species. The proportion of forest specialists and generalists varied according to the context of the landscape and habitat sampled. In general, forests showed more forest-specialist species, while generalists were richer in cocoa agroforest. As expected, alpha diversity was always greater in forest habitat than in cocoa agroforest in all regions. The beta component varied between landscapes and habitat, as agroforest showing a higher beta for forest specialists, whereas generalist species showed a higher beta when considering forest habitat. We emphasize that the regional diversity of each of the three contexts was maintained by different ways. Deforested landscape with open areas maintained its diversity by high beta, while the landscape with high agroforest coverage was thru the alpha component. In this sense, landscapes with high agricultural coverage show better comparisons with landscapes with low forest cover in the conservation of birds, particularly forest specialists as well as the persistence of long-term communities.

keywords: beta-diversity, bird assemblages, cocoa agroforest, cabrucas, tropical forest

INTRODUÇÃO GERAL

As crescentes modificações do ambiente natural pelo homem têm transformado grandes extensões de florestas em paisagens antrópicas, geralmente com remanescentes florestais reduzidos e separados uns dos outros por matrizes inóspitas para grande parte das espécies (MATSON et al., 1997; RIBEIRO et al., 2009; FAHRIG, 2013) Entre as consequências mais drásticas para a biodiversidade está o isolamento espacial dos remanescentes, reduzindo a conectividade entre estas manchas (METZGER; DECAMPS, 1997). Este isolamento pode afetar o fluxo das espécies, principalmente das mais sensíveis às perturbações antrópicas, que tem capacidade de dispersão reduzida ou suprimida, principalmente pela ocorrência de matrizes que as desfavorecem, aumentando a dissimilaridade entre as manchas de habitat (*i.e.* diversidade beta local) (WANG et al., 2013, 2018; MORANTE-FILHO et al., 2016; COELHO et al., 2018).

Nas regiões tropicais, onde é reportado uma intensificação desses processos, os fragmentos florestais remanescentes sofreram diferentes níveis de isolamento, bem como estão estruturados em diferentes tamanhos e formatos (GIBBS et al., 2010; PARDINI et al., 2010; FAHRIG, 2013). No entanto, pode ser atenuado pela composição da matriz, ou o conjunto de hábitats modificados no entorno dos fragmentos (BOESING; NICHOLS; METZGER, 2018). Entre as matrizes mais amigáveis à biodiversidade estão as agroflorestas (FARIA et al., 2006; VAN BAEL et al., 2007; FERREIRA et al., 2018). Dessa forma, sistemas agroflorestais de café (*Coffea arabica* L.) e cacau (*Theobroma cacao* L.), por exemplo, tem sido reportados como eficientes atenuantes da perda de biodiversidade, principalmente nas regiões tropicais (TSCHARNTKE et al., 2011; MERTENS et al., 2018).

Diferente de outros métodos de agricultura não sombreadas (*e.g*. pastagem e monoculturas), as agroflorestas se destacam, principalmente, pelo seu potencial de manutenção de elevada riquezas de diferentes grupos: plantas (SAMBUICHI, 2006; FARIA et al., 2007), aves e morcegos (PINEDA et al., 2005; FARIA et al., 2006), mamíferos (FERREIRA et al., 2018), anuros e lagartos (FARIA et al., 2007), bem como de invertebrados (formigas, escaravelhos e borboletas) (PERFECTO et al., 2003; PINEDA et al., 2005).

Na região tropical do Brasil, a floresta Atlântica que uma vez cobriu quase toda sua extensão costeira, foi reduzida a menos de 12%, suprimidas pelo avanço da urbanização e de áreas destinadas a agropecuária (RIBEIRO et al., 2009; BARLOW et al., 2018). No sul da Bahia, região de floresta atlântica com grande riqueza de espécies e níveis altos de endemismo para a fauna e a flora, as plantações sombreadas de cacau são exemplos de matrizes com grande capacidade de reter biodiversidade (FARIA et al., 2006, 2007; CASSANO et al., 2009; CASSANO; BARLOW; PARDINI, 2012). De fato, parte da cobertura florestal no sul da Bahia é composta por floresta nativas e por agroflorestas de cacau, principalmente as conhecidas como cabruca (*i.e*. sistema tradicional de cultivo do cacau). Nestas cabrucas o cacau (*T. cocoa* L.) substituiu o sub-bosque da floresta nativa e algumas árvores nativas são deixadas para sombreamento (SCHROTH et al., 2011). Embora ocorra uma grande perda de espécies vegetais, as cabrucas ainda mantém complexidade estrutural similar a das florestas, com diferentes estratos de vegetação. Esta semelhança estrutural das cabrucas permite seu uso por várias espécies florestais, embora este ambiente também favoreça as espécies generalistas (FARIA et al., 2007; DELABIE et al., 2011).

No entanto, o potencial destas agroflorestas de cacau em abrigar espécies depende do contexto de paisagem no qual a agrofloresta está inserida. Faria e colaboradores (2006, 2007) mostraram que estas agroflorestas inseridas em paisagens com grande representatividade de florestas possuem mais espécies, cuja composição é mais semelhante a encontrada nas florestas, do que paisagens com grande predominância de agroflorestas. De fato, além das características do habitat local, a diversidade presente em um dado habitat é função da diversidade regional, onde cada mancha apresenta comunidades insaturadas, resultado da dinâmica de extinções locais e colonização do pool de espécies presentes na paisagem (TSCHARNTKE et al., 2005). Desta forma, diferentes habitats (*e.g.* florestas e agroflorestas) podem abrigar uma diversidade de espécies dependendo de caraterísticas locais, da diversidade alfa, – capacidade de prover habitat para estas espécies – e do contexto de paisagem, servindo de fonte de colonização. Além disso, dada a heterogeneidade das paisagens e de aspectos estocásticos da dinâmica de colonização e extinção local, existe uma diferença na composição de espécies entre manchas (diversidade beta) de mesmo habitat (intra-habitat) e, especialmente, entre manchas de hábitats diferentes (inter-habitat). Portanto, a diversidade regional de espécies se dá pela contribuição da diversidade local nos habitats (alfa) e pela diferença da composição de espécies entre hábitats ou manchas (beta).

Neste sentido, apenas riqueza e métricas taxonômicas comuns não permitem uma avaliação mais detalhada sobre a manutenção da diversidade regional de uma dada região. Assim, a utilização dos componentes das partições de diversidade permite a avaliação de processos importantes para manutenção das espécies (*e.g.* dispersão, colonização, extinções locais e aninhamento). Uma vez que a diversidade taxonômica pode ser mais sensível do que a avaliação de componentes funcionais e filogenéticos para perda da biodiversidade em paisagens fragmentadas (BOESING; NICHOLS; METZGER, 2018) a utilização da partição de diversidade mostra-se uma boa ferramenta para avaliação de remanescentes de floresta atlântica e agroflorestas. Os componentes da partição de diversidade taxonômica em diferente tipos de paisagens agrícolas e remanescentes florestais tem sido amplamente estudada (GOLODETS; KIGEL; STERNBERG, 2011; ESTRADA; RABOY; OLIVEIRA, 2012; MERTENS et al., 2018), sobretudo nos trópicos (FARIA et al., 2006; ARROYO-RODRÍGUEZ et al., 2013; MORANTE-FILHO; ARROYO-RODRÍGUEZ; FARIA, 2016) onde o papel das agroflorestas na manutenção de serviços ecossistêmicos e conservação de espécies tem sido analisado (SCHROTH; HARVEY, 2007).

Neste estudo, investigamos os padrões de partição hierárquica da diversidade, além da contribuição das florestas e das cabrucas para a manutenção da diversidade de aves no sul da Bahia afetadas por diferentes contextos de paisagem. Para tal, utilizamos as aves, pois representam um grupo conspícuo e bastante rico dos vertebrados, com grande importância na funcionalidade das florestas (STOTZ et al., 1996), além disso, mostram-se um excelente grupo bioindicador, dada sua sensibilidade à perturbações antrópicas (BETTS et al., 2019) bem como por sua alta diversidade e especialização (BELMAKER et al., 2012). Para tanto 3 paisagens antrópicas com diferentes contextos foram selecionadas. Posteriormente, a partir de uma base pré-selecionada de 80 sítios, 18 agroflorestas de cacau foram selecionadas aleatoriamente, tendo a mesma quantidade de sítios de floresta pareados. Todos os sítios amostrais estão localizados na floresta Atlântica do sul da Bahia, brasil. Região conhecida por deter uma das maiores biodiversidade do mundo, além de um elevado número de casos de endemismos (MYERS et al., 2000). Não obstante, a maior parte da extensão original desse bioma foi convertida em outros tipos de uso do solo para atender, principalmente, as demandas da crescente população humana na região (RIBEIRO et al., 2009). Todavia, no que concerne a trajetória do sul da Bahia, as transformações do uso do solo foram mais específicas e direcionadas ao cultivo tradicional de cacau, plantações de eucalipto e pastagem. Porém, apesar de seu histórico de perda da cobertura florestal original, a região abriga um dos maiores remanescentes de floresta atlântica do nordeste brasileiro, bem como importantes áreas de proteção da biodiversidade (IUCN, 2019). De maneira geral, esperamos encontrar uma diversidade alfa maior nas florestas do que nas agroflorestas de cacau, principalmente no que se refere a espécies florestais. Também esperamos encontrar uma diferença maior entre a composição de espécies (beta diversidade) inter-habitat do que intra-habitat. No entanto, prevemos que estes padrões sejam influenciados por diferentes contextos de paisagem.

OBJETIVOS GERAIS

Nosso trabalho tem por objetivo geral analisar a partição da diversidade taxonômica de aves em remanescentes florestais e agroflorestas de cacau em três contextos de paisagem, sendo 1. alta cobertura florestal e baixa representatividade de cabrucas; 2. baixa cobertura florestal e alta representatividade de cabrucas e 3. baixa cobertura florestal e baixa representação de cabrucas.

Como objetivos específicos:

- Avaliar a contribuição de cada tipo de habitat (cabruca e florestas nativas) e dos componentes alfa e beta na diversidade regional (gama) de aves;
- Identificar como mudanças no contexto de paisagem, principalmente no que diz respeito a redução da cobertura florestal afeta os padrões de partição da diversidade (alfa, beta e gama);

- Analisar a resposta dos grupos: especialistas florestais e generalistas de habitat frente as mudanças do contexto de paisagem.

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Capitulo I*

**Este capitulo será submetido a uma revista internacional e, na sua versão final, contará com a inclusão de co-autores*

The value of cacao agroforest and native forests to the maintenance of bird diversity in anthropogenic landscapes in the Atlantic Forest

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SUMMARY

The rapid and increasing human impact over tropical forests worldwide is a major driver of conversion of native forest into agricultural landscapes. Under these deforested and disturbed anthropogenic landscapes, biotic assemblages face new challenges to persist, making imperative to understand and identify how assemblages respond to such changes. Herein we assessed whether landscape context can affect bird assemblages in southern Bahia Atlantic rainforest, a region under high conservation priority. Using point count, we sampled bird assemblages in native forests and cacao (*Theobroma cacao* L.) agroforests in southern Bahia in three landscapes with distinct elements predominating: 1. Native forests, 2. Agroforests and 3. Open areas. We assessed the gamma (landscape-scale) diversity and partitioned into different components, alpha and beta diversity applying a multiplicative approach. As expected forested landscape showed the highest gamma diversity followed by agroforest and deforested landscape. Forest-specialist species were more related to forest while generalist to agroforest. Landscape immersed in agroforest showed as much local richness as high forested landscape, meanwhile more similarity within sampled sites due to connectivity capability. Interestingly, both forested and deforested landscapes showed the highest values of beta component, probably due distinct reasons. Our findings indicate that forest cover play a major role providing connectivity and enhancing diversity, especially of forest-specialist species. Despite cacao agroforest can smooth biodiversity loss they are not substitutes for native forest. Regional bird diversity is shaped by different trajectories of land-use change resulting in unsure long-term persistence of species, but also directly impacting on the perspective of regional conservancy. Once both cacao agroforest and forest remains are undergoing threats by law changes and unbridled deforestation. Therefore, conservation strategies should prevent either deforestation and retain the value of cacao agroforest by barring regulations that allows reduction of native tree per hectare.

Keywords: tropical forest; bird assemblage; land use change; taxonomic diversity; agroforest

INTRODUCTION

Human demands for natural resources have been increasing in the last decades (SALA et al., 2000). As a result of such pressure, forests around the world are being degraded and converted to other land uses, mainly for agriculture (STEFFEN et al., 2015). Such human-driven activities are increasingly reshaping biological communities across the world, particularly in tropical zones, which concentrate the highest amount of terrestrial biodiversity (FISCHER; LINDENMAYER, 2007; BARLOW et al., 2018). More and more, the remaining biodiversity is confined in anthropogenic landscapes in which not only forest amount decreases but, quite often, remnants are small and immersed within a variety of human-modified land uses that are often not avoided by the native biota (HOEKSTRA et al., 2005; RIBEIRO et al., 2009). In such deforested and fragmented landscapes, we often observe an erosion of habitat specialists due to a combined result of habitat loss and forest fragmentation effects, such as the increasing distance among remnants and the larger proportion of edge habitats (CARRARA et al., 2015; MORANTE-FILHO et al., 2015).

However, some types of man-made land-uses are known to host high levels of biodiversity (WALDRON et al., 2012). This is the case of some agroforest systems, in which crops such as coffee (*Coffea arabica* L.) and cacao (*Theobroma cacao* L.) are shaded by canopy species (FARIA et al., 2006; MERTENS et al., 2018). By maintaining a vertical structure, more simplified but similar to native forest, and in some cases species of native trees, these agroforests maintain environmental conditions similar to their original habitats including local microclimate (RICE; GREENBERG, 2000; LIN, 2007; DE BEENHOUWER; AERTS; HONNAY, 2013). For instance, the cacao agroforests are known to provide supplementary or additional habitat for a variety of species, and might function as corridors between habitat patches (*i.e.* this system is considered a biodiversity-friendly matrix) (RICE; GREENBERG, 2000; SCHROTH; HARVEY, 2007; CASSANO et al., 2009; DELABIE et al., 2011; ESTRADA; RABOY; OLIVEIRA, 2012). Although cacao agroforests hold a high richness of species, even some forest specialists, the species assemblages are most composed by habitat generalists, resulting that agroforest systems are not replaced of native forests (PARDINI et al., 2009; FERREIRA et al., 2018).

The species diversity reported in a given agroforest is partially mediated by the landscape context and partially by local management. For instance, the amount of landscape forest cover surrounding the patch (FARIA et al., 2007), distance of nearest forest patch (LAUBE et al., 2008; CLOUGH et al., 2009) and local vegetation structure (SAATCHI et al., 2001; FARIA et al., 2006), will determine local species composition (ARROYO-RODRÍGUEZ et al., 2007; VIEIRA et al., 2009; CABRERA-GUZMÁN; REYNOSO, 2012). This is in accordance with the general idea that the extent to which a human-modified landscape can maintain biodiversity is the result of different processes operating at distinct spatial scales, including the intrinsic features of local habitats and the landscape-scale composition. The knowledge of the actual contribution of each spatial scale to overall diversity remains among the important information required to adequately support conservation actions. For instance, the gamma diversity (γ) or the total number of species in a given landscape is a function of two diversity components: alpha and beta diversity ($\alpha + \beta$ or $\alpha * \beta$, following JOST, 2007) that are scale-dependent. Thus, the partition of species diversity has been widely applied to assess and identify the contribution of multiple spatial and temporal scales to regional species diversity in fragmented landscapes (*e.g.*, WAGNER et al., 2000; RIBEIRO et al., 2008).

In order to design strategies to curb the current erosion of biodiversity and ecosystem services, it is important to understand how different components of biodiversity are affected by local and landscape-scale changes. Particularly, it is also key to identify whether different combination of habitat types and landscape contexts could optimize biodiversity representation in anthropogenic landscapes. Herein we addressed these questions assessing bird diversity in southern Bahia. We hypothesized that the diversity of bird assemblages in agricultural landscapes, including forest specialists and habitat generalists, is modulated by regional features of different habitat categories and by the amount of forest cover remaining in the landscape, that ultimately affect alpha and beta diversity. Specifically, alpha diversity would be enhanced in more structurally complex habitats (such as native forests), particularly for those forest specialists and with an increasing representation of such complex habitats in the matrix, thus providing constant influx of migrants. Similarly, beta diversity is magnified by a higher structural contrast between a given habitat and its surrounding matrix (FAHRIG, 2003). We then accessed the differential response of total bird assemblages, habitat specialists and habitat generalists in two habitat types, *i.e.* native forests and areas of cacao agroforests, immersed in three distinct landscapes: 1. dominated by open areas, with low amount of both forest and agroforests (low forest cover - LFC); 2. dominated by agroforests, with low amount of native forests and open areas (high agroforest cover – HAC); 3. dominated by native forests, with low representation of agroforest and open areas (high forest cover – HFC). We expect that: 1. overall, bird diversity in forests will be higher than the observed in cacao agroforests, 2. particularly for those forest specialists while 3. habitat generalists will be higher in cacao agroforest than forest, showing an opposite pattern to forest-specialist. We also predict that: 4. gamma and alpha diversity of birds will increase in landscapes with higher levels of forest cover (*i.e.* forest + agroforest cover), particularly native forest cover. In addition, 5. in landscapes with a higher amount of open areas, beta diversity will be higher compared with the other two landscape contexts, due to a higher species turnover of forest-specialists, particularly among forest sites compared with cacao agroforests, with 6. alpha diversity being higher in forest patches than cacao agroforest. By pinpointing how different spatial components can optimize bird diversity in biodiversity-rich region is an important step to address strategies to safeguard its conservation.

MATERIALS AND METHODS

STUDY AREA

This study was carried out in southern Bahia state, in northeast Brazil (Figure 1), within the Atlantic forest hotspot (MYERS et al., 2000). This region had its native forest converted into a plantation of rubber trees, eucalyptus and cacao agroforest (*Theobroma cacao* L.) and open areas for cattle pasture and human settlements (PARDINI, 2009). The cacao agroforest, most composed by traditional systems (*i.e*. understory removed and replaced by cacao trees) – the shade plantation as known as cabruca – is the main land use and their region is considered the centre of cacao production of Brazil (SCHROTH et al., 2011). The vegetation in southern Bahia is classified as a lowland rainforest (OLIVEIRA-FILHO; FONTES, 2000). The weather in this region is hot and humid, with 1500 mm of mean annual rainfall, an average temperature of 24 ºC, and no dry season (MORI et al., 1983).

STUDY LANDSCAPES

We used ArcGIS software and recent satellite images (QuickBird and WorldView, from 2011; RapidEye, from 2009 to 2010), we created digital maps with a scale of 1:10 000, which is adequate for identifying land cover patches based on the visual inspection of differences in colour, texture, shape, location, and context. The remaining patches were classified according to different forest types following the typologies provided by IBGE (2006). Then, we selected three regions established as landscapes based on differences in land use patterns described below:

1. HFC - High forest cover: The first landscape is located in Una municipality (15°17’36’’S e 39°04’31’’W; Figure 1- a). It is characterized by a higher percentage of forest cover (57%), including two protected areas: Reserva Biológica and Refugio da Vida Silvestre de Una; low agroforest cover (9%), and low extension of open area (20%);
2. HAC – High agroforest cover: The second one is located in Ilhéus and Uruçuca municipalities (14°35’35’’S e 39°17’04’’W; Figure 1- b). It is characterized by low forest cover (22%), high agroforest cover (48%), with a low extension of open areas (14%);
3. LFC – Low forest cover: The third one is located in Belmonte municipality (15°51’47’’S e 38°52’58’’W; Figure 1- c). It is characterized by low forest cover (34%) and low agroforest cover (<1%), with the presence of eucalyptus plantation (4%) and larges extension of open areas (60%).

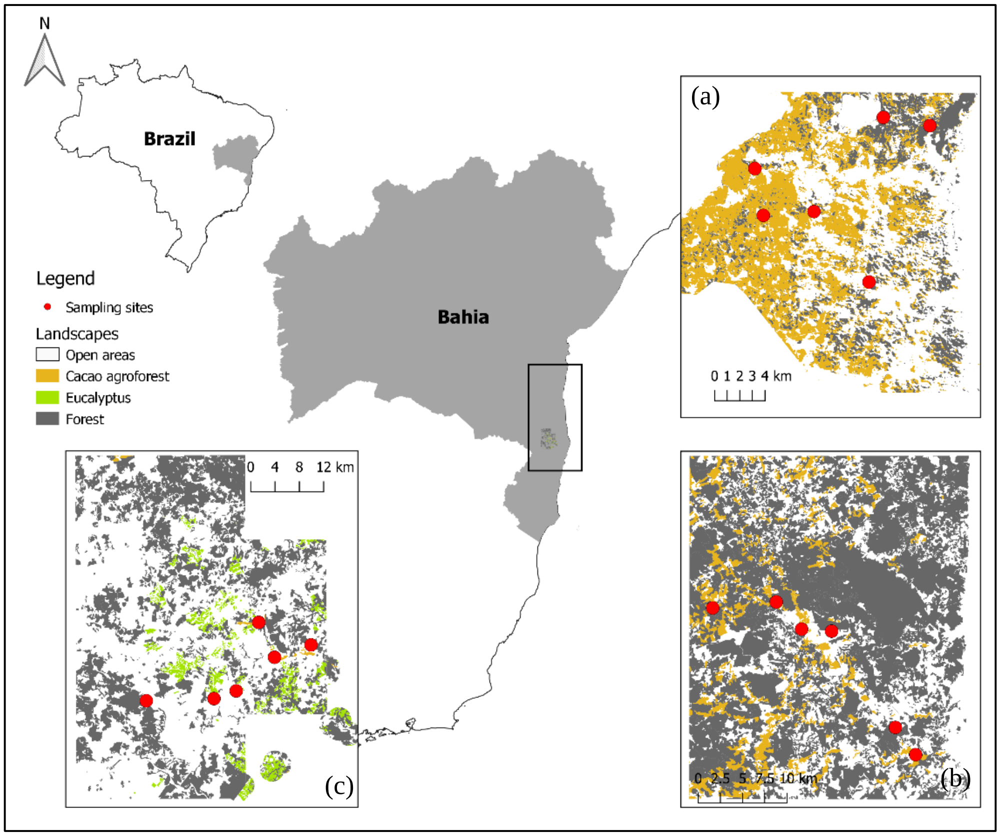


Figure 1. Study area in the southern Bahia, Brazil. We show land cover classes and sampling sites distribution across the landscapes studied. (a) municipality of Ilhéus – HAC; (b) Una – HFC; and (c) Belmonte – LFC.

To choose the sample sites, we preselected 80 agroforest sites. Subsequently, within each landscape, we randomly selected six cacao agroforest sites and six paired forest sites. The minimum distance between two sample sites of the same habitat was 2 km to ensure sample independence and avoiding a minimum of 100 m from the nearest edge, to minimize edge effects. Therefore, we sampled 12 sites in each landscape, totaling 36 sites. The Euclidian distance between sites was similar among our three landscapes (ANOVA, F = 0.64, *P*-value: 0.053), ranging 3.75 to 19.4 km in HCA (11.3 ± 4.81 km, mean ± SE), from 3.40 to

28.3 km in HFA (14.0 ± 7.98 km, mean ± SE) and from 2.44 to 28.6 km in HOA (13.4 ± 7.01 km, mean ± SE).

BIRD SAMPLING

We used the point-count method (BIBBY et al., 1992) for sampling bird assemblages in two field campaigns: February to April 2019 and May to July 2019. All sites (agroforest and forest) were sampled once in each campaign. Within each site, we established four sampling points, with a 30 m radius each, separated by a minimum distance of 150 m apart. We recorded all birds seen and heard (presence and abundance of each species) at each point-count during 15-min throughout the periods of greatest bird activity: between 05h30 and 08h30, and between 14h00 and 17h00. Therefore, our sampling effort per site was 4 h (2 field campaigns x 4 point-counts x 2 periods x 15-min). We used a 10 x 42 Bushnell binoculars to identify the birds and a digital recorder to record their vocalizations. When necessary we confirmed bird identification by our own collection. We also used field guides (RIDGELY et al., 2015) for identification. We adopted the scientific nomenclature used by the Brazilian ornithological records committee (PIACENTINI et al., 2015). Finally, we classified bird species as forest specialist and habitat generalist species based on previous study in the region (MORANTE-FILHO, et al., 2016) and scientific literature (STOTZ et al., 1996). Endemic species of Atlantic forest but also species from forested habitats of the Atlantic and Amazon forests were classified as forest species. Whereas species from other biomes or those that uses a variety of habitats including open areas and anthropogenic areas were classified as generalists.

DATA ANALYSES

We analyzed birds assemblages into two ways: considering the entire community and separating bird community according to two habitat use categories: forest-specialist and generalist of habitat with multiplicative diversity decompositions of Hill numbers: ${}^{q}D_{\gamma} = {}^{q}D_{\beta} * {}^{q}D_{\alpha}$. Here, ${}^{q}D_{\gamma}$ corresponding to the total pool of species observed (gamma diversity), ${}^{q}D_{\alpha}$ representing the average number of species at a local-scale (alpha diversity) and ${}^{q}D_{\beta}$ accounting to the differences in species' composition between local assemblages (beta diversity). In this case, each component of diversity depends of the q (*i.e.* q = 0, 1 or 2), which determines the sensitivity of component into different criteria (see JOST, 2007). Here we addressed our analyses giving $q = 0$. We used the package *entropart* (MARCON; HÉRAULT, 2015) for R free software (R Development Core Team 2018) to conduct our analysis of meta-community. Our sampling efforts were reasonably accurate once our sample coverage were all above 0.8 (see Appendix S1 in supporting information).

RESULTS

We recorded 7001 specimens of birds belonging to 17 orders, 42 families, 141 genera and 183 species across all 36 sites. Ninety-five species were classified as forest-specialist and 85 habitat generalist. The number of species: was higher in the most forested landscape (HFC– 164 species), followed by the landscape with highest cacao agroforest cover and low open areas (HAC – 127 species), and the landscape with the lowest forest cover and highest open area cover (LFC– 123 species). Indeed, HFC was composed by 52% of forest specialist (n = 85) and 48% of generalist of habitat (n = 78); likewise, HAC exhibited 57% of forest-specialist (n = 72) and 43% generalist of habitat (n = 54); while LFC was showed 49% forest-specialist (n = 59) against 51% generalist species of habitat (n = 62).

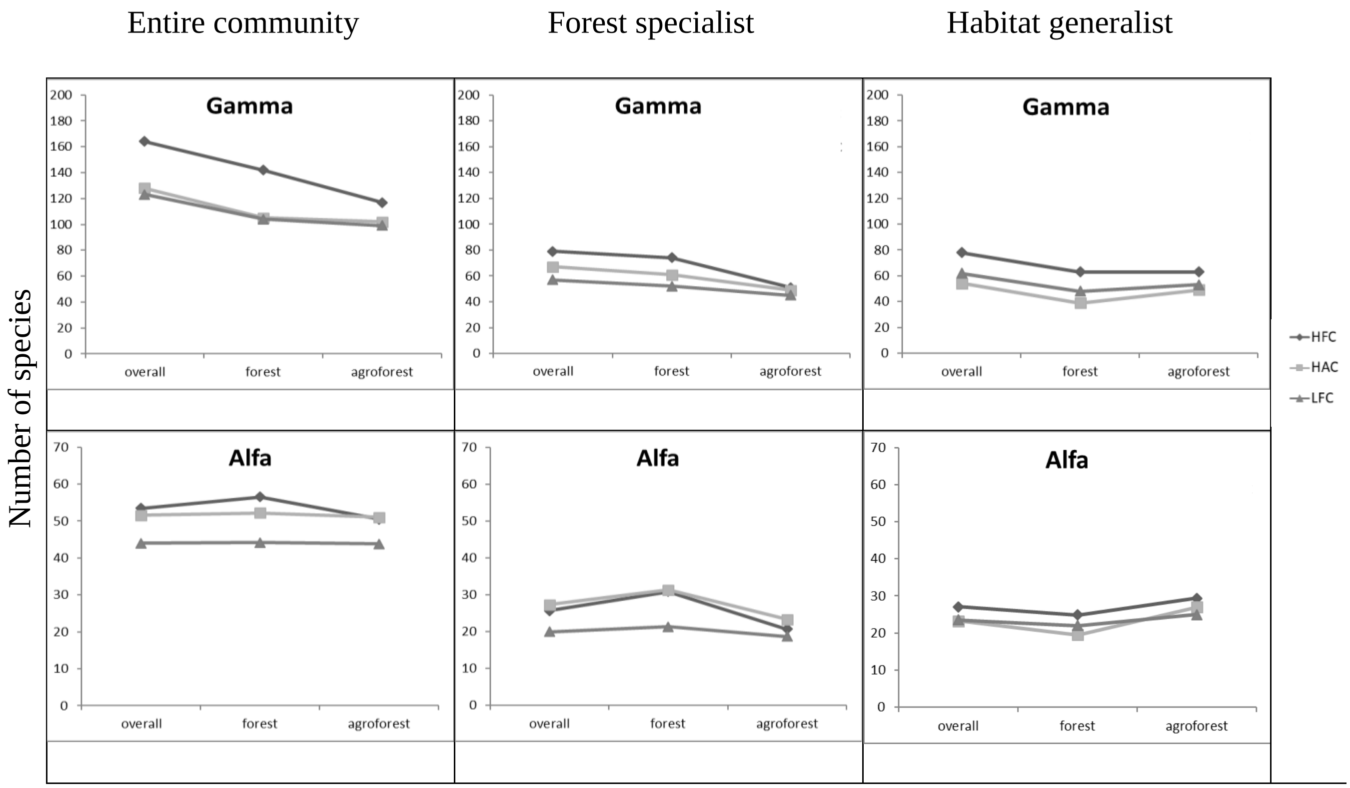
The most commonly detected species, varied by in each landscape as follow: HFC – with *Brotogeris tirica*, *Eupsitulla aurea*, *Aratinga auricapillus* as generalist of habitat and *Pionus maximiliani*, *Cacicus cela* as forest-specialist; HAC – three out of five most abundant species were forest specialist (i.e *Pyrrhura leucotis*, *C. cela* and *Tangara seledon*) and the other were generalists (*B. tirica* and *E. aurea*); and LFC – of five most abundant species four were generalist species being all of them parrots (*i.e. A. auricapillus*, *E. aurea*, *Diopsittaca nobilis* and *B. tirica*) and only *C. cela* as forest specialist.

Components of taxonomic diversity

Bird diversity, assessed through the different taxonomic components, varied according to the landscape-scale context. Overall, total species richness in each landscape context and habitat type was composed by similar representation of habitat specialist and generalists (Figure 2). Interesting, this pattern remains when accounting for total species, and when the assemblages are considered separately, *i.e.* either forest specialists or habitat generalists (Figure 2).

In general, forests supported more species, and more forest specialists, than agroforests, particularly when immersed in HFC but with similar values considering both HAC and LFC. Landscapes with higher amount of forest cover (HFC) comprised higher gamma diversity compared with other two assessed contexts - HAC and LFC – which showed similar values.

The partitioning of gamma diversity, however, revealed that for landscape context each component distinctively contributed to the detected patterns. The high gamma diversity observed on HFC landscapes is due to a combination of high number of average species richness within sampling sites (alpha) and a high degree of species turnover among sampling sites (beta). In such landscape, forests and agroforests showed high values of alpha and beta diversity of forest-specialists, but sites of both habitats also showed high levels of species turnover. Interesting, HFC values of alpha and beta diversity components were similar, respectively, to those observed for HAC and LFC.



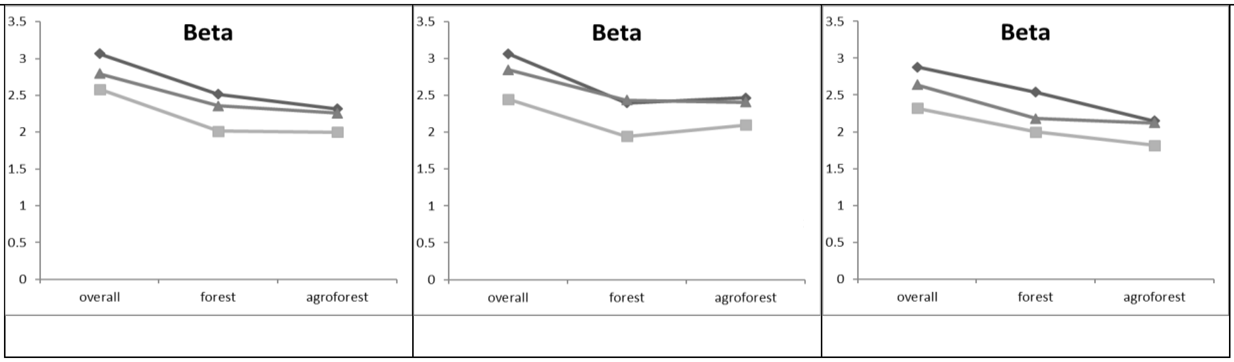


Figure 2. Components of multiplicative partition of bird species diversity of total species and those forest specialists and habitat generalists along sampling sites of two habitat categories (native forests and cacao agroforests) within three distinct landscape contexts (HFC: highly forest cover, HAC: high agroforest cover and LFC: low forest cover, see legend). We measured species diversity considering the Hill numbers (q = 0, thus not considering species abundance); Y axis of gamma and alpha components shows richness, while y axis of beta component shows the amount of effective communities and varied from 0 to 6 (number of sampled communities).

DISCUSSION

Our findings corroborated the key role played by native stands in maintaining diverse bird assemblages in anthropogenic tropical landscapes. This supports the general idea that habitat loss is one of the main threats to biodiversity (FAHRIG, 2013). Our study highlights three important findings: (i) native forests harbor a higher number of species, particularly forest-specialist, but landscape-scale context is key to mediate patterns of bird diversity in anthropogenic landscapes, (ii) highly forested landscapes, optimize bird species diversity due to high levels of local diversity (alpha) and a high dissimilarity among different patches (beta), and that (iii) even highly modified landscapes can still hold high levels of gamma diversity due to different contributions of alpha and beta components, which are dependent of the landscape-scale context.

Responses of species assemblages and diversity components

It is well known that species respond idiosyncratically to anthropogenic disturbances (BARLOW et al., 2016). In general, endangered species were associated more with forest habitat than agroforests, especially within more forested landscapes. This is the case of the endangered species a hummingbird – *Glaucis dohrnii* and ten vulnerable species of which representatives of parrots, toucans, cotinga and antbirds by IUCN categories (see Appendix S2 in supporting information).

Highly forested landscapes showed the highest gamma diversity, most hosted within forest habitats, compared with the other two landscapes assessed. Overall, deforestation and disturbance lead to a considerable loss of diversity of forest-dependent species (FAHRIG, 2013; BREGMAN et al., 2014). In such landscape context, it is clear the larger contribution to gamma is attributed to the forest specialists within the forest habitats. Indeed, despite the structurally complex nature of the agroforests, previous studies in the region (FARIA et al., 2006, 2007) and elsewhere (HARVEY; GONZÁLEZ VILLALOBOS, 2007; SEKERCIOGLU, 2012) have shown that many forest birds specialists can only be reported in native stands, some of which only in most preserved ones. By contrast, the cacao agroforests are described as an ecotone, often comprising a mix of forest-specialists and open area species, with a particular larger representation of the latter group (FARIA et al., 2006).

Yet, this abovementioned pattern is considerably altered depending on the landscape-context. Despite differences in the representation of native and modified habitats, gamma diversity was similar in high agroforest and deforested landscapes, with both habitat types equally contributing to such pattern. But when analysing each ecological group, forest specialists contributed more to gamma diversity in agroforest landscapes while the opposite pattern – more generalists – was observed contributing to gamma in deforested landscapes. Quite often, as disturbance levels increases, the loss of specialists due to disturbance is followed by an increasing representation of generalists. This compensatory dynamic illustrates a situation in which a significant turnover in species composition, rather than the numeric change in overall species richness or abundance, represents the signature of disturbance (MORANTE-FILHO et al., 2015). Therefore, even considering that both landscape contexts can host similar species richness and that the cacao agroforests can harbor more generalist species, the high representation of forest coverage at the landscape-scale enhances the representation of forest-dwellers.

The partitioning of the gamma diversity into alpha and beta components reveals key features explaining the observed patterns. The high gamma diversity reported for high forest cover landscape is a combination of high values of alpha (mean local species richness) and beta (high species turnover among sites) diversity. Thus, each site immersed within these highly forests landscapes harbor an average high number of species, particularly due to the contribution of forest sites hosting on average a high number of overall species, but mostly from forest-dwellers, while shade plantations host relatively lower species richness, but a high representation of generalists. Interesting, these values and the overall pattern of alpha diversity are similar for the high forest cover and high agroforest cover landscapes.

It is well stablished that landscapes composed by high amount of forest cover decrease inter-patch distance facilitating movement of species. In such a context of continuous influx of individuals, patches can maintain high levels of local diversity (alpha), particularly regarding forest specialist species. Because structurally complex matrices such as cacao agroforests may also increase landscape connectivity, landscape context favors maintain the influx of individuals among patches, thus the alpha diversity. Therefore, the connectivity provided by the presence of a large arboreal cover at landscape scale – native stands or agroforests – is key to allow high levels of local diversity (LAURANCE, 1997; HARVEY; GONZÁLEZ VILLALOBOS, 2007; CASSANO et al., 2009; JOSE, 2009). Indeed, similar levels of alpha diversity were not enough to result in the same gamma diversity in both landscape context, which reinforce the importance of the maintenance of forest habitats as the ultimate source of forest species. However, it does illustrate the potential of forest matrices to somehow mitigate the negative impact of the loss of native habitats, increasing the potential of local patches to provide habitat for many species (JOSE, 2012). By contrast, it is clear that dispersal limitation within a more hostile matrix such as pastures on the low forested landscape is limiting the alpha diversity. Despite their ability to fly, many bird species are poor dispersers (FAHRIG, 2007; PÜTTKER et al., 2015). Matrix quality can actually restring sensitive species, generally forest-dwellers, to movement through the matrix surrounding forest patch, which become more isolated in those patches or even agroforest (BÉLISLE; DESBOCHERS; FORTIN, 2001). Accordingly, the nature of the matrix is a strong predictor of species persistence (MORANTE-FILHO et al., 2016), and therefore, species tolerance on the use of the matrix is a major ecological correlate to vulnerability in modified landscapes (BREGMAN et al., 2014). In contrast with the more permeable matrices, in landscapes dominated by pastures and other deforested habitats there is an increasing likelihood of stochastic extinction in small habitat patches, which is not offset by migrants as the isolation among patches increases (HANSKI, 1998; SCHOEREDER et al., 2004). This dynamic may explain the low capacity of sites within deforested landscape to harbor high levels of local (alpha) diversity.

We observed that both high and low forested landscapes showed similar values of beta diversity, higher than those observed for the high agroforest cover landscape. In both former landscapes, the high value of beta diversity considering all species is characterized by an increasing in the number of effective communities of generalists among forest sites, particularly in the highly forested landscape. The isolation among habitat patches – both agroforests and native stands – provided by a predominant inhospitable matrix of open areas (pastures, annual crops) is probably a major feature increasing the dissimilarity level of bird assemblages in the more deforested landscape. Indeed, Morante-Filho et al., (2016) have already reported high levels of beta diversity of bird assemblages among forests sites in this deforested landscape, a pattern mainly explained by local (differences in forest structure among sites) and landscape-scale (more homogeneous) features, but also accounted by the variability of forest-specialists – not generalists – among sites. By contrast, landscapes with high forest coverage may have a high beta diversity due to a high range of niche due to the presence of different forest stages present in the region; or yet, factors such as the size of the forest remnants may have influenced the high beta diversity in this landscape, since small fragments are poorer in wealth compared to large blocks (VIEIRA et al., 2009).

CONCLUSIONS

This study highlights the importance of partitioning the diversity components to understand patterns of regional diversity and to detect which component most contribute to maintain species diversity. Altogether our study provide evidence for the importance of native stands to assure species persistence, but it also reinforces the key role of landscape-scale connectedness and heterogeneity to enhance biodiversity. Such knowledge is key to support conservation recommendations to anthropogenic landscapes.

As the representation of native forests decrease in the landscape, gamma diversity decreased. Nevertheless, even when the total amount of landscape-scale forest cover is dramatically reduced (<34%, see study landscapes section), different landscape context can maintain part of the local biota, by either providing permeable matrices or comprising habitat islands with dissimilar but representative species subset. Our study reinforces the early notion that, in our region, dispersal limitation and environmental filtering are important forces shaping bird assemblage (MORANTE-FILHO et al., 2016). We also highlight that cacao agroforests are not substitutes for native stands but their presence as economically productive and structurally complex matrices play an important role buffering biodiversity loss. These agroforests may provide main or secondary habitats, supplying food and other resources to a large number of animal species (FERREIRA et al., 2018). At the same time, these agroforests also increase habitat heterogeneity at landscape-scale, thus increasing the regional species diversity. These habitats can be particularly important in highly deforested landscapes, by increasing the representation of disturbed but structurally complex habitats that may serve as refugee for many species. Indeed, these agroforests showed similar levels of alpha diversity of forest-specialists to the observed in nearby native forests, despite a higher representation of generalist species.

However, it is important to note that the remaining Atlantic forest in southern Bahia, as well as the cacao agroforests are under threat. The region championed the highest deforestation level from all the Atlantic forest in 2016 (*i.e.* 12.288 hectare lost) (FUNDAÇÃO SOS MATA ATLÂNTICA, 2017), and no major efforts are seeing to curb such illegal trend. Meanwhile, a recent law allows farmers to decrease shading levels of cacao agroforests by selective cutting the shading trees, possibly decreasing the value of such system to host biodiversity. It is therefore imperative to address the possible impact of such trends in land use changes and how different components of diversity could mitigate species loss.

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SUPPORTING INFORMATION

The value of cacao agroforest and native forests to the maintenance of bird diversity in anthropogenic landscapes in the Atlantic Forest

José Clemensou dos Reis Junior and Deborah Faria

Appendix S1 Sample coverage by *entropart*.

We run *MetaCommunity* function from entropart package - MetaCommunity(Abundances, Weights = rep(1, ncol(Abundances))) - to create each object and then analysed the taxonomic components. Then, we run the function *summary* with the object from our meta-community created. This function allows us to see outputs of sample coverage values from a given meta-community. Our sample efforts were above 0.80 in all landscapes, habitats and bird's groups. Overall coverage can be viewed in the plot bellow:

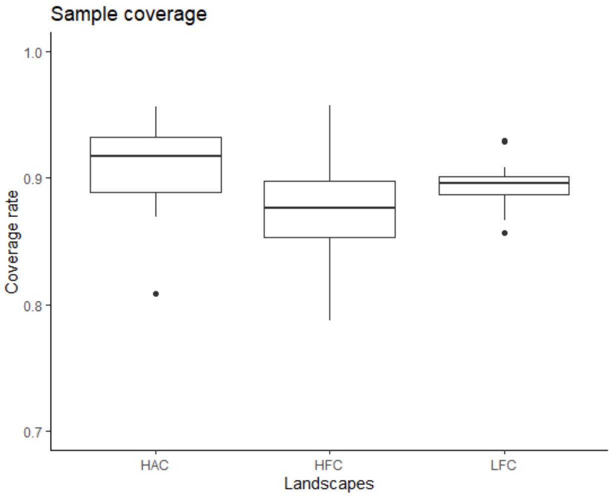

Figure 1. Sample coverage vary from 0 to 1 where 0 is insufficient sample effort while nearby 1 is a completely sampling community.

Figure 1 S1. As described in methods, we used the multiplicative approach of partitioning of taxonomic diversity with Hill numbers. This is in accordance with (JOST, 2007, 2010) that showed multiplicative method is the best way to decompose gamma diversity into independent alpha and beta components. Besides Hill numbers covered q=0, 1 and 2 but here we used only q=0 that correspond to species richness in a given assemblage.

Appendix S2. List of endangered species of bird by IUCN.

The forest-specialist species were analyzed by their threat degree as described in the IUCN Red List of Threatened Species. Version 2019-3. Categories comprise Data Deficient - DD, Least Concern - LC, Near Threatened - NT, Vulnerable - VU, Endangered - EN, Critically Endangered - CR, Extinct in the Wild - EW and Extinct - EX.

Table 1. List of threatened species. Values correspond to presence and abundance in each sampled landscape /habitat. HFC - High forest cover landscape; HAC - High agroforest cover landscape and LFC - Low forest cover landscape. Agro and For are short term to Agroforest and Forest habitats, respectively. Col "status" correspond to IUCN categories as described above.

Taxa	HFC agro	HFC for	HAC agro	HAC for	LFC agro	LFC for	STATUS
Acrobatornis fonsecai	1	0	0	0	0	0	VU
Amadonastur lacernulatus	0	1	0	0	0	0	VU
Amazona rhodocorytha	4	3	0	6	17	19	VU
Carpornis melanocephala	0	2	0	0	0	0	VU
Glaucis dohrnii	1	1	0	0	0	0	EN
Myrmotherula urosticta	0	4	0	3	0	0	VU
Procnias nudicollis	0	5	0	3	0	0	VU
Pyrrhura leucotis	55	26	160	67	36	12	VU
Ramphastos vitellinus	4	6	1	13	0	3	VU
Touit surdus	5	4	0	4	0	0	VU
Xipholena atropurpurea	1	0	0	0	0	0	VU