PPG Ecologia & Conservação

Universidade Estadual de Santa Cruz

Aves em paisagens antrópicas: desvendando os impactos de mudanças na cobertura do solo sobre grupos ecológicos e processos ecossistêmicos

Birds in human-altered landscapes: unraveling the impacts of land cover change on ecological groups and ecosystem processes

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Ilhéus, Brasil

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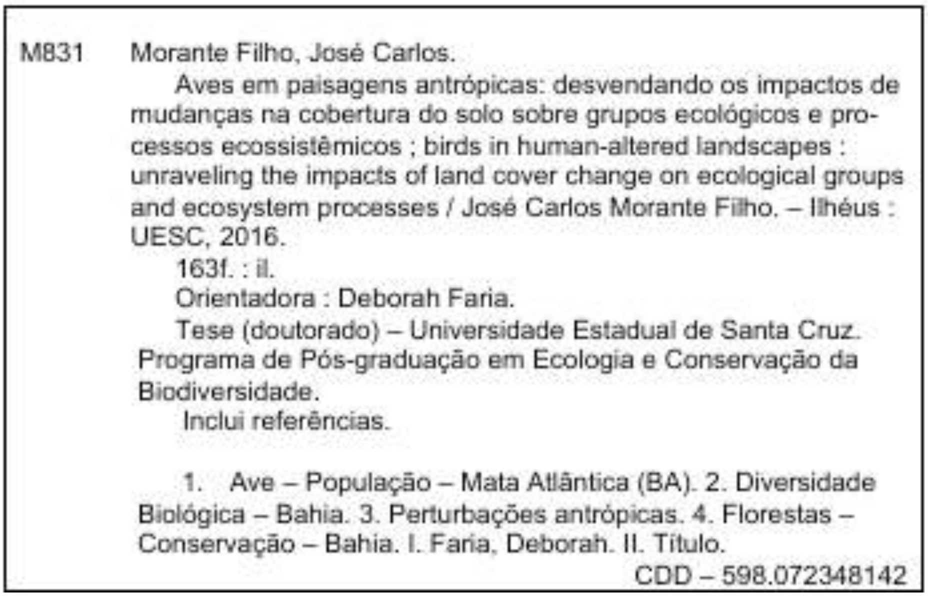

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Resumo

Mudanças na quantidade e qualidade dos hábitats naturais tem impactado negativamente a biodiversidade, especialmente em florestas tropicais que continuam sendo desmatadas a taxas alarmantes para suprir as necessidades da população humana. Apesar de haver uma extensa literatura dos efeitos da fragmentação e perda de hábitat sobre a biodiversidade, não existe um consenso acerca da dinâmica das comunidades biológicas em paisagens antrópicas, e principalmente falta informações de como processos ecológicos essenciais para o funcionamento dos remanescentes florestais são mantidos em tais paisagens. Nesse contexto, o objetivo geral dessa tese foi avaliar os efeitos de mudanças ambientais na escala local e de paisagem sobre a dinâmica e estruturação da comunidade de aves, bem como buscar entender como os processos ecossistêmicos realizados pelas aves pode ser alterados por tais mudanças. O estudo foi desenvolvido em 40 paisagens antrópicas com diferentes quantidades de cobertura florestal, localizadas na Floresta Atlântica do sul da Bahia, Brasil. Os resultados mostram que: (i) a redução na quantidade de floresta afeta negativamente a diversidade de diferentes grupos ecológicos de aves, existindo um limiar de extinção, i.e. perda abrupta de espécies, quando 50% da cobertura florestal é perdida dentro das paisagens; (ii) perda de floresta age como um filtro ambiental, alterando a composição de espécies de aves em paisagens antrópicas; (iii) a diversidade gama de aves nas paisagens pode ser mantida através da mudança na composição de espécies (diversidade beta) entre localidades, porém essa alteração depende do grupo ecológico, da escala espacial e da heterogeneidade da paisagem; (iv) alterações na estrutura da floresta e na composição da paisagem são importantes preditores da estrutura das assembleias de aves em paisagens fragmentadas; e (v) a redução da quantidade de floresta, além de afetar negativamente a diversidade de espécies, pode causar alterações significativas nos processos ecológicos desempenhados pelas aves. Especificamente, detectamos que a perda de floresta aumenta o nível de herbivoria foliar em plantas no subosque de fragmentos florestais. Portanto, os resultados apresentados aqui demonstram os efeitos negativos das mudanças na cobertura do solo sobre a diversidade de aves, e enfatizam que muitas espécies necessitam de grande quantidade de cobertura florestal para persistirem em paisagens antrópicas. Futuras estratégias de conservação devem adotar medidas para evitar o desmatamento de fragmentos remanescentes, com concomitante manejo e restauração de paisagens severamente fragmentadas, para tentar manter a diversidade de aves e consequentemente suas funções ecológicas.

Summary

Changes in the quantity and quality of natural habitats have negatively affected the biodiversity, especially in tropical forests that continue to be deforested at alarming rates to supply the needs of human population. Despite an extensive literature about the effects of fragmentation and habitat loss on biodiversity, there is no consensus on how the dynamics of biological communities in human-altered landscapes occur, and particulary how key ecological processes for the ecosystem functioning can be maintained in such landscapes. In this context, the general aim of this thesis was to evaluate the effects of environmental changes at local and landscape scales on the bird community structure, as well as to understand how ecosystem processes performed by birds can be altered by these changes. The study was conducted in 40 human-altered landscapes with different forest cover amount, located in the Atlantic Forest of southern Bahia, Brazil. The results show that: (i) a decrease in the amount of landscapes-scale forest cover negatively affects the diversity of different ecological groups of birds, with an extinction threshold when 50% of the forest cover is lost in the landscapes; (ii) the forest loss acts as an environmental filter, altering the composition of bird species in human-altered landscapes; (iii) the gamma diversity of birds on landscapes can be maintained by species turnover (beta diversity) between sites, although it depends on the ecological group, spatial scale and landscape heterogeneity; (iv) changes in forest structure and landscape composition are major drivers struturing bird assemblages in fragmented landscapes; and (v) changes in species diversity triggered by the reduction of landscape-scale forest cover significantly effect the ecological processes mediated by such assemblages. Specifically, forest loss increases the herbivory levels in understory plants of forest patches. In summary, the results presented here show the negative effects of land cover changes on the bird diversity, and emphasize that many species require extensive forest cover to persist in human-altered landscapes. Future conservation strategies should take measures to avoid futher deforestation of remnants patches, with concomitant management and restoration of severely fragmented landscapes, in order to maintain the bird diversity and consequently their ecological functions.

Introdução geral

Mudanças na cobertura do solo provenientes principalmente da perda e a fragmentação de hábitats naturais são os principais fatores responsáveis pelas atuais taxas de extinção de espécies, especialmente nas florestas tropicais que além de abrigarem grande parte da biodiversidade do planeta também têm sido desmatadas a taxas alarmantes (Sala et al. 2000, Millennium Ecosystem Assessment 2005, Tabarelli et al. 2012). Atualmente cerca de 4/5 dos ecossistemas terrestres foram convertidos em áreas antropizadas devido as necessidades da população humana (Hobbs et al. 2009, Ellis 2011, Malhi et al. 2014). Isso tem gerado uma grande pressão sobre a biodiversidade pois as comunidades ecológicas se encontram confinadas em paisagens antrópicas com baixa representatividade de hábitats naturais (Gardner et al. 2009). Além disso, os hábitats remanescentes nestas paisagens estão frequentemente fragmentados, modificados e sujeitos a constante pressão antrópica (Gardner et al. 2009, Malhi et al. 2014).

Quando o hábitat é reduzido de tamanho e suas porções remanescentes são espacialmente separadas, a estrutura da paisagem é drasticamente alterada, desencadeando uma série de efeitos frequentemente sinergéticos que determinam os padrões de biodiversidade em paisagens antrópicas (Fahrig 2003, Didham et al. 2012, Walz & Syrbe 2013). Em paisagens com baixa representatividade de hábitat natural tem sido observado que quando a conectividade entre grandes fragmentos é mantida, a redução da riqueza de espécies é frequentemente lenta e linearmente relacionada com a quantidade de hábitat remanescente (Ewers & Didham 2006, Brook et al. 2013). Entretanto, quando a disponibilidade de hábitat é reduzida a menos de 60%, tende a ocorrer um decréscimo abrupto no tamanho médio dos fragmentos, aumentando exponencialmente a probabilidade de extinções estocásticas dentro dos fragmentos remanescentes (Andrén 1994). Entre 10-30% de hábitat remanescente na paisagem, os fragmentos tendem a ser tão pequenos e isolados que as extinções locais não são compensadas pela chegada de migrantes, já que a dispersão é reduzida ou totalmente impedida (Andrén 1994, Fahrig 2002). Nesta situação de extrema redução de disponibilidade de hábitat em escala de paisagem, os efeitos combinados da diminuição do tamanho médio dos fragmentos e concomitante aumento do grau de isolamento entre eles devido ao processo de fragmentação *per se* desencadeiam mudanças drásticas e não-lineares na riqueza de espécies; evento conhecido como limiar de extinção (Andrén 1994, Fahrig 2002). Desta forma, é de suma importância que os estudos ecológicos busquem compreender primeiramente a natureza da relação entre métricas de diversidade biológica e quantidade de hábitat remanescente, uma vez que o tipo relação (linear ou não-linear) pode ser fundamental para decisões mais precisas para a manutenção da biodiversidade e estratégias de manejo em paisagens antrópicas.

Embora os estudos que avaliaram repostas não-lineares para perda de hábitat apontem a existência de limiares de extinção em torno de 10-30% de hábitat remanescente (Andrén 1994, Fahrig 1997, Pardini et al. 2010, Estavillo et al. 2013), uma generalização deste valor pode ser limitada (Swift & Hannon 2010) ou improvável de ocorrer considerando diferenças entre paisagens, grupos biológicos ou mesmo processos ecológicos (Lindenmayer & Luck 2005), devido a pelo menos três principais razões. Primeiro, os limiares são profundamente contexto-dependentes, ou seja, a resposta das espécies à perda e fragmentação do hábitat, ou conectividade, depende até certo ponto de características específicas das paisagens estudadas (Lindenmayer & Luck 2005, Swift & Hannon 2010). Assim, a disponibilidade de hábitats adequados na paisagem e o grau de isolamento entre fragmentos não são só uma função da área e a distância linear entre remanescentes, mas altamente determinadas pela qualidade da matriz (Fahrig 2013). A matriz circundante pode afetar os padrões de diversidade alfa e beta e consequentemente ser um fator determinante da manutenção diversidade total (gama) presente em paisagens antropizadas (Watling et al. 2011, Eycott et al. 2012, Arroyo-Rodríguez et al. 2013). Por exemplo, em paisagens heterogêneas nas quais as matrizes são compostas por ambientes florestais modificados, porém estruturalmente complexos, a diversidade alfa, inclusive de espécies tipicamente florestais de diferentes grupos biológicos, é semelhante entre pequenos e grandes fragmentos (Pardini et al. 2009); e a diversidade beta (diferença na composição de espécies) entre fragmentos tende a ser baixa devido a capacidade das espécies em se dispersarem e utilizarem a matriz (Arroyo-Rodríguez et al. 2013).

Segundo, muitos processos e padrões ecológicos são intrinsecamente dependentes de escala, tanto no espaço quanto no tempo (Fahrig 2013). Diferenças nos traços ecológicos, como a longevidade, tamanho corpóreo e capacidade de dispersão influenciam fortemente a escala apropriada em que a paisagem deve ser definida para uma dada espécie (Fahrig 2013). Embora alguns estudos tenham mostrado que a resposta à escala é bastante consistente dentro de certos grupos biológicos (Flick et al. 2012), quando diferentes espécies respondem a distintas escalas, a relação entre riqueza de espécies e estrutura da paisagem pode não ser consistente devido a definição inadequada de escala (Smith et al. 2001, Fahrig 2013, Arroyo-Rodríguez & Fahrig 2014). Finalmente, existe um alto nível de idiossincrasia na resposta e vulnerabilidade de cada espécie frente às mudanças estruturais em nível de paisagem (Lindenmayer et al. 2005). De fato, como a própria definição de “hábitat” é um conceito espécie-específico, a ideia de limiares de extinção para a riqueza de espécies sustenta que todas espécies devem responder a variável explanatória “perda de hábitat” de forma similar. Entretanto, as espécies são conhecidas por mostrar uma ampla gama de respostas frente às modificações da paisagem, com algumas espécies sendo afetadas de maneira positiva, outras negativamente e algumas até mesmo sem qualquer influência das mudanças estruturais na paisagem (Banks-Leite et al. 2012, 2013, Bregman et al. 2014).

Compreender os padrões e processos que levam as modificações na estrutura e composição das paisagens, e como a biodiversidade pode ser mantida nessas paisagens antrópicas é um grande desafio para biólogos da conservação por diversas razões (Gardner et al. 2009). Primeiro, embora exista um amplo conhecimento acerca da resposta geral da biodiversidade frente a perturbação no hábitat, este padrão difere entre espécies e grupos ecológicos (Ewers & Didham 2006), e este conhecimento é muito concentrado em poucos táxons, principalmente em regiões temperadas (Fahrig 2003). Tais respostas podem também variar entre paisagens e regiões, dependendo da heterogeneidade da paisagem (Arroyo-Rodríguez et al. 2009) e da escala espacial analisada (Arroyo-Rodríguez et al. 2013, Carrara et al. 2015). Infelizmente, muitos estudos de biodiversidade em paisagens antrópicas são conduzidos em uma única paisagem e usualmente na escala de fragmento (Fahrig 2003). Segundo, a extirpação de espécies sensíveis a perturbações pode ser compensada pela proliferação de espécies adaptadas à hábitats perturbados (evento conhecido como dinâmica compensatória), mascarando assim a resposta em nível de comunidades diante dos distúrbios existentes em paisagens antrópicas (Supp & Ernest 2014). Finalmente, apesar de ser bem estabelecido que o número de espécies que as paisagens e regiões podem acumular (diversidade gama) depende parcialmente da mudança na composição (diversidade beta) entre localidades (Arroyo-Rodríguez et al. 2013), a grande maioria dos estudos em paisagens antrópicas avaliam somente as mudanças na diversidade local (alfa), portanto subestimando os impactos que as alterações nos hábitats naturais podem ocasionar sobre a diversidade beta ao longo de diferentes escalas espaciais (Karp et al. 2012, Püttker et al. 2015). Desta forma, entender o impacto que mudanças na cobertura do uso do solo podem ter sobre a heterogeneidade ambiental e a resposta da diversidade beta para tais mudanças é urgentemente necessário para delinear adequadas estratégias de conservação.

Outro ponto importante que necessita de mais atenção é que a conversão de extensos remanescentes florestais em paisagens antrópicas, além de ocasionar a extinção de espécies, incluindo a perda de assembleias ecológicas inteiras (Clavel et al. 2011, Tabarelli et al. 2012), pode também alterar relações ecológicas complexas através de mudanças nas forças *top-down* e *bottom-up* (Terborgh et al. 2001, Dirzo et al. 2014). Entretanto, nosso conhecimento sobre o efeito em cascata que a perda de floresta pode exercer na manutenção da biodiversidade e funcionamento do ecossistema é muito limitado (Martinson and Fagan 2014, Mitchell et al. 2015), com muitos estudos em paisagens antrópicas focando em entender os padrões de diversidade, em especial a taxonômica, e negligenciando os efeitos negativos sobre os processos ecológicos (Tscharntke et al. 2005, Galetti et al. 2013, Mitchell et al. 2015). Dentre os animais, as aves estão entre os mais diversos grupos de vertebrados em florestas tropicais e devido a sua elevada abundância local elas estão envolvidas em processos ecológicos essenciais, como o controle de artrópodes, polinização e dispersão de sementes (Sekercioglu 2006). Entretanto, como a diversidade de aves frequentemente declina devido a mudanças na cobertura do solo, as funções ecológicas por elas executadas podem também ser perdidas ou alteradas (Sekercioglu 2006, Bregman et al 2014, De Coster et al. 2015). Alguns estudos destacam a importância da posição trófica e tipo de guilda alimentar como fatores primordiais para predizer a sensibilidade das espécies a perda de hábitat e alterações na estrutura e composição da paisagem (Murphy & Romanuk et al. 2012, Newbold et al. 2013, Bregman et al. 2014). Guildas tróficas específicas, em particular as aves insetívoras florestais (Sekercioglu et al. 2002) e aves frugívoras de grande porte (Galetti et al. 2013, Moran & Catterall 2014), são provavelmente os primeiros grupos ecológicos a reduzir sua diversidade em paisagens antrópicas (Bregman et al. 2014). O declínio desses grupos ecológicos pode afetar negativamente o funcionamento do ecossistema, uma vez que: o desaparecimento de aves insetívoros pode reduzir a predação de insetos herbívoros e indiretamente contribuir para o aumento do dano foliar nas plantas (Van Bael et al. 2003), e o declínio de aves frugívoras pode reduzir a dispersão de sementes e portanto afetar a regeneração da floresta, com consequências significativas para estrutura da floresta e características genotípicas e genéticas das plantas (Silva & Tabarelli 2000, Sekercioglu 2006, Markl et al. 2012, Galetti et al. 2013).

Diante do exposto acima, há uma carência em estudos realizados em paisagens com diferentes composições e quantidades de hábitats naturais cujos resultados possam ser utilizados para prever de forma mais ampla: i) a quantidade de hábitat remanescente necessária para manter comunidades ecológicas em paisagens antrópicas; ii) a relativa sensibilidade de diferentes grupos ecológicos diante da perda de hábitat; iii) os principais fatores ambientais preditores da diversidade taxonômica; e iv) se a perda de grupos funcionais pode afetar processos ecológicos essenciais para o funcionamento do ecossistema. Esta tese buscou responder as questões abordadas acima através da avaliação dos efeitos de mudanças ambientais na escala local e de paisagem sobre a dinâmica e estruturação da comunidade de aves, bem como sobre algumas funções ecológicas desempenhadas por esse grupo. O estudo foi desenvolvido em 40 paisagens antrópicas com diferentes quantidades de cobertura florestal, localizadas na Floresta Atlântica do sul da Bahia, Brasil. Apesar da Floresta Atlântica ser considerada um dos biomas com maior número de espécies do planeta e elevado número de endemismo (Myers et al. 2000), a maior parte da sua extensão foi convertida em áreas antrópicas para suprir as necessidades da população humana, restando atualmente apenas 12% da sua cobertura original (Ribeiro et al. 2009). Especificamente, o sul da Bahia possui apenas 0,4% da cobertura original de floresta, porém ainda abriga os maiores remanescentes de Floresta Atlântica do nordeste brasileiro (Thomas et al. 1998). Ainda, essa região possui paisagens antrópicas com diferentes níveis de heterogeneidade, com grande variação na quantidade de floresta remanescente e com fragmentos florestais com diferentes graus de degradação e inseridos em diferentes matrizes

(Pardini et al. 2009). Diante dessas características, as paisagens da Floresta Atlântica do sul da Bahia apresentam condições ideais para testar a influencia da perda e degradação do hábitat em diferentes escalas espaciais sobre a biodiversidade. Por fim, utilizou-se as aves como o grupo de estudo devido a sua alta diversidade, taxonomia bem definida e fácil identificação. Além disso, as aves são intrinsecamente ligadas aos ambientes em que vivem, fazendo deste grupo um excelente indicador de alterações na quantidade e qualidade do hábitat (Canterbury et al. 2000).

Objetivos

O objetivo geral da tese foi avaliar os efeitos de mudanças ambientais na escala local e de paisagem sobre a dinâmica e estruturação da comunidade de aves, bem como buscar entender como os processos ecossistêmicos realizados pelas aves pode ser alterados por tais mudanças. Especificamente, buscou-se responder as seguintes perguntas:

1. Qual é o tipo de relação (linear ou não-linear) entre riqueza/abundância de aves e quantidade de floresta na escala de paisagem?
2. Como a redução de cobertura florestal pode afetar diferentes grupos ecológicos?
3. Quais fatores ambientais são determinantes da diversidade beta de aves especialistas florestais e generalistas de hábitat?
4. Como a escala espacial pode afetar a diversidade beta de aves especialistas e generalistas?
5. Existe suficiente informações na literatura científica sobre as funções ecológicas executadas pelas aves e como alterações ambientais podem afetá-las?
6. Quais as consequências diretas e indiretas da redução de cobertura florestal sobre a variação no nível de herbivoria foliar em paisagens antrópicas?

Organização da tese

A tese esta dividida em duas seções. A primeira seção é composta por dois artigos já publicados (capítulos 1 e 2), e cujo o objetivo foi entender como ocorre a dinâmica e estruturação da comunidade de aves em paisagens antrópicas. No **Capítulo 1** foi avaliado como a riqueza e abundância de diferentes grupos ecológicos de aves são afetados pela redução de cobertura florestal na escala de paisagem. Além disso, verificou-se qual o tipo de relação (linear e não-linear) entre as métricas de diversidade e quantidade de floresta, e se o limiar de extinção para quantidade de floresta pode variar entre grupos ecológicos de aves. No **Capítulo 2** foi investigado como a diversidade beta de aves especialistas florestais e generalistas de hábitat é afetada por características locais e de paisagem, e se a diversidade beta pode variar ao longo de diferentes escalas espaciais (dentro de fragmentos florestais, entre fragmentos e entre paisagens). Por fim, na segunda seção (capítulos 3 e 4) buscou-se entender como alterações ambientais podem influenciar as funções ecológicas executadas pelas aves. O **Capítulo 3** apresenta uma revisão crítica de como funções ecológicas realizadas pelas aves estão sendo abordadas pela comunidade científica, além de discutir se existem informações suficientes que permitam uma boa compreensão dos efeitos de mudanças ambientais sobre as funções ecológicas das aves. Finalmente, no **Capítulo 4** avaliou-se os efeitos diretos e indiretos da redução de cobertura florestal sobre a herbivoria foliar; um importante processo ecológico que influencia o funcionamento das florestas e que pode ser mediado pelas aves via a predação de insetos herbívoros.

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Seção I

Estrutura e dinâmica da comunidade de aves em paisagens antrópicas

Capítulo 1

Birds in anthropogenic landscapes: the responses of ecological groups to forest loss in the Brazilian Atlantic Forest [#]

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Abstract

Habitat loss is the dominant threat to biodiversity and ecosystem functioning in terrestrial environments. In this study, we used an *a priori* classification of bird species based on their dependence on native forest habitats (forest-specialist and habitat generalists) and specific food resources (frugivores and insectivores) to evaluate their responses to forest cover reduction in landscapes in the Brazilian Atlantic Forest. From the patch-landscapes approach, we delimited 40 forest sites, and quantified the percentage of native forest within a 2 km radius around the center of each site (from 6 - 85%). At each site, we sampled birds using the point-count method. We used a null model, a generalized linear model and a four-parameter logistic model to evaluate the relationship between richness and abundance of the bird groups and the native forest amount. A piecewise model was then used to determine the threshold value for bird groups that showed nonlinear responses. The richness and abundance of the bird community as a whole were not affected by changes in forest cover in this region. However, a decrease in forest cover had a negative effect on diversity of forest-specialist, frugivorous and insectivorous birds, and a positive effect on generalist birds. The species richness and abundance of all ecological groups were nonlinearly related to forest reduction and showed similar threshold values, i.e., there were abrupt changes in individuals and species numbers when forest amount was less than approximately 50%. Forest sites within landscapes with forest cover that was less than 50% contained a different bird species composition than more extensively forested sites and had fewer forest-specialist species and higher beta-diversity. Our study demonstrated the pervasive effect of forest reduction on bird communities in one of the most important hotspots for bird conservation and shows that many vulnerable species require extensive forest cover to persist.

Introduction

Habitat loss and fragmentation are the major drivers of current rates of biodiversity decline [1]. Although habitat loss generally increases the likelihood of stochastic extinction and declines in population sizes at local and landscape scales, fragmentation effects, i.e., the transformation of the original habitat into a number of isolated fragments in a matrix of habitats that is unlike the original [2], can have positive and/or negative effects depending on species characteristics [1], [3]. Further, although habitat loss and fragmentation are different processes and have different adverse effects on biodiversity, population persistence in anthropogenic landscapes is a result of the interaction of both processes [4], [5].

Ecological studies have shown that the relationship between habitat loss at the landscape scale and extinction of species can be nonlinear [6]–[8]. The extinction threshold hypothesis states that many species require a given amount of suitable habitat to persist in the landscape. Fragmentation has its most pronounced effects at values that are below this threshold and can lead to abrupt decreases in species population size [4], [9], [10]. Extinction thresholds are proposed to occur when less than 30% of habitat remains, due to a decrease in mean patch size and to an exponential increase in the distance between patches [4], [8]. Attempts to uncover the relative importance of fragmentation and habitat amount have proved a difficult task particularly because there is generally high correlation of most fragmentation metrics to habitat loss, but empirical studies have identified habitat amount as the prevailing driver of species loss [8], [11].

The concept of extinction thresholds was primarily derived from simulations of population responses to habitat loss in neutral landscapes, and current empirical studies have focused more on populations than on communities [4], [12]. The existence of thresholds in communities in response to habitat loss has not always been supported by the published results of empirical studies and is still controversial [12]-[14]. Threshold values for remaining habitat that range from 5% to 90% have been documented [12], [15], [16]. Such variation might be due to species characteristics, the different measures used to test thresholds (e.g., habitat amount, patch isolation and patch size), the duration and intensity of changes in the landscape, the nature of the matrix and the spatial scale of the studies [9], [14], [17]. Thresholds can also vary among study regions for the same species [18]. Establishing threshold values for an entire community is especially difficult because of the idiosyncratic responses of ecologically different species to habitat loss and landscape structure [19]. Environmental disturbance and changes in habitat quality may decrease the population size of habitat-specialist species but favor an increase of generalist species [20]. Species richness values could therefore be maintained despite variation along the disturbance gradient, such as variation in habitat loss [21].

Responses may vary according to specific ecological traits (e.g., body mass, home range size, migratory status and habitat affinity) [22], [23], even among those groups of species, such as forest-specialist birds, that are usually considered to be sensitive to anthropogenic disturbance. Some studies have highlighted the importance of dietary niche and trophic level as factors that influence the sensitivity of species to disturbed landscapes [23], [24]. Specific trophic guilds, such as understory insectivorous birds [25] and large frugivores [26], are likely to be the first groups to decline in forest landscapes with a reduced amount of habitat. However, the proneness to extinction of even sensitive species varies. For example, frugivorous species show a greater capacity for dispersal and a greater ability to use complementary habitats to obtain food [27] compared with insectivorous species, which require specific local forest characteristics [28]-[30]. These declines in specific ecological groups can lead to further changes in ecosystem functions in the remaining natural patches [31], [32]. For example, a decline in insectivorous birds may trigger overall changes in trophic cascades [33], the extinction of some frugivorous species may change patterns of seed dispersal [27], and the disappearance of nectarivorous species can lead to a decrease in gene flow among plants, which can then become more susceptible to stochastic extinctions [34].

To address the challenges of preventing biodiversity loss and maintaining ecosystem functioning in human-altered landscapes, it is important to understand how birds that play different ecological roles are affected by habitat loss [35], [36]. In a context of nonlinear relationships, understanding how and where thresholds can occur provides insights to guide landscape planning, management and conservation [37]. In this study, we used an *a priori* classification of bird species according to the available published data and expert opinion, that is based on their dependence on forest (forest-specialists and habitat generalists) and on the specificity of their food resources (frugivorous and insectivorous) to evaluate the responses of these groups to forest cover reduction at 40 forest sites in landscapes that have remaining forest cover that ranges from 6% to 85%. The study was conducted in anthropogenic landscapes in the Brazilian Atlantic Forest, a biome that is highly deforested and disturbed but that still possesses high levels of species richness and endemism [38]. We tested four hypotheses. (i) For all of the species combined, the overall species richness and abundance of birds would not be affected by reductions in forest cover at the landscape scale because of the highly idiosyncratic responses of species of different ecological groups. (ii) The richness and abundance of species of the different groups would vary, e.g., forest-specialist birds would show a strong negative response to forest reduction, generalists would respond positively, and both groups would show nonlinear responses with specific threshold values. (iii) There would be a more abrupt decrease in the species richness and abundance of insectivorous birds that would be triggered at lower levels of habitat loss than there would be for frugivorous species. Previous studies emphasize that habitat loss can be extremely damaging to insectivorous forest birds, due to their low dispersal ability, and habitat and diet specificity [25], [26], [28]. Therefore, if both guilds are nonlinearly affected by habitat loss at the landscape scale, threshold values for insectivorous species are most likely to be higher than those for frugivorous species. We finally expect that (iv) bird communities of different ecological groups would have different species compositions in landscapes with low forest cover. Changes in species composition may occur at high levels of habitat loss due to drastic reduction in species richness (extinction threshold), which will form a subset of species able to survive in disturbed landscapes [39].

Materials and Methods

Study area

This study was conducted in southern Bahia State, northeastern Brazil (Fig. 1). This region is a mosaic of forested habitats that includes remnants of mature forests, secondary forests at different successional stages, shade plantations of cacao (*Theobroma cacao*), rubber trees (*Hevea brasiliensis*) and *Eucalyptus* spp. [20]. The dominant vegetation is classified as Lowland Wet Forest and is characterized by a clear vertical stratification into lower, canopy (25-30 m) and emergent layers (up to 40 m); an abundance of epiphytes, ferns, bromeliads and lianas; and high levels of endemism of different groups [40], [41]. The average annual temperature is 24°C, and the mean annual rainfall is 1500 mm. There is no defined seasonality, although a rainless period may occur from December to March [42].

Sampling design

This study is part of REDE SISBIOTA, a major research network designed to investigate how the reduction of forest cover affects regional biodiversity patterns and processes in anthropogenic landscapes. We had previously identified a region between the Jequitinhonha and Contas Rivers that still harbor large, representative forest tracts, and these forests have similar soil, topography and floristic composition [40].

We mapped this region by analyzing satellite images that were specifically acquired for our work (QuickBird and WorldView, from 2011) or were already available (RapidEye, from 2009-2010). The mapping was created by manually digitizing the land cover features visually interpreted at scale of 1:10000, which is adequate for identifying patches based on the visual inspection of differences in color, texture, shape, location and context. Patches were delimited as polygons, and a digital map was created using ArcGIS software. Polygons were classified according to different forest types following the typologies provided by IBGE [43]. After intensive ground-truthing, we developed a map of the land use of a 3500 km^2 area that encompasses the municipalities of Belmonte, Una, Santa Luzia and Mascote. The coordinates of the center of the sampled area are 15° 28’S and 39° 15’W. At a regional scale, there was a north-to-south gradient in forest cover within the mapped region (Fig. 1). Although there are open areas within the mapped region, most of the large and continuous forests in the northern area are concentrated around the Una Biological Reserve and the Una Wildlife Refugee, two federally protected conservation units that have a total area of 34804 ha, which includes the municipality of Una. In contrast, the southern part of the mapped area is clearly more deforested than the northern part, but there are still some large forest tracts in the southern part.

Based on this map, we identified 58 potential sampling sites that were located in forest patches. We adopted the patch-landscape approach [44], in which the response variables are evaluated within forest patches, and the landscape variables are measured within a specific area surrounding the each sampling site. To characterize the landscape, we quantified the percentage of forest cover using ArcGIS software within a 2 km radius from the center of each sampling site (which yields a surface area of each site of approximately 13 km^2). We considered only native forests in our estimations of the amount of forest cover within the landscape. Therefore, forest cover included all of the native forest types, encompassing the mature and successional forests types described above but excluding shade plantations of cacao and rubber trees. This classification may be a simplification of the ecological requirements of bird species, but we believe that this broad definition is the most appropriate because many recommendations for the conservation and management of landscapes are based on fragmentation or habitat loss in general [45].

We excluded those sites that were located at a distance of less than 1 km from the closest site to avoid recounting individuals that have high dispersal ability and large home ranges (e.g., falcons and parrots). We randomly selected 40 sites that had 6% to 85% forest cover within a radius of 2 km. Twelve sites had 6% to 30% forest cover, 13 sites had 31% to 50%, and 15 sites had 51% to 85%. The distance between sites ranged from 1 to 105 km. We did not sample in either of the protected areas, and no specific permission was required for the selected locations. However, we secured permission to conduct fieldwork in all sampling sites that were located on private land.

Bird survey

We sampled bird communities in three field campaigns: January to April 2013, May to September 2013, and October 2013 to April 2014. The climatic conditions during the campaigns did not affect the sampling of birds, since there is no seasonality defined in the study region [42]. Moreover, each site was sampled once during the bird breeding season (September to January) to avoid any bias, since the birds are more active this period of the year.

We used the point-count method [46], and at each sampling site we established four sampling points that each had a radius of 50 m and that were separated by a distance ranged from 150 to 550 m [46]. We assigned sampling points inside each forest area that were at least 100 m from the edge to avoid effects of adjacent habitats and to ensure that the documented bird community was representative of the site.

All sites were covered in each field campaign, and sampling at each point was conducted for 15 min at sunrise (between 0600 and 0900 hr) and at sunset (between 1500 and 1700 hr), which are the periods of greatest bird activity. Therefore the sampling effort at each sampling site was 6 hours. We recorded each bird that was seen or heard at each sampling point. We avoided sampling on rainy and windy days because such conditions reduce bird detectability [46]. We excluded birds that were flying over the forest and birds that could not be located precisely.

We used 8x42 binoculars to identify the birds and a digital recorder to record their vocalizations. We confirmed vocalization-based bird identifications by playback or by comparing the recordings with an existing database. Field guides [47], [48] were used for identification. The scientific nomenclature used conforms to that of the South American Classification Committee [49].

Data analysis

We designated bird communities as forest-specialist and generalist species based on the scientific literature [23], [50]. The endemic birds of the Atlantic Forest and those that occur in forested habitats of the Atlantic and Amazon Forests, according to Stotz et al. [50], were classified as forest-specialist species. Species that also occur in open vegetation habitats, such as grasslands, of the Cerrado, Caatinga, Pampa and anthropogenic areas were classified as generalists. The forest-specialist species were also grouped according to their trophic guild (i.e., insectivores, frugivores, nectivores, omnivores, carnivores, and granivores). Trophic categories reflect the main food source of the species, and birds were categorized as omnivores if their diet is composed of different classes of food items. These classifications were based on our prior knowledge about the ecology of the species, information available on the literature and after consulting specialists.

We first evaluated the effect of variation in bird diversity based on biogeographical factors by means of a Mantel test between the geographical distance matrix and two matrices of differences in species richness and abundance between pairs of sampling sites. We then assessed the relationship between the number of species (richness) and the total number of individuals (abundance) of the most representative groups (overall species, generalists, forest-specialist, forest frugivores and forest insectivores) and forest amount in the 40 sites. Total richness and abundance in each site were considered as the sum of the number of species and individuals, respectively, recorded during the three field campaigns in the four counting points. We used a null model, a generalized linear model and a logistic model with four parameters to evaluate the bird response types (linear and nonlinear). We assumed a Poisson error distribution for the abundance and species richness data in each of the models.

Null models were used to test the absence of effects, and GLMs were used to test the existence of a continuous change in the biological response related to forest cover. The four-parameter logistic regression, which is expressed in the formula $F(x) = d + (\frac{a}{1+e\left((b-x)\right)})$, is a nonlinear model that has a sigmoidal shape that is appropriate to fit to threshold curves [51]. This model has a lower asymptote (d), which is the lower value of the response variable, and an upper asymptote (a + d). The parameter “a” represents the difference in the response variable before and after the decay phenomena expressed in the model, and “b” is the inflection point, the point at which the curve tends to change from one asymptote to another. The parameter "c" is proportional to the slope of the ascending part of the curve or to the speed at which it reaches the asymptote near the inflection point "b" [51], [52].

The models were subjected to model selection using models’ Akaike weights, calculated using Akaike information criterion corrected for small sample sizes (AICc) [53]. The AICc weights or model probabilities (ranging from 0 to 1), express the normalized relative likelihood of each model. Models that present Akaike weights with more than half the value of the best model (higher weight) was considered to further investigation. After model selection, we analyzed the residual distributions of the best models and the confidence intervals of the parameters.

In the case where the most likely relationship was represented by nonlinear models, we used piecewise models to determine the inflection point correspondent to extinction threshold values. A piecewise model identifies two or more straight lines that are joined at an unknown point, called the breakpoint [52], and can be considered the indicator of the bird extinction threshold [54], [55].

We used nonmetric multidimensional scaling (NMDS, two axes) to analyze differences in bird communities among landscapes. We used presence-absence data and the Jaccard similarity index to perform an ordination of landscapes that was based on their similarities in species composition. An analysis of similarities (ANOSIM) was performed to test for differences in bird composition between landscapes that had amounts of forest cover that were below and above the threshold values that had been determined with the piecewise model. The NMDS and ANOSIM analyses were performed for the most representative bird groups (generalists, forest-specialist, forest frugivores and forest insectivores). We also performed direct gradient analysis [56] that used presence-absence data to verify the replacement in bird species along the gradient of forest cover and to determine which species occur in landscapes that are located below and above the extinction threshold. All the statistical analyses and graphs were carried out in R software [57] using vegan [58], mass [59], nlme [60], bbmle [61] and segmented [62] packages, with an adopted alpha of ≤ 0.05 considered significant. Custom R scripts for the analyzed data are provided in S1 File.

Results

Bird community

The total sampling effort involved 240 hours that were equally distributed among sampling sites. We recorded 5931 individuals that belonged to 184 species and 39 families at the 40 sampling sites. The families Tyrannidae (19 species, n = 889), Thraupidae (17 species, n = 697) and Thamnophilidae (15 species, n = 724) had the greatest abundance and species richness. The species with the greatest abundance were *Cacicus cela* (n = 238), *Tolmomyias flaviventris* (n = 173), *Machaeropterus regulus* (n = 163) and *Thamnophilus ambiguus* (n = 159). Only one individual was recorded for each of 11 other species (*Celeus torquatus*, *Coccyzus euleri*, *Cyanerpes cyaneus*, *Euphonia cyanocephala*, *Myrmotherula minor*, *Myiothlypis rivularis*, *Anabacerthia lichtensteini*, *Pionus menstruus*, *P. maximiliani* and *Sclerurus mexicanus*). These birds were observed mainly in landscapes that had high forest cover. In contrast, species such as *Patagioenas speciosa*, *Phaethornis ruber* and *T. flaviventris* were frequently observed in landscapes that had different amounts of forest cover. These species were recorded in 37, 35 and 33 landscapes, respectively.

Overall, approximately 60% of birds were forest-specialist species (103 species, n = 3715). Insectivorous birds showed the greatest richness (56 species, n = 1935), followed by frugivores (34 species, n = 1165). The other trophic guilds were poorly represented (Table 1) and therefore were not used in the analyses.

The effect of forest cover reduction on the bird community

We found no spatial correlation between geographical distances and differences in species richness (r = 0.05, p = 0.07) and abundance (r = 0.009, p = 0.30) among sampling sites. The greatest richness (62 species) and abundance (205 individuals) were observed in landscapes with 71% and 65% of forest cover, respectively, whereas the poorer (28 species) and less abundant sites (102 individuals) were observed in sites with 25% and 50% landscape scale forest cover, respectively. Overall abundance and species richness were not affected by differences in forest cover at the landscape level (Fig. 2). Although the AICc weight showed that GLMs were the best models (Table 2), its correlation coefficients were very low (0.002 for richness and 0.0009 for abundance). This finding indicates that the models showed straight lines that were almost parallel to the x axis, which is very similar to the null models. Therefore, both models showed the lack of relationship between the dependent variables and forest cover.

The effect of forest cover was evident when the species were classified into *a priori* ecological groups (Table 2). Forest-specialist bird diversity showed a nonlinear relationship and was negatively affected by a reduction in forest cover at the landscape scale (Fig. 2). The piecewise model showed that an abrupt decrease in forest-specialist diversity occurs in landscapes that have an amount forest cover that is less than 46%±3.9% (for richness) and 44%±2.2% (for abundance). Conversely, forest cover reduction positively affected generalist birds, with significant nonlinear responses of species richness and abundance along the gradient of forest cover. There was a rapid change in the richness of generalist birds when the amount of forest at the landscape scale reaches 50%±10.2% (Fig. 2). There was a decline in the diversity of bird generalists in landscapes that have an amount of forest cover that is above this value, and landscapes with less forest cover have more generalists. Additionally, specific threshold values were quite similar for generalist abundance (49%±4.3%).

As with forest-specialist species, forest frugivores and insectivores were also negatively associated with forest cover. The abundance and species richness of both groups declined in a nonlinear pattern (Fig. 3). Piecewise models indicated thresholds of loss of frugivorous species and individuals respectively at 46%±5.4% and 44%±3.7% of forest cover at the landscape scale. For insectivorous birds, the extinction threshold for richness occurred in landscapes with 44%±4.9% forest cover, and abundance decreased quickly in landscapes with forest cover of less than 34%±2.6%. There was substantial variation in the number of individuals (i.e., abundance) of both groups along the forest cover gradient. Landscapes with similar amounts of forest cover sometimes had different bird abundance. For example, 37 insectivorous birds were counted in a landscape with 63% forest cover and 105 insectivorous birds were counted in a landscape with 65% forest cover (Fig. 3).

Change in bird species composition

The bird species composition of all ecological groups was also affected by forest cover. The first two axes of the NMDS had a stress value of 0.15 for forest-specialist, 0.19 for generalists, 0.17 for frugivorous, and 0.16 for insectivorous birds. This finding indicates that our data were represented well in these two dimensions. The two axes of the NMDS showed a clear separation between landscapes (Fig. 4). One group was composed of landscapes that had forest cover that was less than the observed threshold values for the different ecological groups (represented by lower scores on the first axis), and another group was composed of landscapes that had forest cover that was greater than the observed threshold values (represented by higher scores on the first axis). Overall, bird species composition among landscapes with low forest cover (below the threshold) showed great dissimilarity (high beta-diversity) compared with those with more forested landscapes and higher variation in scores on the second axis (Fig. 4). In addition, comparisons of the ANOSIM analysis showed significant differences in the species composition of forest-specialist ($R = 0.39$, $p = 0.001$), generalists ($R = 0.28$, $p = 0.001$), insectivores ($R = 0.33$, $p = 0.001$) and frugivores ($R = 0.36$, $p = 0.001$) in landscapes with an amount of forest cover that was less than, and greater than, the threshold.

The direct ordination showed a replacement of species of different groups with forest cover (S1-S4 Figs.). Twenty-six species of forest-specialist occurred exclusively on landscapes with high forest cover (S1 Fig.). Eight of these species are frugivorous (e.g., *Carpornis melanocephala*, *Turdus albicollis*, *Xipholena atropurpurea* and *Euphonia pectoralis*), and 16 are insectivorous (e.g. *Drymophila ferruginea*, *Eleoscytalopus psychopompus*, *Formicarius colma* and *Philydor atricapillus*). All of these species disappeared in landscapes with less than 50% of their original forest cover (S3 and S4 Figs.). Conversely, from the total of generalist birds, 30 species are favored by the decrease in forest. These species occur exclusively in landscapes with low forest cover (S2 Fig.).

Discussion

Forest cover and species diversity

We found that forest reduction at the landscape scale triggers major changes in the bird communities that inhabit anthropogenic landscapes in the Brazilian Atlantic Forest. As hypothesized, when all species combined were considered, bird richness and abundance were not affected by forest cover reduction at the landscape scale. This pattern occurred because the bird community was composed of species that have different responses to environmental perturbation. There was species that are not affected by a decrease in forest cover and species that are positively or negatively affected by the change [19]. One can therefore expect that overall richness and abundance are maintained along the gradient of forest cover by the replacement of sensitive bird species by those that are favored by deforestation [63].

The compensatory response of birds was clear when different ecological groups were considered, which indicated that overall richness and abundance can mask striking changes in community patterns and can be misleading as biodiversity indicators of meaningful conservation value [64]. Forest-specialist birds showed an abrupt decrease in species richness in landscapes that had a forest cover that was less than 50%, but there was a concomitant increase in the richness of generalist birds. Our results therefore demonstrated how bird community structure changes when forest is lost. The diversity of forest-specialist birds is maintained when more than 50% of the forest cover remains. However, a decrease in forest cover below this critical value (<50%) creates novel habitats that favor generalist bird species, which may be better adapted to use disturbed habitats [23]. Forest reduction also triggered a major loss in the species richness of frugivorous and insectivorous birds. Frugivorous and insectivorous birds, regardless of their specific ecological characteristics, showed extinction threshold values that were representative of all forest-specialist.

Alpha diversity tended to be lower with progressive habitat loss, and the remaining species assemblages constituted a subset of more tolerant or disturbance-adapted species [65], [66]. By contrast, there was high species replacement (beta diversity) in these deforested landscapes, which helped to maintain relatively rich and abundant bird assemblages in a regional scale (gamma diversity). Further, the species composition of all ecological groups changed in landscapes with reduced amount of forest cover. Thus, habitat loss can act as an environmental filter and select species with ecological traits able to survive in landscapes with reduced amount of forest [39].

The level of functional redundancy among bird species is not obvious, and it is therefore necessary to understand how and whether this clear pattern of species decline and replacement can lead to the loss of ecosystem functioning [67]. For example, the disappearance of frugivorous birds may change seed dispersal patterns and thus affect forest structure [68], and the decline of insectivorous birds may increase the population of herbivorous insects and consequently affect leaf damage and photosynthesis [69].

Bird extinction threshold

In simulated landscapes that have a low proportion (usually less than 30%) of original habitat, the mean patch size is reduced and, as habitat loss continues, there is an exponential increase in the mean distance between patches [4]. Species extinctions within small patches are not offset by migration among patches in such highly deforested and fragmented landscapes, which triggers a threshold of species extinction [4]. This extinction threshold in landscapes that have less than 30% of remaining habitat has been reported empirically in studies of different taxonomic groups in anthropogenic landscapes in various regions [8], [19], [37], [70]. Within the Atlantic Forest, extinction thresholds that range from 10% to 40% of forest cover have been reported in studies that focused on plants [70], [71] and mammals [8], [72].

However, our results indicated that landscapes that still have a large proportion of forest (~50%) may exhibit a sharp decline in species diversity. Similar results for birds were observed in the southeastern Atlantic Forest [73], which indicates that these effects are not unique to our study. Martensen et al. [73] reported an abrupt decrease in the species richness of sensitive birds when there is less than 50% of forest cover in a landscape. One possible reason for this high threshold value is that most tropical bird communities are composed of rare and specialized species that are more sensitive to alterations in their habitat and therefore require more forest [73]. Indeed, southern Bahia is rich in bird species, even compared with the northern and southern portions of the Atlantic forest, and most of the birds that were observed in the present study were forest-specialist that are often sensitive to forest loss [50].

In a recent conceptual model, Villard and Metzger [65] proposed that extinction thresholds can be influenced by the configuration of the elements that comprise the landscape, with the most vulnerable species being those that have a narrow range within which habitat loss can be mitigated in part by favorable habitat configurations. Although our estimates of forest cover included only native vegetation, the matrix of some of our landscapes also included shade cacao plantations, which is an anthropogenic forest category in which many bird species are reported to occur [20]. It is therefore surprising that, even in landscapes that have such relatively permeable matrices as shade plantations, a large amount of native habitat is still required to maintain different ecological groups of birds. It is also important to highlight that the habitat categorization that we used may have influenced the threshold values. We used the total of all forest types in different successional stages when calculating the percentage of remaining forest. Previous studies conducted in the region [20], [74], [75] document that the different categories of native forest mosaics contain different species communities. It is possible that the amount of forest that is effectively used by forest-specialist species is less than the amount of forest that is actually available in the landscape. However, it may be impossible in empirical analyses to quantify the conditions that limit the occurrence of every species [76]. This is particularly true in neotropical regions because of their high species diversity and inadequate scientific knowledge of the ecological requirements of the birds.

All ecological groups of birds showed nonlinear responses to the relationship between abundance and forest cover reduction. The abrupt decreases in abundance that follow small changes in the amount of forest cover can be extremely important for conservation. Even when certain species are present in landscapes that have an amount of forest that is less than the observed threshold, their density may be so low that the species is functionally extinct, which is a stage that precedes the actual extinction of the species [77], [78]. Additionally, frugivorous and insectivorous birds showed large variation in abundance in landscapes that had similar amounts of forest. This variability may indicate that there was random variation or that there are other factors that are important for maintaining populations of these species. Insectivorous birds, especially those that use the understory, have a low capacity for dispersal and are affected by local modifications of vegetation structure [25]. Local characteristics of a forest can therefore be as important as variables at the landscape scale. Frugivores depend on seasonal resources and must therefore move daily to obtain food and are likely to rely on the use of multiple habitats [79]. However, the degradation of natural habitats may lead not only to habitat loss but also to a simplification of the matrix structure, which makes the landscape less permeable to species movement [80]. An inhospitable matrix and increasing distance between patches can impede species dispersal because of higher energetic demand and high predation risk [27], which would lead to a low abundance of frugivores in some landscapes [35], [81]. Although shade plantations provide complementary habitats for a variety of bird species in our region [82], these agroforests may negatively affect insectivorous and frugivorous birds that live in the understory because the native understory is completely replaced by cacao plants.

Implications for conservation

The use of extinction thresholds can be an important tool to help natural resource manager to biodiversity conservation [17]. Identifying thresholds, it is possible to propose appropriate management of the landscape to maintain or restore forest cover values above that threshold, which is more likely to retain a greater species diversity [83], [14].

Current Brazilian environmental laws require that the amount of protected areas within the Atlantic forest domain be equivalent to 20% of the total area of private rural properties [84]. However, even assuming that property-scale habitat amount could somehow reflect overall landscape-scale spatial patterns, extinction threshold values that were found in the present study indicate that more forest should be protected to ensure the persistence of most habitat-sensitive birds, such as forest-specialists, frugivores and insectivores. Bird species belonging to those groups require that approximately 50% of a given site be occupied by protected forest to maintain their diversity. The agroforestry systems that are present in the study region do provide complementary habitats for many species [20], [74], [82], and can therefore mitigate the effects of habitat loss at some extent, but many of the bird species sampled here are very habitat specific, thus exclusively depending on native forest habitats to survive. Currently, the remaining forest cover of the Brazilian Atlantic Forest is only 11% of its original extent [85]. The best preserved areas are located in the southern states at Serra do Mar, which has 36.5% of its original vegetation, and the remnants that still exist in Bahia State (17.7%) [85]. These values suggest that there is an urgent need for forest restoration policy at both state and national scales to ensure that there is enough forest to conserve bird diversity dependent on forested environments [86].

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Figure Legends

Fig 1. Map of the study area in southern Bahia, northeastern Brazil.

A: Atlantic Forest remnants (gray areas) and the 40 sampling sites (black circles). Dashed lines show the areas that were mapped for this study. Images of areas that are outside of the dashed lines were obtained from forest cover map "Atlas dos Remanescentes Florestais da Mata Atlântica" of open access [87]. B: Detail of some sampled landscapes (2 km radius), highlighting the percentage of forest cover (gray areas).

Fig 2. Total richness and abundance of forest-specialist and generalist species in the 40 sampling sites.

Landscapes vary in the amount of remaining forest cover from 6% to 85%. Lines correspond to the best fitting models.

Fig 3. Richness and abundance of frugivorous and insectivorous birds in the 40 sampling sites.

Landscapes vary in the amount of remaining forest cover from 6% to 85%. Lines correspond to the best fitting models.

Fig 4. NMDS ordination of the 40 sites that were sampled in the Brazilian Atlantic Forest.

Black points represent the scores of landscapes and the numbers indicate the percentages of forest cover (from 6% to 85%). A: Forest-specialist birds, B: Generalist birds, C: Frugivorous birds, D: Insectivorous birds. Pairwise ANOSIM tests showed significant differences ($p < 0.05$) between the bird compositions of landscapes with percentages of forest cover that were less than (left polygons) and greater than (right polygons) the threshold values.

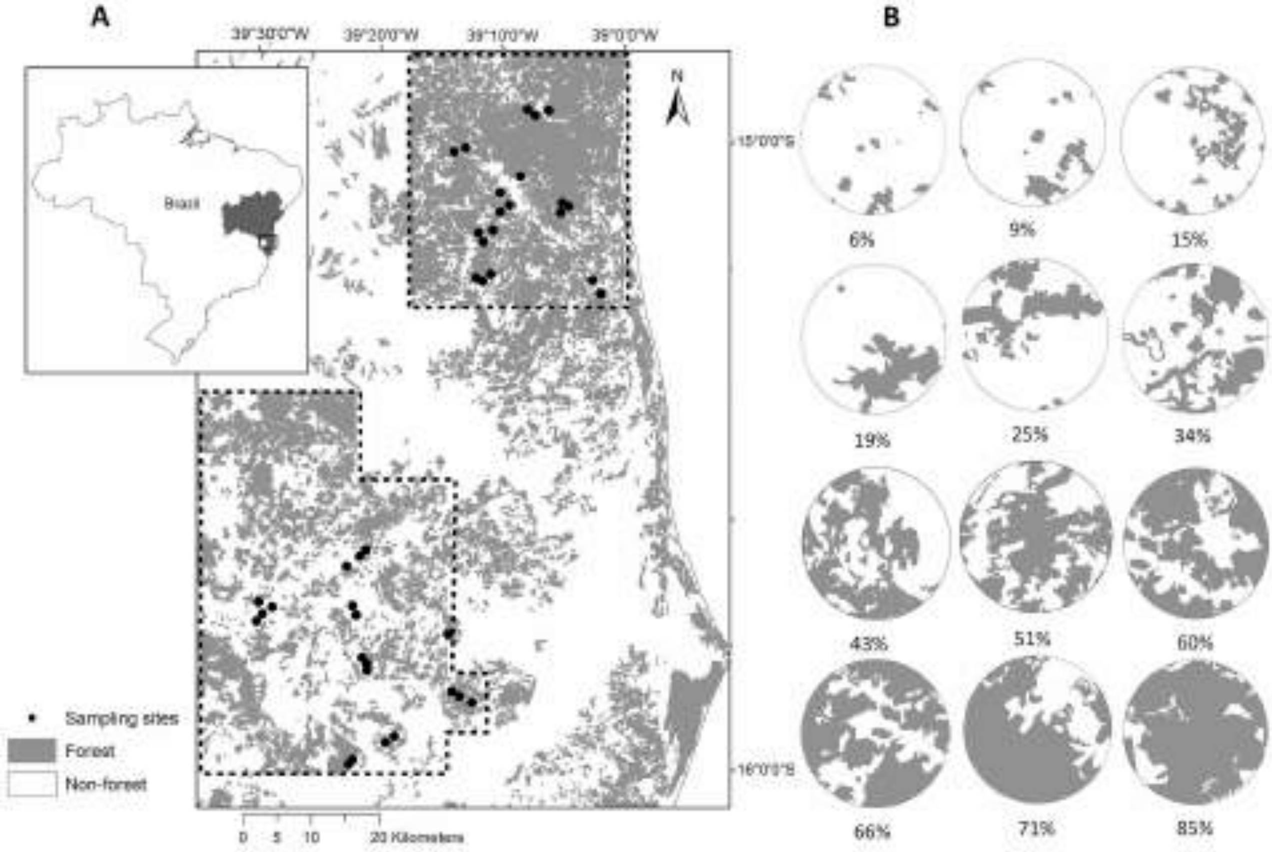
A
39°30'0"W
39°20'0"W
39°10'0"W
39°0'0"W
N
15°0'0"S
16°0'0"S
Brazil
Sampling sites
Forest
Non-forest
0 5 10 20 Kilometers
B
6%
9%
15%
19%
25%
34%
43%
51%
60%
66%
71%
85%

Figure 1

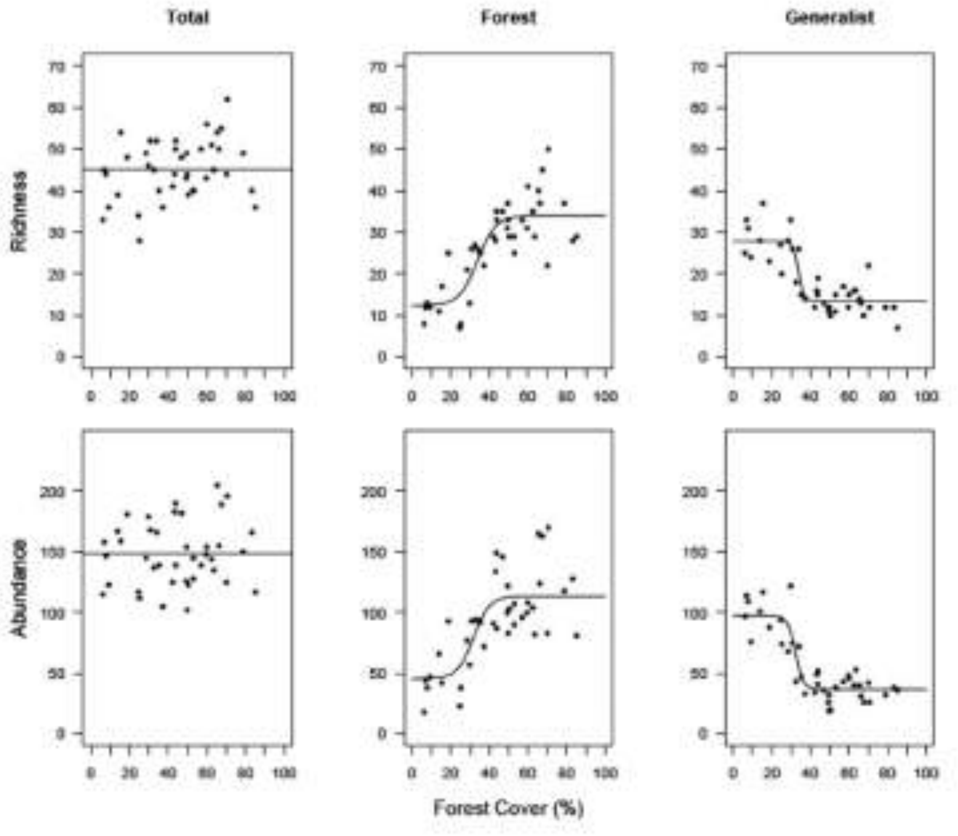
Total
Forest
Generalist
Richness
Abundance
0
10
20
30
40
50
60
70
0
50
100
150
200
0
20
40
60
80
100
Forest Cover (%)

Figure 2

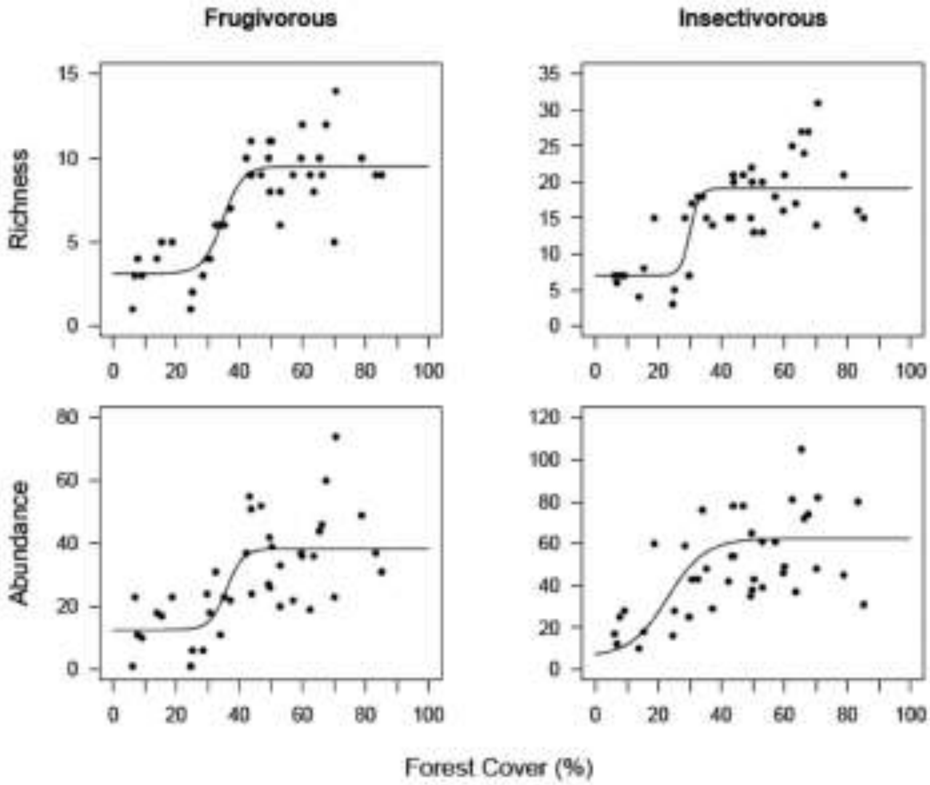
Frugivorous
Insectivorous
Richness
Abundance
Forest Cover (%)
0
20
40
60
80
100
15
10
5
35
30
25
20
120

Figure 3

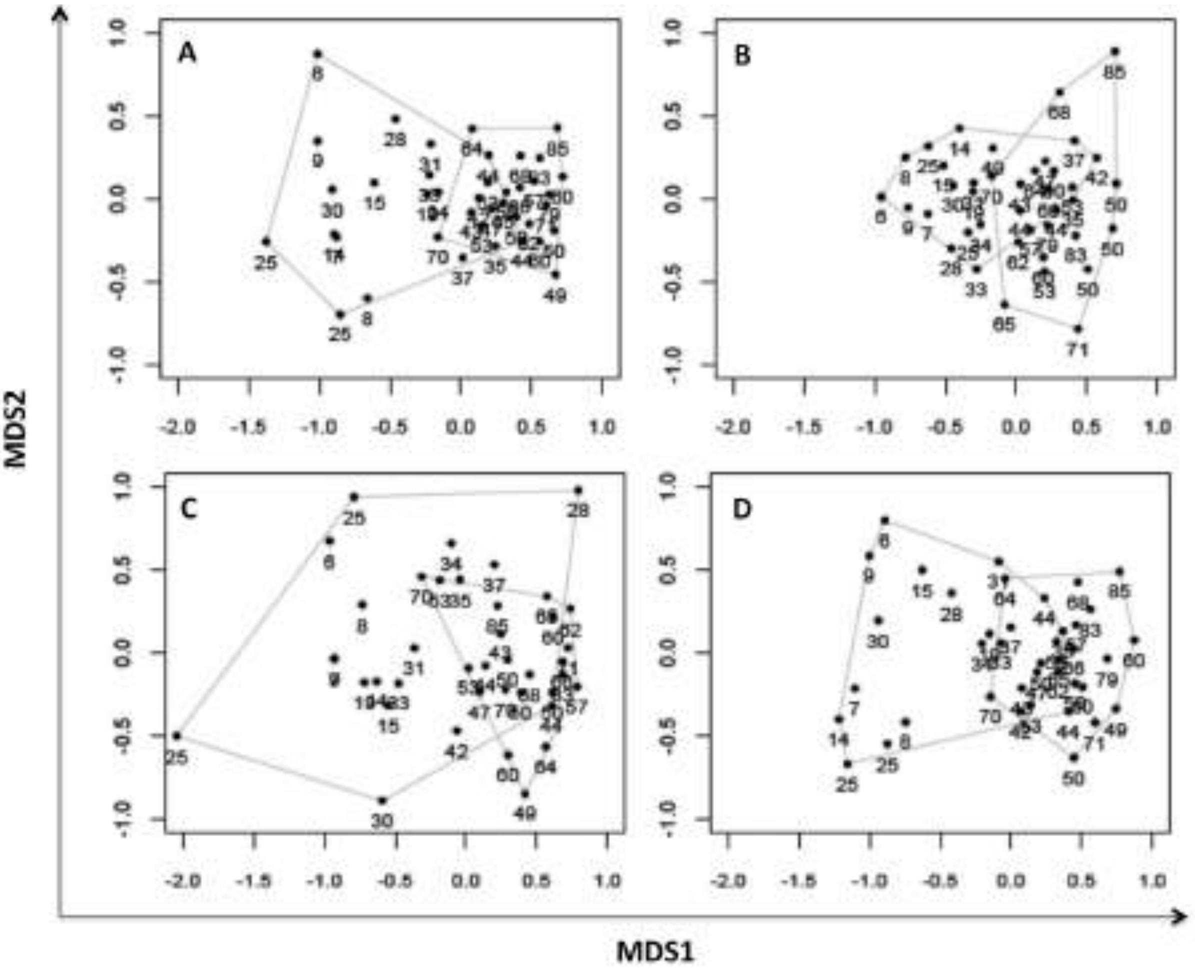

Figure 4

Tables

Table 1. Richness and abundance of birds of different ecological groups.

Ecological groups	**Richness**	**Abundance**
Generalist	81	2216
Forest-specialist	103	3715
Trophic guilds of forest-specialist		
Frugivorous	34	1165
Insectivorous	56	1935
Omnivorous	6	452
Nectarivorous	3	136
Carnivorous	3	13
Granivorous	1	14

Table 2. Best models (in bold) for explaining the relationship between richness and abundance of ecological groups of birds and the amount of forest cover.

	Richness					Abundance				
Species group	Model	AICc	Δ_i	k	w_i	Model	AICc	Δ_i	k	w_i
Total	**GLM**	**270.91**	**0**	**2**	**0.64**	**GLM**	**457.59**	**0**	**2**	**0.49**
	NULL	**272.58**	**1.67**	**1**	**0.27**	**NULL**	**457.79**	**0.2**	**1**	**0.46**
	FLM	275.03	4.12	4	0.09	FLM	462.56	4.97	4	0.04
Forest-specialist	**FLM**	**264.57**	**0**	**4**	**1**	**FLM**	**526.84**	**0**	**4**	**1**
	GLM	287.97	23.4	2	<0.01	GLM	606.03	79.2	2	<0.01
	NULL	380.62	116.1	1	<0.01	NULL	889.98	363.1	1	<0.01
Generalists	**FLM**	**226.27**	**0**	**4**	**0.98**	**FLM**	**350.09**	**0**	**4**	**1**
	GLM	233.69	7.5	2	0.02	GLM	420.67	70.6	2	<0.01
	NULL	305.53	79.4	1	<0.01	NULL	789.34	439.2	1	<0.01
Frugivores	**FLM**	**174**	**0**	**4**	**0.99**	**FLM**	**405.92**	**0**	**4**	**1**
	GLM	184.69	10.7	2	0.01	GLM	447.87	42	2	<0.01
	NULL	216	42	1	<0.01	NULL	598.69	192.8	1	<0.01
Insectivores	**FLM**	**236.56**	**0**	**4**	**0.99**	**FLM**	**475.9**	**0**	**4**	**1**
	GLM	250.2	13.6	2	0.01	GLM	517.74	41.8	2	<0.01
	NULL	304.65	68.1	1	<0.01	NULL	657.63	181.7	1	<0.01

Models: Null model (NULL), generalized linear model (GLM) and logistic model with four parameters (FLM). AICc: Akaike information criterion corrected; Δ_i: difference in AICc between the best model and the ith model; k: parameter number of the model; w_i: AICc weight. Models are ranked by AICc values.

Supporting Information

S1 File. Commands executed in R Program to conduct the data analysis of bird ecological groups.

```
#packages
library("vegan")#[1]
library("MASS")#[2]
library(nlme)#[3]
library("bbmle")#[4]
library("segmented")#[5]

#loading table
Tabela_aves=read.table("c:/data frame/Tabela_aves.txt", header= T, sep="")

#loading variables
#total richness of birds
tot.rich=Tabela_aves$Riq_total
#total abundance of birds
tot.abu=Tabela_aves$Abund_total
#generalist birds richness
gen.rich=Tabela_aves$Riq_generalista
#generalist birds abundance
gen.abu=Tabela_aves$Abund_generalista
#forest-dependent birds richness
for.rich=Tabela_aves$Riq_florestais
#forest-dependent birds abundance
for.abu=Tabela_aves$Abund_florestais
#frugivorous birds richness
fru.rich=Tabela_aves$Riq_FRU
#frugivorous birds abundance
fru.abu=Tabela_aves$Abund_FRU
#insectivores birds richness
ins.rich=Tabela_aves$Riq_INS
#insectivores birds abundance
ins.abu=Tabela_aves$Abund_INS
```

```
#forest cover
cover=Tabela_aves$Por

############

#First - Evaluated the bird response types (linear and nonlinear)

#Models: total richness

#Generalized Linear model
modTR.glm=glm(tot.rich~cover, family=poisson)

#four parameter logistic regression with poisson error
logip=function(p,lambda,x){
  a=p[1]
  b=p[2]
  c=p[3]
  d=p[4]
  Riq1 = d+(a/(1+exp((b-cover)/c)))
  -sum(dpois(x,lambda=Riq1, log=TRUE))
}
parnames(logip)=c("a","b","c","d")
modTR.log=mle2(minuslog=logip, start= c(a=30,b=30, c=3,d=20), data=list(x=tot.rich))

#null model
modTR.null=glm(tot.rich~1, family=poisson)

#model selection
AICctab(modTR.glm,modTR.log, modTR.null, weights=T, nobs=40)

##null and glm are almost equiprobable, let us see the points, the models and residuals

#plots:
plot(cover,tot.rich, xlab="Forest cover", ylab="Total Richness")#original data
```

```
abline(h=mean(tot.rich))#null model
points(cover, modTR.glm$fit, type="l", col="dark gray")##glm model

#investigating the glm parameters
coef(modTR.glm)

#a very low value of correlation coeficient.
#null model explins better

#residual analysis
plot(modTR.glm$res, cover)
plot(modTR.null$res, cover)

##########
```

#Models: total abundance

```
#Generalized Linear model
modTA.glm=glm(tot.abu~cover, family=poisson)

#four parameter logistic regression with poisson error
logip=function(p,lambda,x){
  a=p[1]
  b=p[2]
  c=p[3]
  d=p[4]
  Riq1 = d+(a/(1+exp((b-cover)/c)))
  -sum(dpois(x,lambda=Riq1, log=TRUE))
}
parnames(logip)=c("a","b","c","d")
modTA.log=mle2(minuslog=logip, start= c(a=70,b=25, c=3,d=80), data=list(x=tot.abu))

##null model
modTA.null=glm(tot.abu~1, family=poisson)
```

```
#model selection
AICctab(modTA.glm,modTA.log, modTA.null, weights=T, nobs=40)

##null and glm área lmost equiprobable, let us see the points, the models and residuals

#plots:
plot(cover,tot.abu, xlab="Forest cover", ylab="Total Abundance")#original data
abline(h=mean(tot.abu))#null model
points(cover, modTA.glm$fit, type="l", col="dark gray")#glm model

#investigating the glm parameters
coef(modTA.glm)

#a very low value of correlarion coeficient, again.
#null model explins better

#residual analysis
plot(modTA.glm$res, cover)
plot(modTA.null$res, cover)

############
```

#Models: generalist birds richness

```
#Generalized Linear model
modGR.glm=glm(gen.rich~cover, family=poisson)

#four parameter logistic regression with poisson error
logip=function(p,lambda,x){
  a=p[1]
  b=p[2]
  c=p[3]
  d=p[4]
  Riq1 = d+(a/(1+exp((cover-b)/c)))#inverse relation
  -sum(dpois(x,lambda=Riq1, log=TRUE))
```

```
}
parnames(logip)=c("a","b","c","d")
modGR.log=mle2(minuslog=logip, start= c(a=40,b=25, c=3,d=10), data=list(x=gen.rich))

##null model
modGR.null=glm(gen.rich~1, family=poisson)
#model selection
AICctab(modGR.glm,modGR.log, modGR.null,weights=T, nobs=40)
#logistic wons

#investigating
#likelihood profile of parameters
pGR=profile(modGR.log)

#plot
plot(pGR)
#Coefficients:
#a        b        c        d
#14.44908 33.80707  1.38481 13.46904

#plots:
#adjusted points
plot(cover,gen.rich, xlab="Forest cover", ylab="Generalists Richness")#original data
curve (13.46904+(14.44908/(1+exp((x-33.80707)/1.38481))), add=T)

#residual analysis
#generating residuals
resGR.log=gen.rich-(13.46904+(14.44908/(1+exp((cover-33.80707)/1.38481))))

#plot raw residuals against x
plot( cover,resGR.log)

################
```

#Models: generalist birds abundance

```
#Generalized Linear model
modGA.glm=glm(gen.abu~cover, family=poisson)

#four parameter logistic regression with poisson error
logip=function(p,lambda,x){
  a=p[1]
  b=p[2]
  c=p[3]
  d=p[4]
  Riq1 = d+(a/(1+exp((cover-b)/c)))#inverse relation
  -sum(dpois(x,lambda=Riq1, log=TRUE))
}
parnames(logip)=c("a","b","c","d")
modGA.log=mle2(minuslog=logip, start= c(a=40,b=25, c=3,d=10), data=list(x=gen.abu))

##null model
modGA.null=glm(gen.abu~1, family=poisson)

#model selection
AICctab(modGA.glm,modGA.log, modGA.null,weights=T, nobs=40)
#logistic wons

#investigating
#likelihood profile of parameters
pGA=profile(modGA.log)

#plot
#get coefficients
modGA.log
plot(pGA)

#Coefficients:
#a         b         c         d
#60.704081 32.253299  2.016751 36.678726
```

```
#plots:
#adjusted points
plot(cover,gen.abu, xlab="Forest cover", ylab="Generalists Abundace")#original data
curve (36.678726+(60.704081/(1+exp((x-32.253299)/2.016751))), add=T)

#residual analysis
#generating residuals
resGA.log=gen.abu-(36.678726+(60.704081/(1+exp((cover-32.253299)/2.016751))))

#plot raw residuals against x
plot( cover,resGA.log)

###########
```

#Models: forest-dependent birds richness

```
#Generalized Linear model
modFR.glm=glm(for.rich~cover, family=poisson)

#four parameter logistic regression with poisson error
logip=function(p,lambda,x){
  a=p[1]
  b=p[2]
  c=p[3]
  d=p[4]
  Riq1 = d+(a/(1+exp((b-cover)/c)))
  -sum(dpois(x,lambda=Riq1, log=TRUE))
}
parnames(logip)=c("a","b","c","d")
modFR.log=mle2(minuslog=logip, start= c(a=40,b=25, c=3,d=10), data=list(x=for.rich))

#null model
modFR.null=glm(for.rich~1, family=poisson)
#model selection
```

```
AICctab(modFR.glm,modFR.log, modFR.null,weights=T, nobs=40)
#logisticn wons

#investigating
#likelihood profile of parameters
pFR=profile(modFR.log)

#plot
plot(pFR)

#get coefficients from logsitic
modFR.log

#Coefficients:
#a         b         c         d
#21.645268 33.826036  4.750837 12.416747

#plots:
#adjusted points
plot(cover,for.rich, xlab="Forest cover", ylab="Forest-Dependent Richness")#original data
curve (12.416747+(21.645268/(1+exp((33.82603-x)/4.750837))), add=T,lwd=1.5)

#residual analysis
#generating residuals
resFR.log=for.rich-(12.416747+(21.645268/(1+exp((33.82603-cover)/4.750837))))

#plot raw residuals against x
#logistic
plot( cover,resFR.log)

########
```

#Models: forest-dependent birds abundance

```
#Generalized Linear model
```

```
modFA.glm=glm(for.abu~cover, family=poisson)

#four parameter logistic regression with poisson error
logip=function(p,lambda,x){
  a=p[1]
  b=p[2]
  c=p[3]
  d=p[4]
  Riq1 = d+(a/(1+exp((b-cover)/c)))
  -sum(dpois(x,lambda=Riq1, log=TRUE))
}
parnames(logip)=c("a","b","c","d")
modFA.log=mle2(minuslog=logip, start= c(a=80,b=35, c=3,d=40), data=list(x=for.abu))

#null model
modFA.null=glm(for.abu~1, family=poisson)

#model selection
AICctab(modFA.glm,modFA.log, modFA.null,weights=T, nobs=40)
#logistic wons

#investigating
#likelihood profile of parameters
pFA=profile(modFA.log)

#plot
plot(pFA)

#get coefficients from logsitic
modFA.log

#Coefficients:
#a         b         c         d
#67.869384 31.759500  3.140008 45.640603
```

```
#plots:
#adjusted points
plot(cover,for.abu, xlab="Forest cover", ylab="Forest-Dependent Abundance")#original data
curve (45.640603+(67.869384/(1+exp((31.759500-x)/4.140008))), col="darkgray", lwd=2,add=T)

#residual analysis
#generating residuals
resFA.log=for.abu-(45.640603+(67.869384/(1+exp((31.759500-cover)/4.140008))))

#plot raw residuals against x
#logistic
plot( cover,resFA.log)

###########
```

#Models: frugivorous birds richness

```
#Generalized Linear model
modFbR.glm=glm(fru.rich~cover, family=poisson)

#four parameter logistic regression with poisson error
logip=function(p,lambda,x){
  a=p[1]
  b=p[2]
  c=p[3]
  d=p[4]
  Riq1 = d+(a/(1+exp((b-cover)/c)))
  -sum(dpois(x,lambda=Riq1, log=TRUE))
}
parnames(logip)=c("a","b","c","d")
modFbR.log=mle2(minuslog=logip, start= c(a=10,b=30, c=2,d=3), data=list(x=fru.rich))

##null model
modFbR.null=glm(fru.rich~1, family=poisson)
```

```
#model selection
AICctab(modFbR.glm,modFbR.log, modFbR.null,weights=T, nobs=40)
#logistic wons

#investigating
#likelihood profile of parameters
pFbR=profile(modFbR.log)

#plot
plot(pFbR)

#get coefficients from logsitic
modFbR.log

#Coefficients:
#a         b         c         d
#6.378173 34.734150  2.264860  3.121281

#plots:
#adjusted points
plot(cover,fru.rich, xlab="Forest cover", ylab="Frugivorous Richness")#original data
curve (3.121281+(6.378173/(1+exp((34.734150-x)/3.121281))), lwd=1.5,add=T)

#residual analysis
#generating residuals
resFbR.log=fru.rich-(7.012601+(12.105213/(1+exp((30.019914-cover)/7.012601))))

#plot raw residuals against x
#logistic
plot( cover,resFbR.log)

##################
```

#Models: frugivorous birds abundance

```
##Generalized Linear model
modFbA.glm=glm(fru.abu~cover, family=poisson)

#four parameter logistic regression with poisson error
logip=function(p,lambda,x){
  a=p[1]
  b=p[2]
  c=p[3]
  d=p[4]
  Riq1 = d+(a/(1+exp((b-cover)/c)))
  -sum(dpois(x,lambda=Riq1, log=TRUE))
}
parnames(logip)=c("a","b","c","d")
modFbA.log=mle2(minuslog=logip, start= c(a=30,b=35, c=4,d=15), data=list(x=fru.abu))

#null model
modFbA.null=glm(fru.abu~1, family=poisson)

#model selection
AICctab(modFbA.glm,modFbA.log, modFbA.null,weights=T, nobs=40)
#logistic wons

#investigating
#likelihood profile of parameters
pFbA=profile(modFbA.log)

#plot
plot(pFbA)

#get coefficients from logsitic
modFbA.log

#Coefficients:
#a         b         c         d
#25.749904 35.931809  2.629633 12.648185
```

```
#plots:
#adjusted points
plot(cover,fru.abu, xlab="Forest cover", ylab="Frugivorous Abundance")#original data
curve (12.648185+(25.749904/(1+exp((35.931809-x)/2.629633))), lwd=1.5,add=T)

#residual analysis
#generating residuals
resFbA.log=fru.abu-(12.648185+(25.749904/(1+exp((35.931809-cover)/2.629633))))

#plot raw residuals against x
#logistic
plot( cover,resFbA.log)

##################
```

#Models: insectivores birds richness

```
#Generalized Linear model
modIR.glm=glm(ins.rich~cover, family=poisson)

#four parameter logistic regression with poisson error
logip=function(p,lambda,x){
  a=p[1]
  b=p[2]
  c=p[3]
  d=p[4]
  Riq1 = d+(a/(1+exp((b-cover)/c)))
  -sum(dpois(x,lambda=Riq1, log=TRUE))
}
parnames(logip)=c("a","b","c","d")
modIR.log=mle2(minuslog=logip, start= c(a=10,b=30, c=1,d=6), data=list(x=ins.rich))

##null model
modIR.null=glm(ins.rich~1, family=poisson)
```

```
#model selection
AICctab(modIR.glm,modIR.log, modIR.null,weights=T, nobs=40)
#logistic wons

#investigating
#likelihood profile of parameters
pIR=profile(modIR.log)

#plot
plot(pIR)

#get coefficients from logsitic
modIR.log

#Coefficients:
#a        b        c        d
#12.105698 30.019599  1.461216  7.012205

#plots:
#adjusted points
plot(cover,ins.rich, xlab="Forest cover", ylab="Insectivores Richness")#original data
curve (7.012205+(12.105698/(1+exp((30.019599-x)/1.461216))), lwd=1.5,add=T)

#residual analysis
#generating residuals
resIR.log=ins.rich-(7.012205+(12.105698/(1+exp((30.019599-cover)/1.461216))))

#plot raw residuals against x
#logistic
plot( cover,resIR.log)

##################
```

#Models: insectivororus bird abundance

```
#Generalized Linear model
modIA.glm=glm(ins.abu~cover, family=poisson)

#four parameter logistic regression with poisson error
logip=function(p,lambda,x){
  a=p[1]
  b=p[2]
  c=p[3]
  d=p[4]
  Riq1 = d+(a/(1+exp((b-cover)/c)))
  -sum(dpois(x,lambda=Riq1, log=TRUE))
}
parnames(logip)=c("a","b","c","d")
modIA.log=mle2(minuslog=logip, start= c(a=40,b=35, c=1,d=20), data=list(x=ins.abu))

#null model
modIA.null=glm(ins.abu~1, family=poisson)

#model selection
AICctab(modIA.glm,modIA.log, modIA.null,weights=T, nobs=40)
#logistic wons

#investigating
#likelihood profile of parameters
pIA=profile(modIA.log)

#plot
plot(pIA)

#get coefficients from logsitic
modIA.log

#Coefficients:
#a       b       c       d
```

```
#56.462531 22.952974 12.643445  5.999742

#plots:
#adjusted points
plot(cover,ins.abu, xlab="Forest cover", ylab="Insectivores Abundance")#original data
curve (5.999742+(56.462531/(1+exp((22.952974-x)/5.999742))), lwd=1.5,add=T)

#residual analysis
#generating residuals
resIA.log=ins.abu-(5.999742+(56.462531/(1+exp((22.952974-cover)/5.999742))))

#plot raw residuals against x
#logistic
plot( cover,resIA.log)
```

#####Plot Figure 2

```
par(mfrow=c(2,3))
plot(cover, tot.rich, xlim=c(0,100), ylim=c(0,70), xaxp=c(0,100,10), ylab="Richness", xlab=NA, col="black", pch=16,cex.lab=1.3,las="1", main="Total")
abline(h=mean(tot.rich))#null model
plot(cover, for.rich,xlim=c(0,100), ylim=c(0,70), xaxp=c(0,100,10), ylab=NA, xlab=NA, col="black", pch=16,cex.lab=1.3, las="1", main="Forest")
curve (12.416747+(21.645268/(1+exp((33.82603-x)/4.750837))), add=T,col=1)##logistic model
plot(cover, gen.rich,xlim=c(0,100), ylim=c(0,70), xaxp=c(0,100,10), ylab=NA, xlab=NA, col="black", pch=16,cex.lab=1.3, las="1", main="Generalist")
curve (13.46904+(14.44908/(1+exp((x-33.80707)/1.38481))), add=T,col=1)##logistic model
plot(cover,tot.abu,xlim=c(0,100), ylim=c(0,240), xaxp=c(0,100,10), ylab="Abundance", xlab=NA, col="black", pch=16,cex.lab=1.3,las="1")
abline(h=mean(tot.abu))##null model
plot(cover, for.abu, xlim=c(0,100), ylim=c(0,240), xaxp=c(0,100,10), ylab=NA, xlab="Forest Cover (%)", col="black", pch=16,cex.lab=1.3, las="1")
curve (45.640603+(67.869384/(1+exp((31.759500-x)/4.140008))), col=1,add=T)##logistic model
```

```
plot(cover, gen.abu,xlim=c(0,100), ylim=c(0,240), xaxp=c(0,100,10), ylab=NA, xlab=NA, col="black", pch=16,cex.lab=1.3, las="1")
curve (36.678726+(60.704081/(1+exp((x-32.253299)/2.016751))), add=T,col=1)##logistic model
```

####Plot Figure 3

```
par(mfrow=c(2,2))
plot(cover, fru.rich,xlim=c(0,100), ylim=c(0,15), xaxp=c(0,100,10), ylab="Richness", xlab=NA, col="black", pch=16,cex.lab=1.3, las="1", main="Frugivorous")
curve (3.121281+(6.378173/(1+exp((34.734150-x)/3.121281))), col=1,add=T)##logistic model
plot(cover, ins.rich,xlim=c(0,100), ylim=c(0,35), xaxp=c(0,100,10), ylab=NA, xlab=NA, col="black", pch=16,cex.lab=1.3, las="1", main="Insectivorous")
curve (7.012205+(12.105698/(1+exp((30.019599-x)/1.461216))), col=1,add=T)##logistic model
plot(cover, fru.abu,xlim=c(0,100), ylim=c(0,120), xaxp=c(0,100,10), ylab="Abundance", xlab=NA, col="black", pch=16,cex.lab=1.3, las="1")
curve (12.648185+(25.749904/(1+exp((35.931809-x)/2.629633))), col=1,add=T)##logistic model
plot(cover, ins.abu,xlim=c(0,100), ylim=c(0,120), xaxp=c(0,100,10), ylab=NA, xlab="Forest Cover (%)", col="black", pch=16,cex.lab=1.3, las="1")
curve (5.999742+(56.462531/(1+exp((22.952974-x)/5.999742))), col=1,add=T)##logistic model

##############
```

#Second - Piecewise model with poisson error for find to threshold value

```
modGR.pic=segmented(modGR.glm,seg.Z=~cover,psi=list(cover=c(40)),control=seg.control(display=F))#generalist richness
summary(modGR.pic)
modGA.pic=segmented(modGA.glm,seg.Z=~cover,psi=list(cover=c(40)),control=seg.control(display=F))#generalist abundance
summary(modGA.pic)
modFR.pic=segmented(modFR.glm,seg.Z=~cover,psi=list(cover=c(40)),control=seg.control(display=F))#forest richness
summary(modFR.pic)
```

```
modFA.pic=segmented(modFA.glm,seg.Z=~cover,psi=list(cover=c(40)),control=seg.control(display=F))#forest abundance
summary(modFA.pic)
modFbR.pic=segmented(modFbR.glm,seg.Z=~cover,psi=list(cover=c(40)),control=seg.control(display=F))#frugivores richness
summary(modFbR.pic)
modFbA.pic=segmented(modFbA.glm,seg.Z=~cover,psi=list(cover=c(40)),control=seg.control(display=F))#frugivores abundance
summary(modFbA.pic)
modIR.pic=segmented(modIR.glm,seg.Z=~cover,psi=list(cover=c(40)),control=seg.control(display=F))#insectivores richness
summary(modIR.pic)
modIA.pic=segmented(modIA.glm,seg.Z=~cover,psi=list(cover=c(40)),control=seg.control(display=F))#insectivores abundance
summary(modIA.pic)

############
```

#Third - Analyze differences in bird composition among landscapes

#Forest bird NMDS and ANOSIM

```
#loading table of forest bird
for_bird=read.table("c:/data frame/for_bird.txt", header= T, sep="")

#loading table forest cover to forest bird
for_cover=read.table("c:/data frame/for_cover.txt", header= T, sep=""))#site with percentage below 46% (peiecewise value) were categorized as low forest cover and site with cover above 46% were categorozed as high

names(for_cover)
#"Sites" "Cover" "Cat"
#Cat = categories of forest cover (low and high)

plan1=t(for_bird)
```

```
plan.pres=plan1
plan.pres[plan.pres>0]=1#transforming the bird records in presence-absence
nmds1=metaMDS(plan.pres,"jaccard", k=2,trymax=20,trace=T)
nmds1$stress

matrix=vegdist(plan.pres)
anosim1=anosim(matrix,for_cover$Cat)
anosim1

#Scores for graphic
scorspec=nmds1$species
scorsitios=nmds1$points
```

#Generalist bird NMDS and ANOSIM

```
#loading table of generalist bird
gen_bird=read.table("c:/data frame/gen_bird.txt", header= T, sep="")

#loading table forest cover to generalist bird
gen_cover=read.table("c:/data frame/gen_cover.txt", header= T, sep=""))#site with percentage below 50% (peiecewise value) were categorized as low forest cover and site with cover above 50% were categorozed as high

plan2=t(gen_bird)
plan.pres2=plan2
plan.pres2[plan.pres2>0]=1
plan.pres2
nmds2=metaMDS(plan.pres2,"jaccard", k=2,trymax=20,trace=T)
nmds2$stress

matrix2=vegdist(plan.pres2)
anosim2=anosim(matrix2,gen_cover$Cat)

#Scores for graphic
scorspec2=nmds2$species
```

```
scorsitios2=nmds2$points
```

#Insectivorous bird NMDS and ANOSIM

```
#loading table of insectivorous bird
ins_bird=read.table("c:/data frame/ins_bird.txt", header= T, sep="")

#loading table forest cover to insectivorous bird
ins_cover=read.table("c:/data frame/ins_cover.txt", header= T, sep=""))#site with percentage below 44% (peiecewise value) were categorized as low forest cover and site with cover above 44% were categorozed as high

plan3=t(ins_bird)
plan.pres3=plan3
plan.pres3[plan.pres3>0]=1
plan.pres3
nmds3=metaMDS(plan.pres3,"jaccard", k=2,trymax=20,trace=T)
nmds3$stress

matrix3=vegdist(plan.pres3)
anosim3=anosim(matrix3,ins_cover$Cat)

#Scores for graphic
scorspec3=nmds3$species
scorsitios3=nmds3$points
```

#Frugivorous bird NMDS and ANOSIM

```
#loading table of frugivorous bird
fru_bird=read.table("c:/data frame/fru_bird.txt", header= T, sep="")

#loading table forest cover to frugivorous bird
fru_cover=read.table("c:/data frame/fru_cover.txt", header= T, sep=""))#site with percentage below 46% (peiecewise value) were categorized as low forest cover and site with cover above 46% were categorozed as high
```

```
plan4=t(fru_bird)
plan.pres4=plan4
plan.pres4[plan.pres4>0]=1
plan.pres4
nmds4=metaMDS(plan.pres4,"jaccard", k=2,trymax=20,trace=T)
nmds4$stress

matrix4=vegdist(plan.pres4)
anosim4=anosim(matrix4,fru_cover$Cat)

#Scores for graphic
scorspec4=nmds4$species
scorsitios4=nmds4$points

############
```

#Plot Figure 4

```
par(mfrow=c(2,2))

treat=c(rep("low", 20), rep("high", 20))
plot(scorsitios,type="n",xlim=c(-2,1),ylim=c(-1,1),font.main=1,cex.axis=0.8,cex.lab=0.8,cex.main=0.8,cex=0.6)#forest bird
ordihull(nmds1, groups=treat, draw="lines", col="gray",label=F)
points(scorsitios[1:20,],pch=16,cex=0.9)
points(scorsitios[21:40,],pch=16, cex=0.9)
text(scorsitios,labels=for_cover$Cover,pos=1,cex=0.8)

treat1=c(rep("low", 22), rep("high", 18))
plot(scorsitios2,type="n",xlim=c(-2,1), ylim=c(-1,1),xlab=NA, ylab=NA, font.main=1,cex.axis=0.8,cex.lab=0.8,cex.main=0.8,cex=0.6)#generalist bird
ordihull(nmds2, groups=treat1, draw="lines", col="gray",label=F)
points(scorsitios2[1:22,],pch=16,cex=0.9)
points(scorsitios2[23:40,],pch=16, cex=0.9)
```

```
text(scorsitios2,labels=gen_cover$Cover,pos=1,cex=0.8)

treat2=c(rep("low", 20), rep("high", 20))
plot(scorsitios4,type="n",xlim=c(-2,1), ylim=c(-1,1),xlab=NA, ylab=NA,
font.main=1,cex.axis=0.8,cex.lab=0.8,cex.main=0.8,cex=0.6)#frugivorous bird
ordihull(nmds4, groups=treat2, draw="lines", col="gray",label=F)
points(scorsitios4[1:20,],pch=16,cex=0.9)
points(scorsitios4[21:40,],pch=16, cex=0.9)
text(scorsitios4,labels=fru_cover$Cover,pos=1,cex=0.8)

treat3=c(rep("low", 20), rep("high", 20))
plot(scorsitios3,type="n",xlim=c(-2,1), ylim=c(-1,1),xlab=NA, ylab=NA,
font.main=1,cex.axis=0.8,cex.lab=0.8,cex.main=0.8,cex=0.6)#insectivorous bird
ordihull(nmds3, groups=treat3, draw="lines", col="gray",label=F)
points(scorsitios3[1:20,],pch=16,cex=0.9)
points(scorsitios3[21:40,],pch=16, cex=0.9)
text(scorsitios3,labels=ins_cover$Cover,pos=1,cex=0.8)
```

#Fourth - Direct ordination using presence-absence

```
#Function to create the graphic
ordination<-function(tabela,gradiente,at,grad,eixoY,eixoX){
tabela<-as.matrix(tabela)
gradiente<-as.matrix(gradiente)
media.pond<-colSums(tabela*gradiente[,1])/colSums(tabela)
sub.orden<-tabela[order(gradiente[,1],decreasing=F),]
sub.orde<-sub.orden[,order(media.pond,decreasing=T)]
dados.pa<-matrix(0,nrow(tabela),ncol(tabela))
dados.pa[tabela>0]<-1
ordenado<-sub.orde[,which(colSums(dados.pa)>0)]
par(mfrow=c(ncol(ordenado)+1,1),mar=c(0,2,0.3,8),oma=c(2.5,1,1,6))
layout(matrix(1:(ncol(ordenado)+1)),heights=c(3,rep(1,ncol(ordenado))))
plot(sort(gradiente[,1]),axes=F,ylab="",mfg=c(21,1),lwd=8,las=2,lend="butt",frame.plot=F,xaxt="n",type="h",col="black",ylim=c(min(gradiente),max(gradiente)))
axis(side=2,at=c(min(gradiente),max(gradiente)),las=2)
```

```
mtext(grad,2,outer=T,font=1,line=-24,padj=-34,las=2,cex=0.8)
for(i in 1:ncol(ordenado)){
barplot(ordenado[,i],bty="l",axisnames=F,axes=FALSE,col="black")
mtext(colnames(ordenado)[i],3,line=-1,adj=0,at=at,cex=.55,font=1)
}
mtext(eixoX,1,outer=T,font=1,line=1.2, cex=1)
mtext(eixoY,2,font=1,outer=T,line=-2,cex=1)
}

#Forest bird-Supplementary material Figure S1
for.bird=read.csv2("for.bird.csv", header = T, check.names=F)#loading the data containing the species names in the column and sample site in the lines
for.bird[for_bird>0]=1#transforming the bird records in presence-absence
for.bird.plot=ordination(for_bird,cover,50,"Forest Cover (%)","Presence-Absence","Sampling Site")

#Generalist bird-Supplementary material Figure S2
gen.bird=read.csv2("gen_bird.csv", header = T, check.names=F)
gen_bird[gen_bird>0]=1
gen_bird.plot=ordination(gen_bird,cover,50,"Forest Cover (%)","Presence-Absence","Sampling Site")

#Frugivorous bird-Supplementary material Figure S3
fru_bird=read.csv2("fru_bird.csv", header = T, check.names=F)
fru_bird[fru_bird>0]=1
fru_bird.plot=ordination(fru_bird,cover,50,"Forest Cover (%)","Presence-Absence","Sampling Site")

#Insectivorous bird-Supplementary material Figure S4
ins_bird=read.csv2("ins_bird.csv", header = T, check.names=F)
ins_bird[ins_bird>0]=1
ins_bird.plot=ordination(ins_bird,cover,50,"Forest Cover (%)","Presence-Absence","Sampling Site")
```

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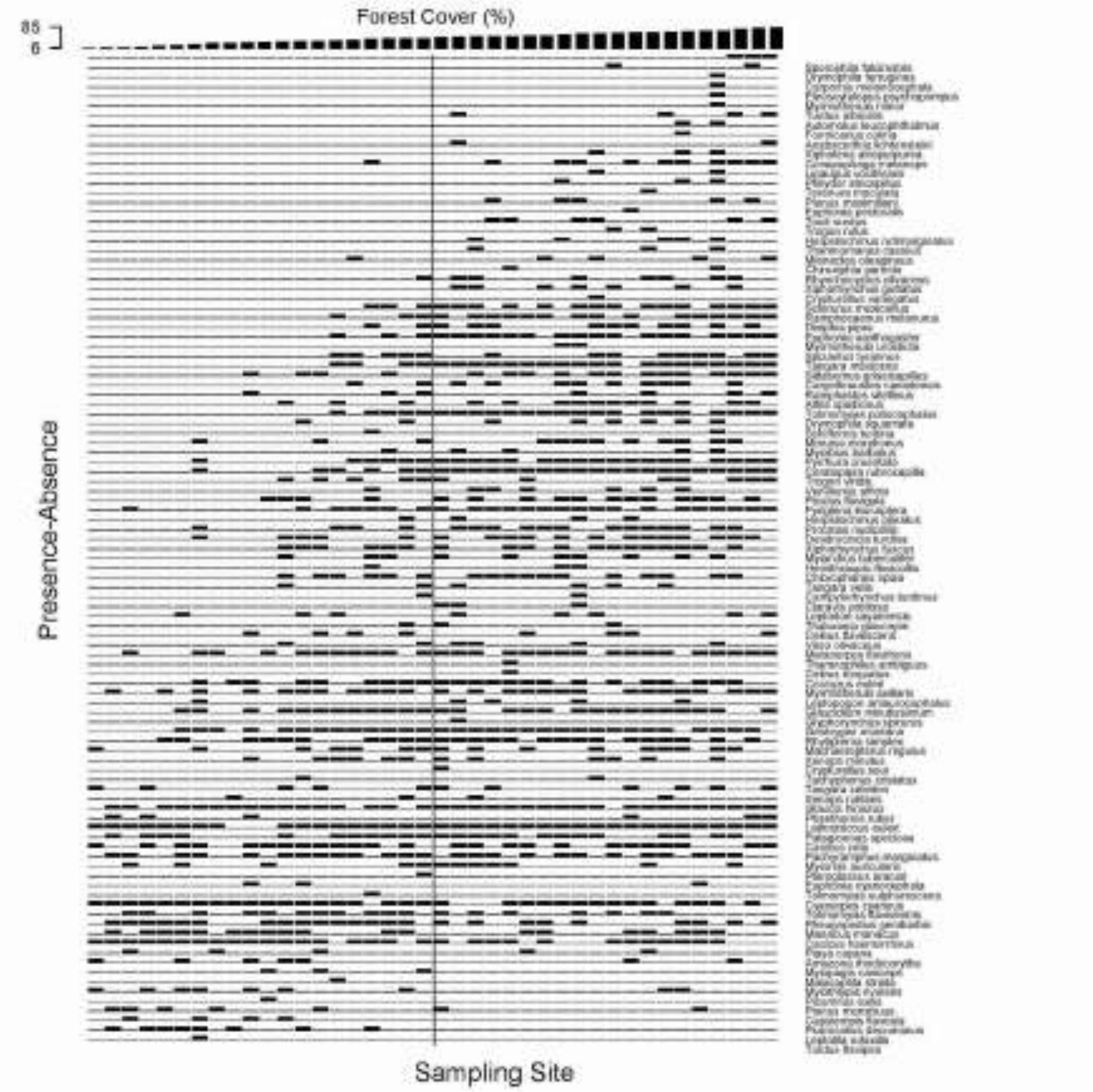
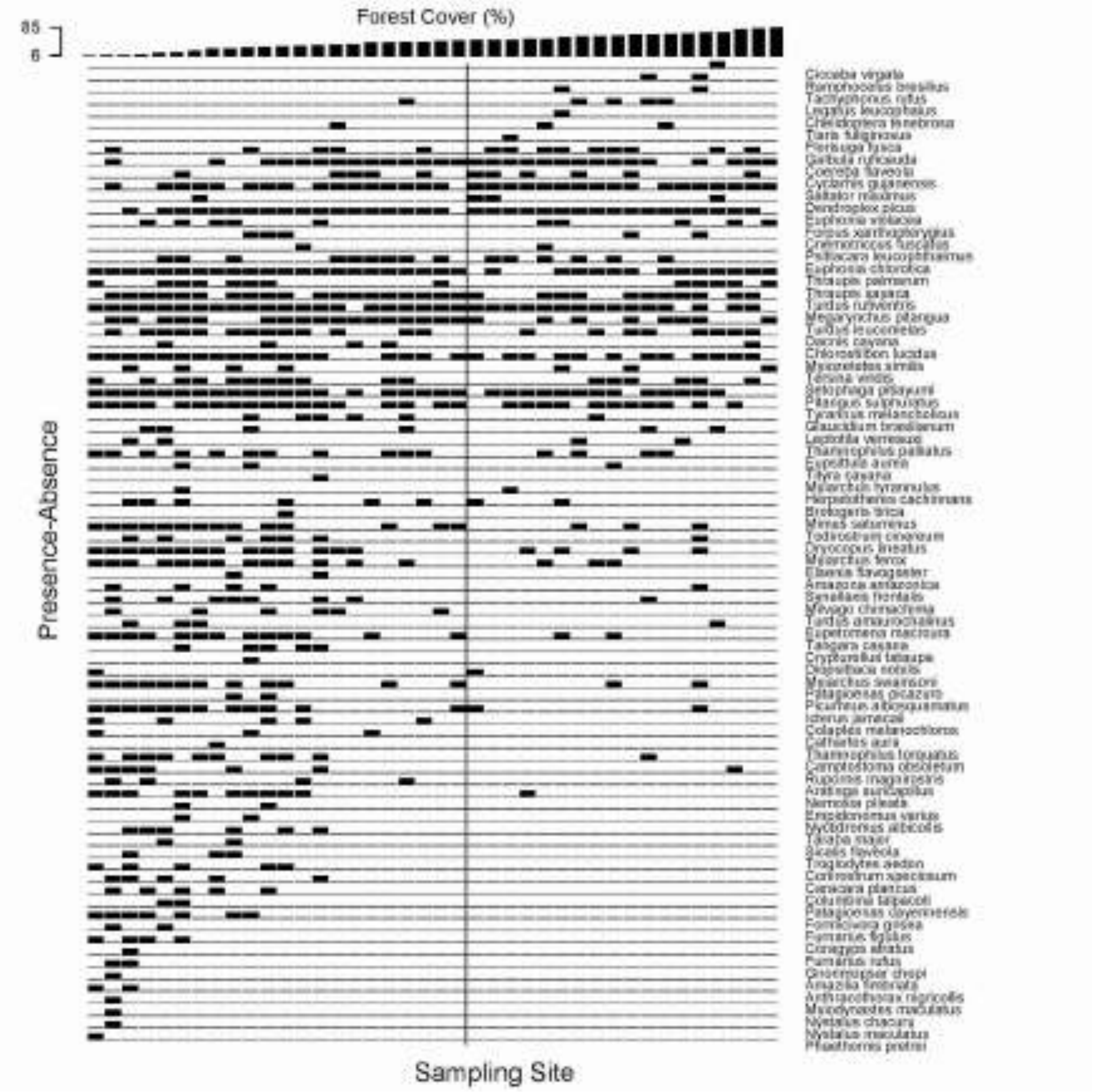
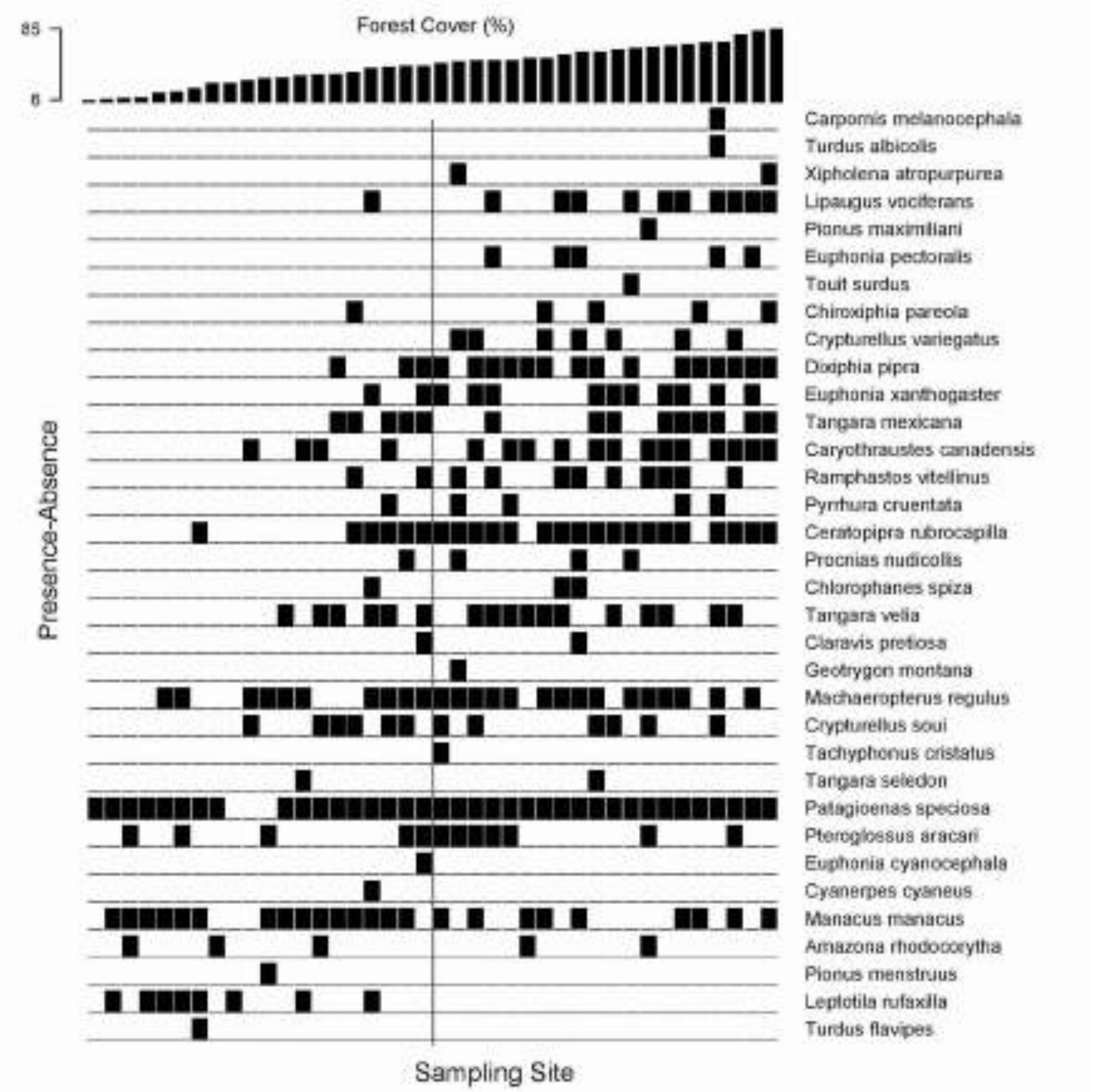


S1 Fig. Occurrence of forest-specialist birds in relation to the amount of forest cover in the 40 sampling sites. The vertical line indicates the threshold value estimated by the piecewise model.



S2 Fig. Occurrence of generalist birds in relation to the amount of forest cover in the 40 sampling sites. The vertical line indicates the threshold value estimated by the piecewise model.



S3 Fig. Occurrence of frugivorous birds in relation to the amount of forest cover in the 40 sampling sites. The vertical line indicates the threshold value estimated by the piecewise model.

S4 Fig. Occurrence of insectivorous birds in relation to the amount of forest cover in the 40 sampling sites. The vertical line indicates the threshold value estimated by the piecewise model.

Capítulo 2

Patterns and predictors of β-diversity in the fragmented Brazilian Atlantic forest: A multiscale analysis of forest specialist and generalist birds [#]

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Running headline: Bird β-diversity in the fragmented Atlantic forest

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Summary

1. Biodiversity maintenance in human-altered landscapes (HALs) depends on the species turnover among localities, but the patterns and determinants of β-diversity in HALs are poorly known. In fact, declines, increases, and neutral shifts in β-diversity have all been documented, depending on the landscape, ecological group and spatial scale of analysis.

2. We shed some light on this controversy by assessing the patterns and predictors of bird β-diversity across multiple spatial scales considering forest specialist and habitat generalist bird assemblages.

3. We surveyed birds from 144 point counts in 36 different forest sites across two landscapes with different amount of forest cover in the Brazilian Atlantic forest. We analysed β-diversity among points, among sites, and between landscapes with multiplicative diversity partitioning of Hill numbers. We tested whether β-diversity among points was related to within-site variations in vegetation structure, and if β-diversity among sites was related to site location and/or to differences among sites in vegetation structure and landscape composition (i.e. percent forest and pasture cover surrounding each site).

4. β-diversity between landscapes was lower than among sites and among points in both bird assemblages. In forest specialist birds, the landscape with less forest cover showed the highest β-diversity among sites (bird differentiation among sites), but generalist birds showed the opposite pattern. At the local scale, however, the less forested landscape showed the lowest β-diversity among points (bird homogenisation within sites), independently of the bird assemblage. β-diversity among points was weakly related to vegetation structure, but higher β-diversity values were recorded among sites that were more isolated from each other, and among sites with higher differences in landscape composition, particularly in the less forested landscape.

5. Our findings indicate that patterns of bird β-diversity vary across scales and are strongly related to landscape composition. Bird assemblages are shaped by both environmental filtering and dispersal limitation, particularly in less forested landscapes. Conservation and management strategies should therefore prevent deforestation in this biodiversity hotspot.

Key-words: Biodiversity crisis, dispersal limitation, environmental filtering, forest specialist, habitat loss, human-modified landscape, species turnover, tropical forest.

Introduction

Land cover change has resulted in human-altered landscapes (HALs) with different level of spatial heterogeneity (Hansen *et al*. 2013). Biodiversity maintenance in these landscapes represents a great challenge for several reasons (Gardner *et al*. 2009). First, the response of biodiversity to habitat disturbance differs among species and ecological groups (Ewers & Didham 2006), but evidence for this only comes from a few taxa, and mainly from temperate regions (Fahrig 2003). Second, such responses also vary among landscapes and regions, depending on landscape heterogeneity (Arroyo-Rodríguez *et al*. 2009) and are only evident within certain spatial scales (Arroyo-Rodríguez *et al*. 2013; Carrara *et al*. 2015). Unfortunately, most studies of biodiversity in HALs have been conducted in one landscape, and at one single spatial scale (i.e., usually the patch scale; Fahrig 2003). Also, the extirpation of disturbance-sensitive species may be compensated for by proliferation of disturbance-adapted species (i.e. compensatory dynamics), thus masking the response of community-level attributes to habitat disturbance in HALs (Supp & Ernest 2014). Finally, although it is well known that the number of species that landscapes and regions can accumulate (γ-diversity) depends on the species turnover (β-diversity) among localities (Arroyo-Rodríguez *et al*. 2013), the vast majority of studies in HALs assess changes in local (α) diversity, overlooking the impact that spatial habitat changes might have on β-diversity across multiple spatial scales (but see Karp *et al*. 2012; Püttker *et al*. 2015, Solar *et al.* 2015). Therefore, we need additional multiscale analyses of β-diversity in tropical landscapes with different spatial structures to attain a better understanding of the relative effects that spatial habitat change may have on tropical biodiversity. Such studies should independently assess disturbance-sensitive and disturbance-adapted species to avoid confusing effects of compensatory dynamics (Supp & Ernest 2014).

Evidence indicates that β-diversity depends on both local and landscape patterns (e.g. vegetation structure, landscape forest cover) directly related to deterministic (e.g. environmental filtering and species interactions) and stochastic (e.g. ecological drift and random extinctions) processes (Chase & Myers 2011). In HALs, deforestation and forest fragmentation are expected to alter such patterns and processes in contrasting ways, depending on the effects of land cover change on environmental heterogeneity and habitat isolation (Karp *et al*. 2012; Tscharntke *et al*. 2012; Püttker *et al*. 2015; Solar *et al.* 2015). For example, the replacement of native forests by extensive monocultures, such as sugarcane, cattle pastures and palm oil, results in landscapes with lower environmental heterogeneity which may provoke concomitant declines in β-diversity (Melo *et al.* 2013; Liu & Slik 2014). In addition, as land cover change is usually concentrated in easily accessible productive areas, the remaining old-growth forest patches in HALs are usually restricted to relatively inaccessible areas, such as steep slopes with poor soils (Arroyo-Rodríguez *et al*. 2009; Liu & Slik 2014). This environmental impoverishment can result in the loss of a large number of disturbance-sensitive species, and the proliferation of a small subset of disturbance-adapted species (Ekroos, Heliola & Kuussaari 2010; Lôbo *et al*. 2011; Tabarelli, Peres & Melo 2012). Therefore, in the absence of dispersal limitation (e.g. when considering good dispersers), such species replacement can lead to the biotic homogenisation (i.e. decreases in β-diversity) across multiple spatial scales (Tabarelli, Peres & Melo 2012). Nevertheless, when considering less vagile species, dispersal limitation can increase β-diversity, promoting compositional differentiation between forest patches and landscapes (Laurance *et al*. 2007; Arroyo-Rodríguez *et al*. 2013; Solar *et al.* 2015).

In mixed-use landscapes, however, environmental heterogeneity can be maintained and even increased, thus contributing to the maintenance or increase of community dissimilarity (Tylianakis *et al*. 2006; Perović *et al*. 2015). We refer, for example, to heterogeneous landscapes composed of old-growth forest patches, secondary forests, biodiversity-friendly crops such as shade cocoa and coffee plantations, and other types of agricultural lands (Pardini *et al*. 2009; Mendenhall *et al*. 2014). Because each land cover patch can present different resources and environmental characteristics, they can be potentially occupied by different species, thus increasing the levels of community divergence between patches and landscapes (Laurance *et al*. 2007; Tscharntke *et al*. 2012; Liu & Slik 2014; Solar *et al.* 2015). Under this scenario, the negative local effects of land cover change on α-diversity can be overridden by the increase of β-diversity, thus allowing the maintenance of γ-diversity (see the “dominance of beta diversity hypothesis”; sensu Tscharntke *et al*. 2012). Therefore, understanding the impact that land cover change may have on environmental heterogeneity and the response of β-diversity to such changes is urgently needed for designing adequate conservation strategies.

We analysed the impact of land cover change on bird β-diversity in the Brazilian Atlantic forest – a biodiversity hotspot that has lost ca. 88% of its original forest cover (Ribeiro *et al*. 2009). Most endangered bird species in Brazil occur in this biome (MMA 2008), and there is evidence that forest loss negatively impacts bird α-diversity in the Atlantic forest, particularly of forest specialist species (Banks-Leite *et al*. 2014; Morante-Filho *et al*. 2015). To our knowledge, however, there is only one study that assesses the impact of land cover change on bird β-diversity in this region (Banks-Leite, Ewers & Metzger 2012), but based purely on presence-absence data. This previous study shows that compositional dissimilarity among patches decreases with forest loss. Yet we still do not know which are the main drivers of bird β-diversity in the region, and if this homogenisation pattern differ (i) among species with different abundance levels (from rare to dominant species), (ii) among species with different vagilities and habitat requirements (e.g. forest specialist vs. habitat generalist species), and (iii) among spatial scales (e.g. within and among patches).

We assessed the patterns and predictors of bird β-diversity using a hierarchically nested sampling design (see Appendix S1 in Supporting Information), i.e. 144 point counts in 36 forest sites in two landscapes with different local and landscape heterogeneity. We tested for differences in β-diversity across spatial scales considering forest specialist and habitat generalist birds. This allowed us to evaluate the impact of dispersal limitation on β-diversity patterns, as species’ vagilities are relatively lower in forest birds than in habitat generalist birds. β-diversity was analysed with multiplicative diversity partitioning of Hill numbers, a novel approach that allows the analysis of β-diversity of rare, common, and dominant species (Jost 2007). We also assessed the relative effects of dispersal limitation and environmental filtering on β-diversity by testing: (i) whether β-diversity among points was related to within-site variations in vegetation structure, and (ii) whether β-diversity among sites was related to site location and/or to differences between sites in vegetation structure and landscape composition (i.e. percent forest and pasture cover surrounding each site). As the less forested landscape had lower environmental heterogeneity (Appendix S2), we predicted that β-diversity within (i.e. among points) and among sites would be lower in this landscape than in the more forested landscape. We expected that this pattern would be particularly evident in habitat generalist birds, whereas the opposite pattern may be expected for forest specialist species because of dispersal limitation. Because most bird species in the tropics have small populations, we also predicted that β-diversity would be higher when considering rare species than when considering dominant species, particularly in the more forested landscape, within which we expected to find a higher number of rare species.

Materials and methods

STUDY AREA

This study was carried out in the southeastern Bahia State, Brazil (Fig. 1); a region originally covered by lowland tropical wet forest (Thomas *et al*. 1998). Average annual temperature in the region is 24 °C, and the mean annual rainfall is 1500 mm. There is no defined seasonality, although a rainless period may occur from December to March. Land-use changes during the last 30 decades have transformed the native forest into a mosaic of tree covers (e.g. old-growth and secondary forest patches, shade cacao plantations, rubber trees and *Eucalyptus* sp.) and open areas (e.g. cattle pasture and human settlements) (Pardini *et al*. 2009; Fig. 1).

STUDY LANDSCAPES

We worked in two landscapes with contrasting land cover changes (Fig. 1; Appendix S2). Using the ArcGIS software and recent satellite images (QuickBird and WorldView, from 2011; RapidEye, from 2009-2010), 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) (Fig. 1).

Both landscapes still harbour very large old-growth forest remnants, and have similar soil, topography and floristic composition (Thomas *et al*. 1998). Yet the landscape with higher forest cover (HFC) occupies 101,900 ha, 50% of which corresponds to native old-growth and secondary forest, principally concentrated around the Una Biological Reserve and the Una Wildlife Refuge –

two federally protected conservation units that have a total area of 34,804 ha. The landscape matrix in HFC is highly heterogeneous, but is dominated by shade cacao plantations (22% of the landscape matrix) and rubber trees (10%) (Fig. 1). In contrast, the landscape with lower forest cover (LFC) occupies 201,910 ha, 30% of which corresponds to old-growth and secondary forest. The landscape matrix in LFC is notably more homogeneous, being dominated by cattle pastures (86% to the landscape matrix) and *Eucalyptus* sp. plantations (7%) (see additional differences in landscape composition in Appendix S2).

STUDY SITES AND PREDICTOR VARIABLES

Within each landscape we randomly selected 18 forest sites (Fig. 1). The Euclidian distance between sites was similar in both landscapes (Student t-test; t = -1.7, $P = 0.09$), ranging from 1.2 to 30 km in HFC (14.3 ± 7.0 km, mean ± SE), and from 1.2 to 32 km in LFC (16.6 ± 8.1 km). Following Fahrig (2013), we used a sample site-landscape approach, i.e. the response variables were evaluated within each forest site, and landscape attributes surrounding sites (i.e., forest and pasture cover) were measured within a specific radius (buffer) from the center of each focal site. In particular, we used a 600-m radius, after verifying that the abundance and richness of bird assemblages were strongly related to forest cover measured at this scale (see a multiscale analysis in Appendix S3), and that such local landscapes did not overlap in space, which is needed to make accurate landscape-scale inferences (Eigenbrod, Hecnar & Fahrig 2011). We also characterised the vegetation structure in four 20 x 4-m plots randomly located in the centre of each site. Within each plot, we recorded all trees with a diameter at breast height (DBH) ≥ 5 cm and all shrubs from 50 to 200 cm in height. We then estimated the density of trees and shrubs, and mean DBH per tree – variables that can be directly related to resource availability (e.g. abundance of fruits; Chapman *et al*. 1992) and foraging sites (Castaño-Villa, Ramos-Valencia & Fontúrbel 2014), and that are positively correlated with bird diversity (Watson 2004; Rosenwald *et al*. 2011).

BIRD SURVEY

We sampled bird communities using the point-count method (Bibby, Burgess & Hill 1992) in three field campaigns: January to April 2013, May to September 2013, and October 2013 to April 2014. All forest sites were sampled once in each field campaign, including the bird breeding season (September-January) in the region. Within each forest, we established four points with a 50-m radius each, separated by 150 to 550 m among each other and placed at minimum distance of 100 m from the nearest forest edge. We recorded all birds seen and heard at each point during 15 min, during the periods of greatest bird activity (between 0600 and 0900 hr, and between 1500 and 1700 hr). Thus, the sampling effort per site was 6 hours (3 field campaigns x 4 points x 2 periods x 15 min). We avoided sampling on rainy and windy days because such conditions reduce bird detectability. We excluded birds that were flying over the forest and birds that could not be located precisely. We used 8x42 binoculars to identify the birds and a digital recorder to record their vocalizations. We confirmed vocalization-based bird identifications by playback after the 15 min were completed or by comparing the recordings with an existing database. Field guides (Mata, Erize & Rumboll 2006; Ridgely & Tudor 2009) were used for identification. The scientific nomenclature used conforms to that of the South American Classification Committee (Remsen *et al*. 2014). Finally, we classified bird species as forest specialist and habitat generalist species based on the scientific literature (Stotz *et al*. 1996; Bregman, Sekercioglu & Tobias 2014). The endemic birds of the Atlantic forest and those that occur in forested habitats of the Atlantic and Amazon forests were classified as forest species. Species that use a variety of habitats including open vegetation, such as the grasslands of the Cerrado, Caatinga, and Pampa, as well as anthropogenic areas were classified as generalists.

DATA ANALYSES

Using the entropart package (Marcon & Herault 2013) for R software (R Core Team 2013), we evaluated the accuracy of bird inventories with the coverage estimator ($\hat{C}_n$) recommended by Chao & Jost (2012), which estimates the proportion of the total number of individuals in an assemblage that belong to the species represented in the sample. Our bird inventories were reasonably accurate with our sampling effort, averaging (± SD) 0.90 ± 0.04 per site in the complete assemblage, 0.91 ± 0.04 in forest specialist birds, and 0.86 ± 0.07 in generalist birds. More importantly, sample coverage did not differ between HFC and LFC when considering the complete assemblage (Student t-test, t = -1.48, $P = 0.15$), and when considering forest birds (t = -0.93, $P = 0.36$) and generalist birds (t = -0.23, $P = 0.82$). This indicates that our results are not biased by differences in sample completeness between landscapes.

Patterns of bird β-diversity across spatial scales (i.e. among points, among sites, and between landscapes) were analysed with multiplicative diversity decompositions of Hill numbers: ${}^qD_\beta = {}^qD_\gamma/{}^qD_\alpha$, where ${}^qD_\gamma$ refers to the observed total (gamma) diversity, and ${}^qD_\alpha$ refers to the mean local (alpha) diversity within the study communities. ${}^qD_\beta$ is interpreted as the ‘effective number of completely distinct communities’, as it ranges between 1 (when all communities are identical) and N (i.e. the number of communities), when all communities are completely different from each other (Jost 2007). The formulae for ${}^qD_\gamma$ and ${}^qD_\alpha$ are detailed elsewhere (Jost 2007; Tuomisto 2010). As described by Jost (2007, 2010), β-diversity is independent of α-diversity and sample size (also see Appendix S4). Nevertheless, it depends on the parameter q, which determines the sensitivity of the measure to species’ relative abundances (Jost 2007; Tuomisto 2010). We considered β-diversity of order 0 ($^{0}D_{\beta}$), 1 ($^{1}D_{\beta}$) and 2 ($^{2}D_{\beta}$). $^{0}D_{\beta}$ is not sensitive to species abundances and so gives disproportionate weight to rare species. $^{1}D_{\beta}$ weights each species according to its abundance in the community, and measures the turnover of 'common' or 'typical' species in the community. $^{2}D_{\beta}$ favours very abundant species, and is therefore interpreted as the turnover of 'dominant' species in the community (Jost 2007; Tuomisto 2010). These three β-diversity measures were calculated using raw estimators with the entropart package, considering the following decompositions, from larger to smaller: (1) β-diversity between landscapes: $^{q}\beta_{land} = {}^{q}\gamma_{region}/{}^{q}\alpha_{land}$; (2) β-diversity among sites: $^{q}\beta_{site} = {}^{q}\gamma_{land}/{}^{q}\alpha_{site}$; and (3) β-diversity among points: $^{q}\beta_{point} = {}^{q}\gamma_{site}/{}^{q}\alpha_{point}$ (Appendix S1). To assess whether the magnitude in β-diversity differed across spatial scales, we compared the relative compositional dissimilarity between communities using the transformation of $^{q}D_{\beta}$ proposed by Jost (2006) for communities with different numbers of samples (i.e. landscapes: N = 2; forest sites: N = 18; point counts: N = 4): $^{q}DS = 1 - [(1/{}^{q}D_{\beta} - 1/N)/(1 - 1/N)]$. ^{q}DS ranges between 0, when all samples are identical, and 1, when all samples are completely distinct.

To test whether patterns of β-diversity within sites (i.e. among points) differed between landscapes, we used linear models (with normal errors) after log-transforming data. Crawley (2012) suggests using generalised linear models with Poisson error for count dependent variables (i.e., $^{0}D_{\beta}$), but recently Ives (2015) demonstrates that this kind of models can lead to increasing Type I statistical errors. Thus, to avoid for potential Type I errors in our models, we decided to use linear models instead of generalised linear models. We used Mantel tests to assess whether the matrix of β-diversity among sites was correlated to site location (i.e. with the matrix of the geographical distances among sites) and/or to the matrices showing the differences among sites in vegetation structure (i.e. density of trees and shrubs, and mean DBH per tree) and in local landscape characteristics (i.e. percent forest and pasture cover surrounding each site). To assess the effect of local variations in vegetation structure on β-diversity patterns, we also tested whether β-diversity within sites was related to inter-site differences in the variance among plots in vegetation structure with Mantel tests. Finally, we also used Mantel tests to assess whether site location was related to inter-site differences in environmental characteristics. All graphs and statistical analyses were carried out with R software, using the vegan package (Oksanen *et al*. 2013).

Results

OVERVIEW

We recorded 5294 birds from 182 species and 39 families. Of those, 101 species (55%) were forest specialists, and 81 species (45%) were habitat generalists. Both landscapes yielded similar bird species richness (138 species in HFC and 145 in LFC), but most species in HFC (92 out of 138, 67%) were forest birds, whereas in LFC only 68 out of 145 species (47%) were forest birds. As 100 species occurred in both landscapes (59 specialists and 41 generalists), the number of species restricted to one landscape was slightly higher in LFC (45 species) than in HFC (38 species). Interestingly, 80% of the species restricted to LFC were generalists, whereas 87% of the species restricted to HFC were forest specialists. Five species dominated bird assemblages in HFC (with 21% of the individuals recorded in this landscapes): 4 forest specialists (*Cacicus cela*, *Drymophila squamata*, *Machaeropterus regulus*, and *Pipra rubrocapilla*) and 1 generalist species (*Coereba flaveola*). Yet, considering the 4 species that dominated the LFC landscape (18% of individuals), 3 species were generalists (*Megarynchus pitangua*, *Pitangus sulphuratus*, and *Thraupis palmarum*) and only one was forest specialist (*Tolmomyias flaviventris*). Regarding rare species, the percentage of singletons (species represented by one individual) and doubletons (species with two individuals) was greater in HFC (30.1% of all species; 37.5% of which were forest birds and 62.5% generalist birds) than in LFC (22.6% of all species; 52.5% of which were forest birds and 47.5% generalist birds).

BIRD β-DIVERSITY ACROSS SPATIAL SCALES

In both bird assemblages, β-diversity at the regional scale (i.e. between landscapes, ${}^{q}\beta_{land}$) was notably lower than at the landscape scale (i.e. among forest sites, ${}^{q}\beta_{site}$) and at the site scale (i.e. among points, ${}^{q}\beta_{point}$) for any order q (Fig. 2). Yet, at the regional scale, β-diversity of dominant species (${}^{2}\beta_{land}$) was 1.08 times higher in forest specialist birds than in generalist species. In fact, at this scale, β-diversity of generalist species was 1.1 times higher when considering rare species (${}^{0}\beta_{land}$) than when considering dominant species.

At the landscape scale, however, β-diversity of rare species was greater than β-diversity of dominant species in both landscapes and bird assemblages (Fig. 2). Interestingly, notable differences between landscapes were found when considering ${}^{q}\beta_{site}$ of generalist and specialist birds. In particular, the less forested landscape (LFC) showed a higher β-diversity among sites (i.e. biotic differentiation at the landscape scale) than the more forested landscape (HFC) when considering forest specialist birds, but the opposite pattern was found when considering habitat generalist species for any order q (Fig 2).

At the forest site scale and for forest specialist birds, β-diversity among points was significantly lower in LFC than in HFC when considering all order q (linear models, $P < 0.01$ in all cases). For generalist birds, β-diversity among points was significantly lower in LFC than in HFC, but only in ${}^{0}\beta_{point}$ ($P > 0.01$). Such patterns of biotic homogenisation within sites in LFC were particularly evident when considering forest specialist birds, within which ${}^{q}\beta_{point}$ in LFC was lower than ${}^{q}\beta_{site}$, whereas in generalist birds ${}^{q}\beta_{point}$ in LFC and HFC were higher than ${}^{q}\beta_{site}$ for all order q

(Fig. 2). Finally, ${}^{q}\beta_{point}$ tended to be higher in generalist birds than in specialist birds, particularly in LFC.

PREDICTORS OF BIRD β-DIVERSITY

β-diversity at the landscape level (i.e. among sites) was more strongly related to the geographical distance among forest sites and to the differences among sites in local landscape characteristics (i.e. forest and pasture cover surrounding each site) than to variations in vegetation structure (Table 1). Independently of the bird assemblage, higher β-diversity values were recorded among sites more isolated from each other, and among sites with higher differences in landscape characteristics, particularly the less forested landscape. Interestingly, in the more forested landscape, only β-diversity of forest specialist species increased among sites more isolated from each other and with higher differences in landscape characteristics. Regarding the vegetation structure, only differences in tree density increased β-diversity among sites, particularly when considering generalist species (Table 1). At the site scale, ${}^{q}\beta_{point}$ of generalist and specialist birds was significantly positively related to increasing differences in the variance of tree DBH, but only in HFC (Table 2). Finally, in HFC site location was only related to inter-site differences in forest cover, but in LFC, higher differences in local (i.e. vegetation structure) and landscape characteristics were recorded among sites more isolated from each other (Fig. 3).

Discussion

Our findings reveal that land cover changes in the Brazilian Atlantic forest have major impact on bird assemblages. Three patterns deserve special attention. First, the extirpation of forest specialist birds was compensated by the colonization and proliferation of habitat generalist species in the less forested landscape. Second, as expected, β-diversity at the landscape scale (i.e. among sites) differed between bird assemblages and landscapes: specialist birds showed the highest compositional differences among sites in the less forested landscape, whereas the highest differentiation among sites in generalist birds occurred in the landscape with higher forest cover. Finally, at the forest site scale, the less forested landscape showed the lowest β-diversity among points (bird homogenisation within sites) in both assemblages. Therefore, in agreement with previous studies carried out with birds (Karp *et al.* 2012), mammals (Püttker *et al.* 2015) and plants (Arroyo-Rodríguez *et al.* 2013), insects (Solar *et al.* 2015), shifts in β-diversity in human-altered tropical landscapes depends on landscape composition and on the spatial scale of analysis. As discussed below, such biotic reorganization was related to both environmental filtering and dispersal limitation.

MAINTENANCE OF BIRD ASSEMBLAGES IN HUMAN-ALTERED TROPICAL LANDSCAPES

Biodiversity maintenance in HALs depends on multiple patterns and processes across different spatial scales (Tscharntke *et al*. 2012). For example, the loss of disturbance-sensitive species can be compensated for by the colonization of disturbance-adapted species, thus allowing the maintenance of regional species diversity (Supp & Ernest 2014; Morante-Filho *et al*. 2015). Our results support this idea as the replacement of forest specialist by habitat generalist birds in the less forested landscape resulted in similar species richness to the landscape with higher forest cover. Also, based on the "dominance of beta diversity hypothesis" (Tscharntke *et al*. 2012), high levels of gamma diversity can be maintained despite local species extinctions if landscapes have a high level of β-diversity among localities. Our findings support this hypothesis, as the loss of species at the site scale (α-diversity) in both landscapes (i.e. loss of generalist species in the more forested landscape, and loss of specialist species in the less forested landscape; Appendix S5 in Supporting Information), was overridden by high levels of β-diversity among sites (i.e. high β-diversity of generalist birds in the more forested landscape, and high β-diversity of specialist birds in the less forested landscape).

The environmental impoverishment associated with intensive land-use change, however, can lead to the biotic homogenisation across multiple spatial scales, thus threatening the maintenance of landscape and regional biodiversity (Lôbo *et al*. 2011; Karp *et al*. 2012; Arroyo-Rodríguez *et al*. 2013). In agreement with this idea, the less forested landscape (dominated by cattle pastures) showed the lowest β-diversity among point counts (i.e., bird homogenisation within sites). This pattern was evident in both bird assemblages. Also, as predicted, this landscape showed a lower β-diversity among sites, but only when considering habitat generalist birds, which are able to use different land cover types across the landscape and have relatively higher vagility (Julliard *et al*. 2006). Nevertheless, as expected (see below), this landscape showed the highest β-diversity among sites when considering forest specialist species, most probably because of dispersal limitation associated with habitat specialization (Julliard *et al*. 2006), which can promote the compositional differentiation between forest patches in highly deforested landscapes (Laurance *et al*. 2007; Arroyo-Rodríguez *et al*. 2013).

THE IMPACT OF ENVIRONMENTAL FILTERING AND DISPERSAL LIMITATION ON BIRDS

Environmental filtering and dispersal limitation are expected to influence patterns of bird assemblages, especially in the less forested landscape. The extensive deforestation suffered by this landscape resulted in a homogenised spatial scenario, with lower forest cover, fewer land cover types, and domination of cattle pastures (Fig. 1; Appendix S2). This scenario is expected to act as an important environmental filter to forest-dwelling birds, thus promoting the selection towards birds with high vagility, larger population sizes, and low habitat specificity (Julliard *et al*. 2006; Ekroos, Heliola & Kuussaari 2010). Suporting this idea, the less forested landscape showed a higher percentage of habitat generalist birds, and considering this group of birds, β-diversity within and among sites were lower in the less forested landscape than in the more forested landscape.

Besides the dispersal limitation can increase the compositional differentiation in landscapes with lower forest cover (Laurance *et al*. 2007; Soininen, McDonald & Hillebrand 2007). In this sense, higher β-diversity values were recorded among sites more isolated from each other, and as expected, this pattern was particularly evident in the less forested landscape. In the more forested landscape, however, only β-diversity of forest specialist species increased among sites more isolated from each other, thus supporting the idea that dispersal limitation can be proportionally more important in forest birds than in habitat generalist species.

Alternatively, this result can reflect the impact of environmental filtering, as we found that, as others (Nekola & White 1999; Soininen, McDonald & Hillebrand 2007), the sites more isolated among each other in less forested landscape showed higher differences in vegetation structure and local landscape composition. Therefore, the sites with higher compositional differentiation of birds were also the sites with higher differences in environmental characteristics (Buckley & Jetz 2008). Furthermore, β-diversity among sites was significantly and positively related to inter-site differences in local tree density and forest and pasture cover surrounding each site, thus showing that environmental filtering is probably more important than dispersal limitation in determining the patterns of bird assemblages in fragmented landscapes (Karp *et al*. 2012).

Yet, in local scale the mean DBH of trees was an important predictor of β-diversity among points only in HFC. In this landscape we find more variation in the mean DBH (Fig. S3; Appendix S3), which may favour the occurrence of different species. For example, occurrence of the bark foragers belonging the Picidae (as *Picumnus exilis* and *Veniliornis affinis*), Furnariidae (*Xenops minutus* and *X. rutilans*) and Dendrocolaptidae (*Dendrocincla turdina* and *Xiphorhynchus guttatus*) is positively correlated with different diameters of trees (Castaño-Villa, Ramos-Valencia & Fontúrbel 2014). However the other environmental characteristics were poorly correlated with β-diversity at this scale. This result may indicate that other factors, such as competition and resource availability, can be more important for determining species turnover within the forest patches in both landscapes (Veech *et al*. 2002).

CONCLUSIONS AND CONSERVATION IMPLICATIONS

Of the total species recorded in our region, 45% of birds are exclusive to one of the studied landscapes. Besides, the replacement of ecological groups combined to increase in β-diversity of forest species among patches contributes to maintain of gamma diversity in the less forested landscape. Effective conservation efforts need to consider the β-diversity patterns, when proposing the creation of new protected areas (Ribeiro *et al.* 2008; Solar *et al.* 2015), ensuring the preservation of forest patches along the entire environmental gradient (Liu & Slik 2014).

Our study highlights the importance of assessing different spatial scales and predictors of diversity. If we had evaluated the diversity in our study region only at a local scale, our results would demonstrate only homogenization of the species composition in less forested landscape, with no effect of environmental variables. Therefore, studies that use only one scale to assess biodiversity patterns should be cautious in their conclusions, since the use of different scales may reveal completely disparate patterns (Tylianakis *et al.* 2006; Arroyo-Rodríguez *et al.* 2013). Furthermore, divergent patterns found within each landscape can indicate that different conservation strategies should be used to maintain bird diversity in each landscape. In the more forested landscape, the high β-diversity at the local scale indicates that the preservation of the vegetation characteristics of forest, especially by prohibiting the wood extraction and logging, may help to maintain the local heterogeneity and consequently increase alpha diversity within patches. However, in landscapes with lower forest cover it is also necessary to preserve as many forest patches as possible, as high spatial discrepancies in species composition among patches (β-diversity) contribute to maintain a high gamma diversity at the landscape scale (Arroyo-Rodríguez *et al.* 2009).

Our study reveals two hazardous finding for the maintenance of bird diversity and forest ecosystem functioning. First, the long-term maintenance of such high gamma is more uncertain in less forested landscape where most forest-specialist species, being restricted to few fragments structurally different from one another, and isolated by a harsh matrix, are more prone to local extinction. Thus, it is possible that extinction debt could be masking the long-term outcome of landscape scale deforestation, here representing rather a transient stage. Second, the replacement of ecological groups due to land cover change can be a severe indicator of the future trajectory of forest patches in our region. As forest specialist should have a long history of co-evolutionary with their habitat, while generalist species are a recent consequence of global change (Julliard *et al.*, 2006), we do not know if this change may decrease resilience of patches to environmental disturbance. Furthermore, forest specialists within a specialized community are likely to show ecological completeness, while generalists in a generalist community must present ecological redundancy (Olden *et al.* 2004). Hence this could result in functional homogenization (Olden *et al.* 2004), with serious implications for the ecological services performed by birds (Sekercioglu 2006). Future studies need to understand whether this clear pattern of ecological group replacement can lead to the loss of ecosystem function, for example, the disappearance of forest-frugivorous birds may change seed dispersal patterns and thus affect forest structure (Silva & Tabarelli 2000).

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Data accessibility

Data are available from the Dryad Digital Repository: doi:10.5061/dryad.r8d10

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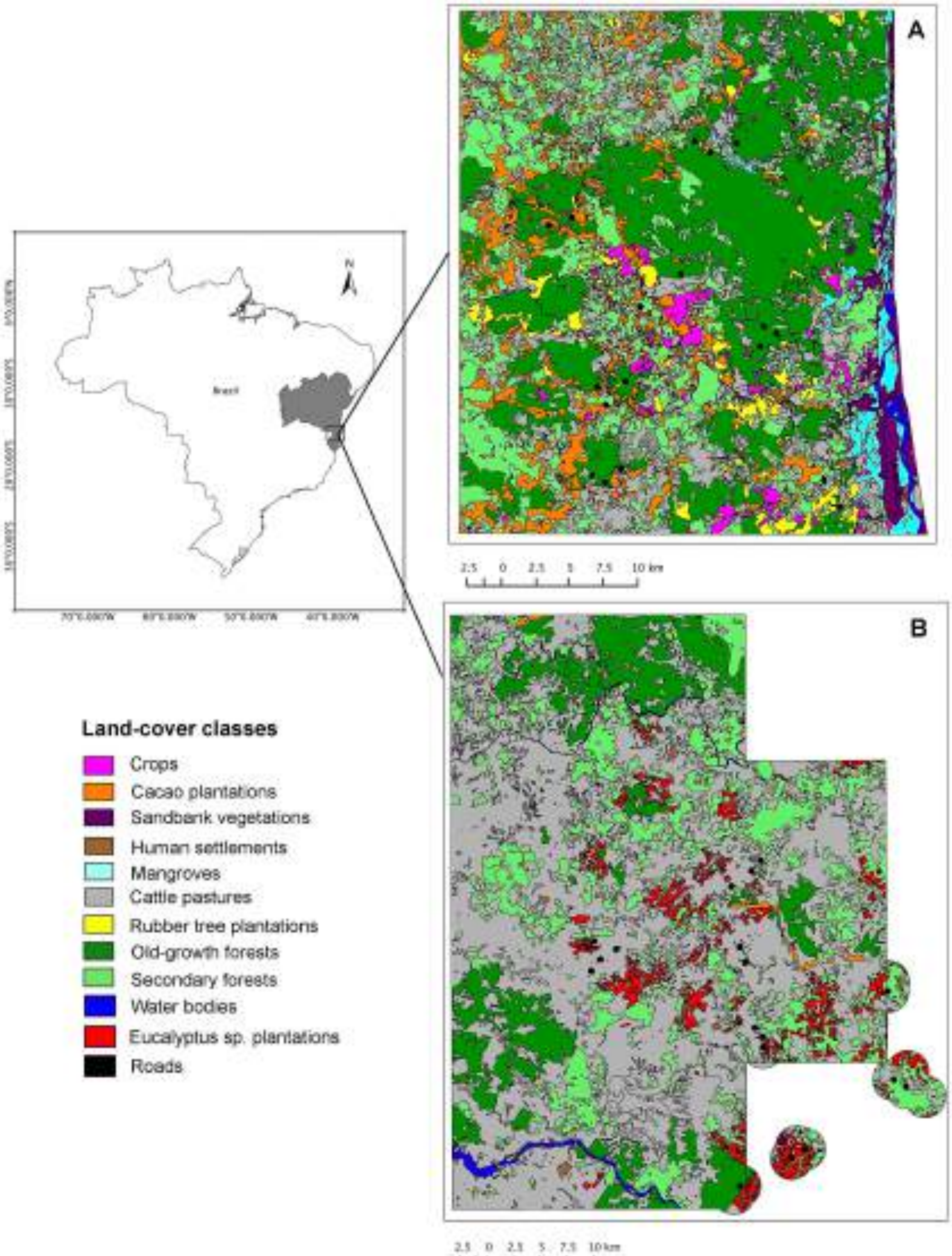
A
B
Brazil
N
2.5 0 2.5 5 7.5 10 km
2.5 0 2.5 5 7.5 10 km
Land-cover classes
Crops
Cacao plantations
Sandbank vegetations
Human settlements
Mangroves
Cattle pastures
Rubber tree plantations
Old-growth forests
Secondary forests
Water bodies
Eucalyptus sp. plantations
Roads

Figure 1

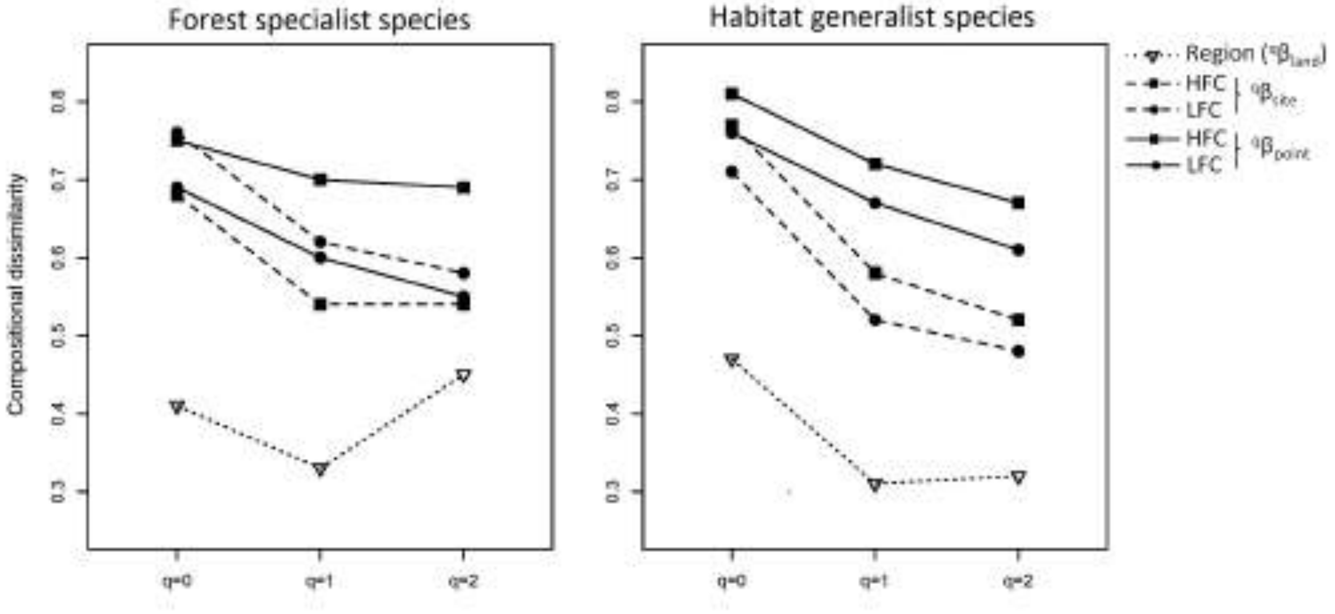
Forest specialist species
Habitat generalist species
Compositional dissimilarity
0.3
0.4
0.5
0.6
0.7
0.8
q=0
q=1
q=2
Region ($^q\beta_{land}$)
HFC
LFC
$^q\beta_{site}$
HFC
LFC
$^q\beta_{point}$

Figure 2

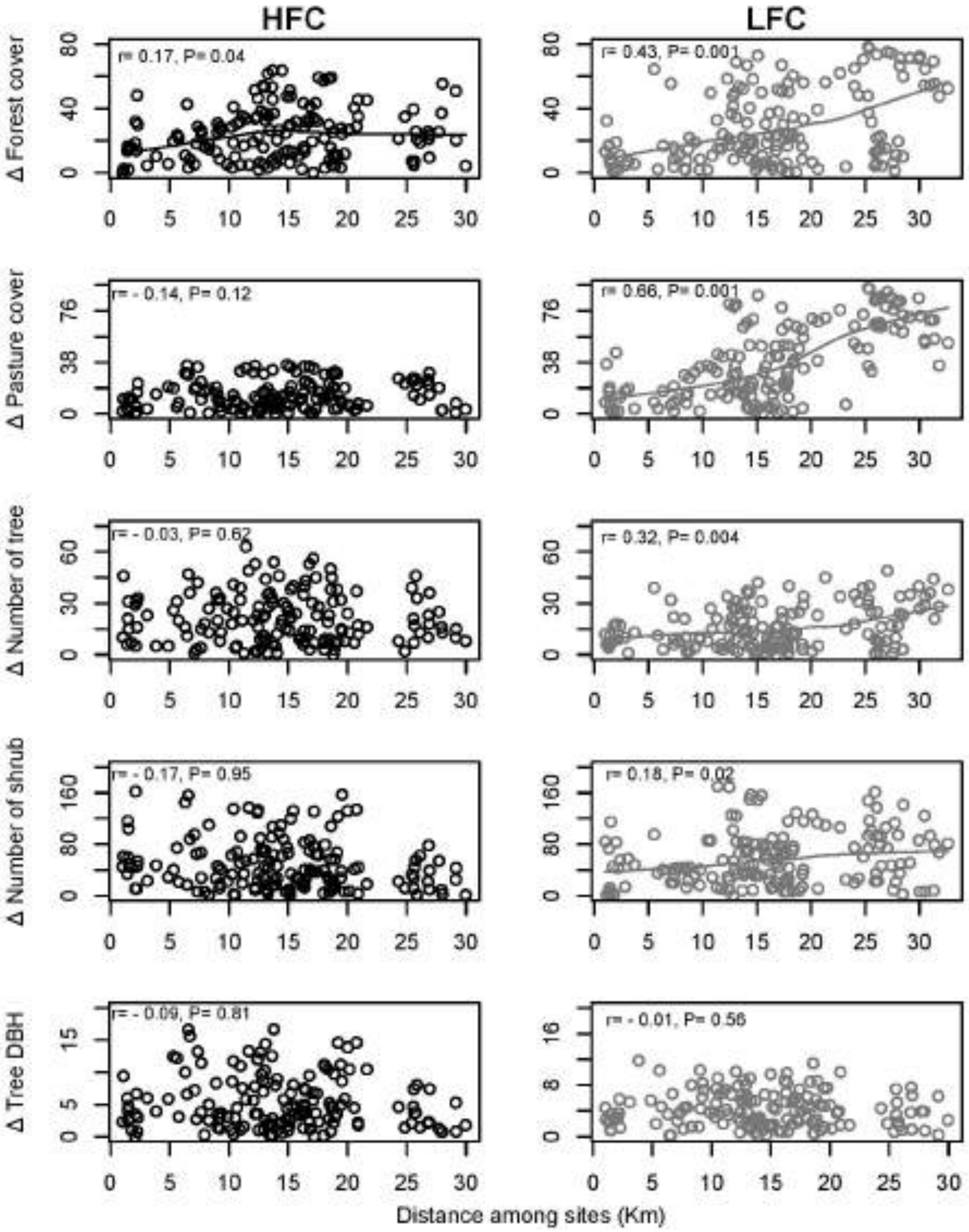
HFC
LFC
Δ Forest cover
Δ Pasture cover
Δ Number of tree
Δ Number of shrub
Δ Tree DBH
r= 0.17, P= 0.04
r= 0.43, P= 0.001
r= - 0.14, P= 0.12
r= 0.66, P= 0.001
r= - 0.03, P= 0.62
r= 0.32, P= 0.004
r= - 0.17, P= 0.95
r= 0.18, P= 0.02
r= - 0.09, P= 0.81
r= - 0.01, P= 0.56
0
40
80
38
76
30
60
160
5
15
8
16
10
20
25
Distance among sites (Km)

Figure 3

Figure legends

Fig. 1. Study area in southern Bahia, Brazil. We show the location and land cover classes of the landscape with higher forest cover (HFC) (A), with 50% of remaining forest cover, and the landscape with lower forest cover (LFC) (B), with 30% of remaining forest cover. We indicate the study forest sites within each landscape with black dots.

Fig. 2. Bird β-diversity between landscapes (i.e. for entire region), among count points, and among forest sites in southern Bahia State, Brazil. We show the transformation of beta (i.e. compositional dissimilarity) proposed by Jost (2007), which ranges between 0 (when all samples are identical), and 1 (when all samples are completely distinct). We indicate the results for forest specialist and habitat generalist birds. β-diversity among sites and among points is separately showed for the landscape with higher forest cover (HFC) and the landscape with lower forest cover (LFC). In all cases, we evaluated three orders of q (0, 1 and 2), which determines the sensitivity of the measure to the relative abundances.

Fig. 3. Correlation between differences (Δ) in local and landscape environmental variables and the geographic distance between forest sites located in the landscape with higher forest cover (HFC) and the landscape with lower forest cover (LFC) in southern Bahia State, Brazil. Smoother lines are shown in the graphs with significant correlations.

Table 1. Correlation between bird β-diversity among forest sites and site location (geographical distance among sampled sites) and inter-site differences (Δ) in landscape and vegetation characteristics in two landscapes with different forest cover (HFC and LFC) in southern Bahia, Brazil. The results are separately showed for forest specialist and habitat generalist species. We considered three orders of *q* (1, 2 and 3), which determine the sensitivity of each β-diversity component to species abundances.

Assemblage/ Landscape	β-diversity component	Site location	Δ Forest cover	Δ Pasture cover	Δ Tree density	Δ Shrub density	Δ Tree DBH
Forest specialist species							
HFC	${}^{0}D_{\beta}$	0.32*	0.13	0.16	0.11	-0.22	-0.02
	${}^{1}D_{\beta}$	0.39**	0.27*	0.19*	0.19*	-0.13	-0.01
	${}^{2}D_{\beta}$	0.28*	0.25*	0.13	0.22*	-0.14	0.08
LFC	${}^{0}D_{\beta}$	0.34**	0.38**	0.37*	0.29*	-0.006	0.02
	${}^{1}D_{\beta}$	0.44**	0.47**	0.48**	0.36*	0.08	0.05
	${}^{2}D_{\beta}$	0.33**	0.41*	0.41**	0.33*	0.15	0.01
Habitat generalist species							
HFC	${}^{0}D_{\beta}$	0.15	0.11	0.04	0.05	-0.04	0.03
	${}^{1}D_{\beta}$	0.15	0.16	-0.1	0.16	0.02	0.02
	${}^{2}D_{\beta}$	0.08	0.19*	-0.14	0.25*	0.11	0.005
LFC	${}^{0}D_{\beta}$	0.41**	0.57**	0.55**	0.39*	0.06	0.07
	${}^{1}D_{\beta}$	0.54**	0.72**	0.63**	0.61**	0.21*	0.05
	${}^{2}D_{\beta}$	0.49**	0.80**	0.58**	0.72**	0.25*	-0.004

We indicate the correlation coefficients calculated with Mantel tests. Significant coefficients are indicated with asterisks (*$P < 0.05$; **$P < 0.001$, after applying a stringent Bonferroni correction to reduce the likelihood of type I statistical errors). The HFC landscape shows a higher forest cover than the LFC landscape. Landscape characteristics included the percentage of native forest cover, and the percentage of the matrix composed of cattle pastures. The vegetation characteristics included the number of trees and shrubs, and the mean DBH (diameter at breast height) per tree.

Table 2. Correlation between bird β-diversity within forest sites (i.e. among point counts) and inter-site differences (Δ) in the variance of several vegetation characteristics in two landscapes with different forest cover (HFC and LFC) in southern Bahia, Brazil. The results are separately showed for forest specialist and habitat generalist species. We considered three orders of *q* (1, 2 and 3), which determine the sensitivity of each β-diversity component to species abundances.

Assemblage/Landscape	Diversity component	Δ Tree density	Δ Shrub density	Δ Tree DBH
Forest specialist species				
HFC	${}^0D_\beta$	0.13	-0.08	0.43*
	${}^1D_\beta$	-0.03	-0.07	0.27*
	${}^2D_\beta$	0.04	0.03	0.03
LFC	${}^0D_\beta$	0.18	-0.11	-0.006
	${}^1D_\beta$	0.13	-0.05	0.03
	${}^2D_\beta$	0.21	-0.09	0.03
Habitat generalist species				
HFC	${}^0D_\beta$	-0.04	-0.07	0.15
	${}^1D_\beta$	0.03	-0.02	0.40*
	${}^2D_\beta$	0.1	0.1	0.44*
LFC	${}^0D_\beta$	-0.13	0.07	-0.02
	${}^1D_\beta$	-0.11	-0.1	-0.03
	${}^2D_\beta$	-0.11	0.01	0.01

We indicate the correlation coefficients calculated with Mantel tests. Significant coefficients are indicated with asterisks (*$P < 0.05$; **$P < 0.001$, after applying a stringent Bonferroni correction to reduce the likelihood of type I statistical errors). The HFC landscape shows a higher forest cover than the LFC landscape. Vegetation characteristics included the number of trees and shrubs, and the mean DBH (diameter at breast height) per tree.

SUPPORTING INFORMATION

Appendix S1 Hierarchical nested sampling design to assess bird β-diversity across different spatial scales.

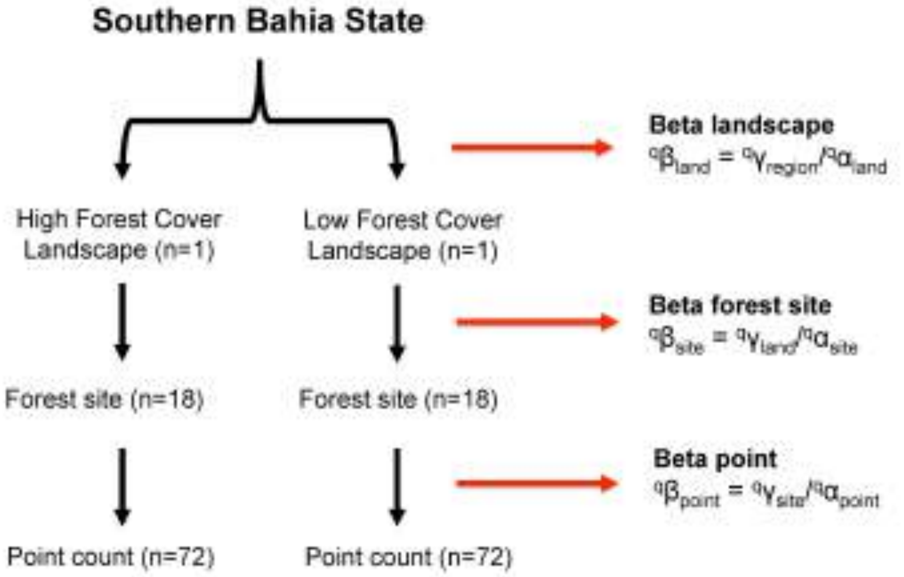

Fig. S1. Spatial scales used to assess differences in bird β-diversity in southern Bahia State, northeastern Brazil. From the largest to the smallest scale β-diversity was assessed (i) between landscapes ($^{q}\beta_{land} = {}^{q}\gamma_{region}/{}^{q}\alpha_{land}$); (ii) among sites within each landscape ($^{q}\beta_{site} = {}^{q}\gamma_{land}/{}^{q}\alpha_{site}$); and (iii) among points within each site ($^{q}\beta_{point} = {}^{q}\gamma_{site}/{}^{q}\alpha_{point}$).

Appendix S2 Differences between landscapes in local and landscape characteristics.

To assess the potential influence of environmental variables on β-diversity patterns, we tested for differences between landscapes in vegetation structure and local landscape characteristics. Vegetation structure was measured in four 20 x 4-m plots randomly located in the center of each of the 18 forest sites. Within each plot, we recorded all trees with diameter at breast height (DBH) ≥ 5 cm, and also all shrubs with 50-200 cm in height. We then estimated the density of trees and shrubs, and the mean DBH per tree within four plots (320 m^2). We did not use the sum of tree DBH because it was significantly related to stem density ($R^2 = 0.84$, $P < 0.001$). Regarding the landscape characteristics surrounding each sites, we considered the percentage of forest cover, the percentage of the matrix composed of cattle pastures and the number of land-cover classes within a 600-m radius from the center of each site (Fig. S2), after verifying that this local landscape size adequately predicts the response of birds to forest loss (see Appendix S4).

The landscape with higher forest cover (HFC) was more heterogeneous than the landscape with lower forest cover (LFC) (Fig. S2). At the landscape scale, the HFC landscape was by far more forested (range = 34 to 98% of forest cover) than the LFC landscape (7% to 85%; Fig. S2). HFC not only showed a significantly greater local forest cover (Mann-Whitney-Wilcoxon test, $U = 281$, $P < 0.001$), but also a lower percentage of cattle pastures in the matrix ($U = 54$, $P < 0.001$) and a greater amount of land-cover classes ($U = 270$, $P < 0.001$) than LFC (Fig. S3). Also, HFC showed a higher density of trees ($U = 270$, $P < 0.001$), shrubs ($U = 272$, $P < 0.001$), and mean DBH per tree ($U = 236$, $P < 0.001$) than LFC (Fig. S3).

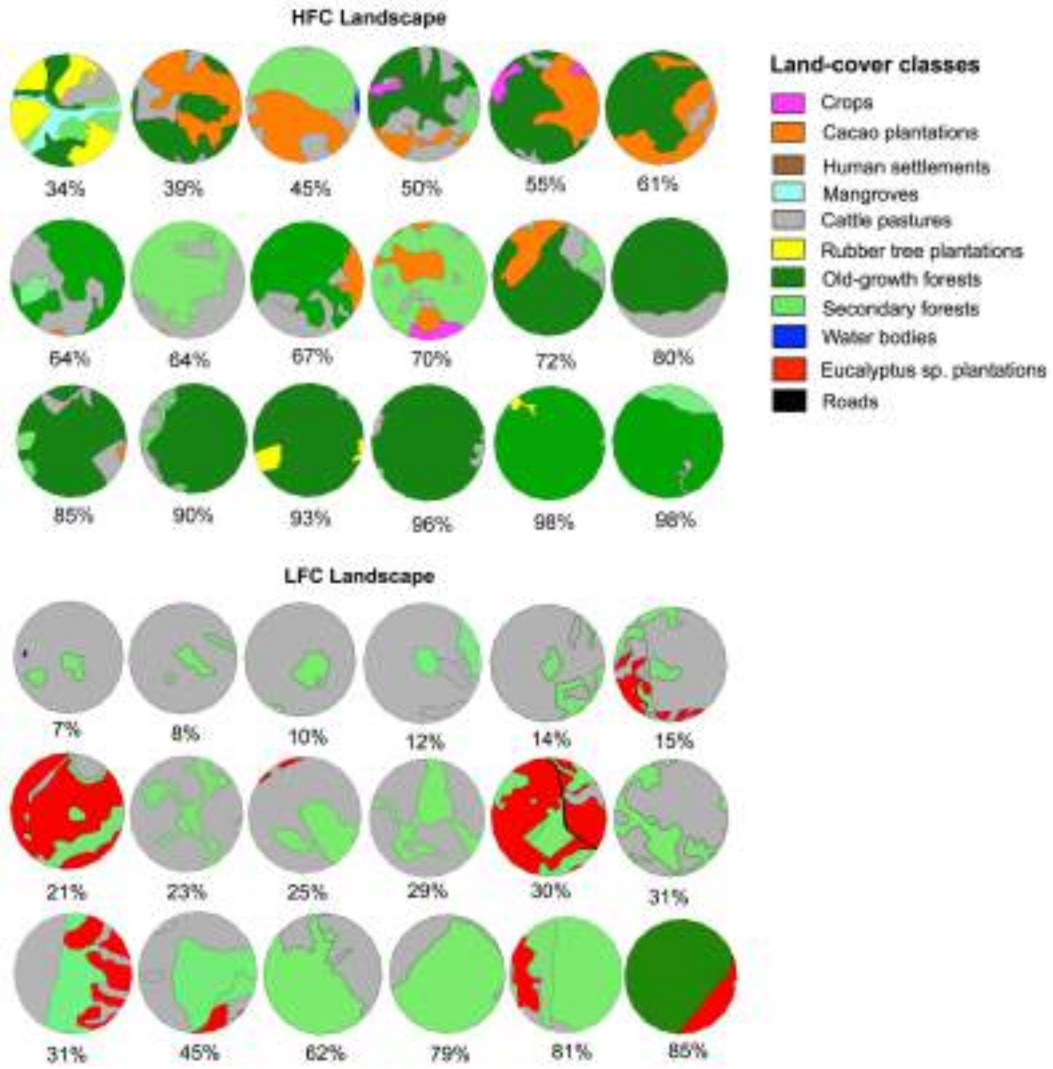

Fig. S2. Spatial structure and land-cover classes of sampled sites in the HFC and LFC landscapes. Figures represent the percentage of native forest cover (old-growth and secondary forest cover) calculated within a 600-m radius (115 ha) from the center of each forest site.

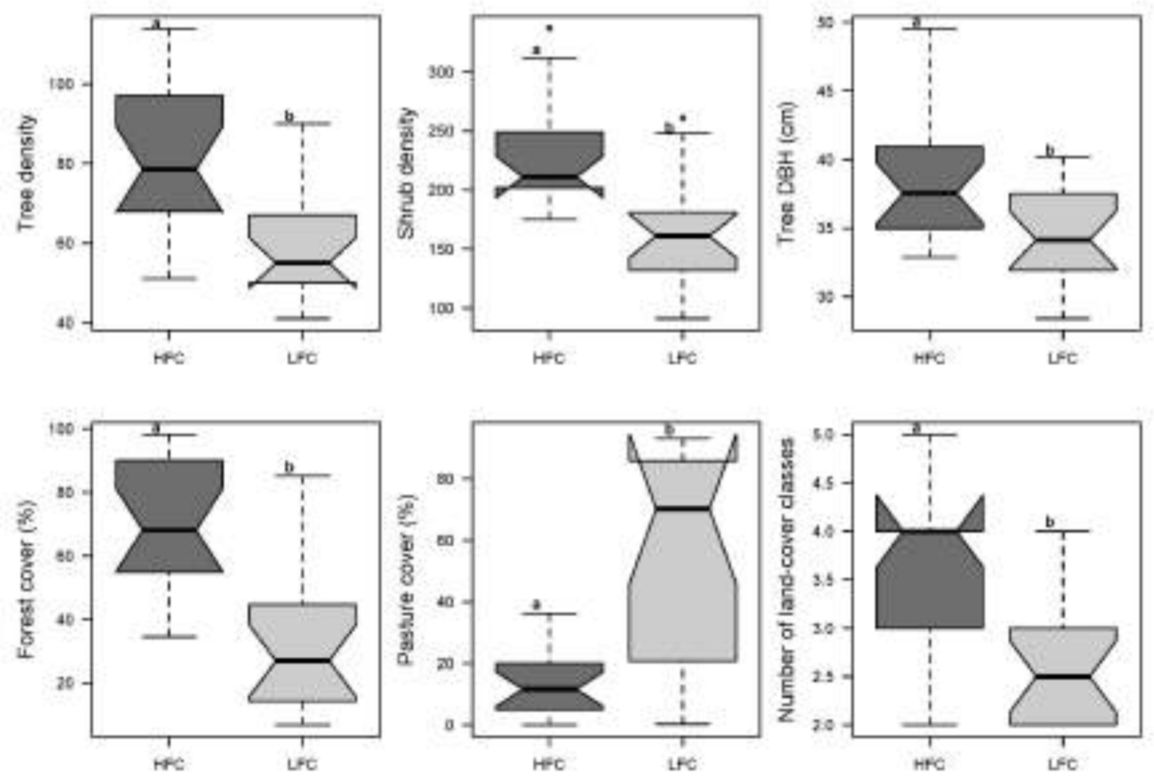

Fig. S3. Differences in vegetation structure and spatial characteristics surrounding each site between a landscape with high forest cover (HFC) and a landscape with low forest cover (LFC) in southern Bahia State, Brazil. The median (solid line), 25th and 75th percentiles (boundaries of boxes), interquartile range (whiskers above and below box plots), and outlier points (value that lies more than one and a half times the length of the box from either end of the box) are indicated for each landscape. Different letters indicate significant differences (P < 0.01) between landscapes according to Mann-Whitney-Wilcoxon test.

Appendix S3 The scale of landscape effects on birds.

Because the effect of forest loss on biodiversity is known to depend on the spatial scale at which forest amount is measured (i.e. the so-called "scale of landscape effects"; sensu Jackson & Fahrig 2012; Fahrig 2013) we calculated forest cover within ten different-sized buffers (i.e., landscapes), ranging from 100 to 1000-m radius. The smallest buffer represents the size of our smallest forest site (ca. 3 ha), and the largest buffer was used based on previous landscape-scale studies of understory birds in the Atlantic forest (Develey & Metzger 2006; Boscolo & Metzger 2009). We then located eight additional buffers with the same size between the largest and the smallest buffer, obtaining thus local landscapes of 3 ha (radius = 100 m), 12.56 ha (200 m), 28.26 ha (300 m), 50.24 ha (400 m), 78.50 ha (500 m), 113.04 ha (600 m), 153.86 ha (700 m), 200.96 ha (800 m), 254.34 ha (900 m) and 314 ha (1,000 m). We considered the percentage of both old-growth and secondary forest in our estimations of native forest cover. This classification may be a simplification of the ecological requirements of bird species, but we believe that this broad definition is appropriate because many recommendations for the conservation and management of landscapes are based on fragmentation or habitat loss in general (Smith *et al*. 2011). Besides, it may be impossible in empirical analyses to quantify the conditions that limit the occurrence of every species (Rueda *et al*. 2013). This is particularly true in Neotropical regions because of their high species diversity and inadequate scientific knowledge of the ecological requirements of the birds.

Following Fahrig (2013), we evaluated the strength of the relationship (R^2) between forest cover surrounding each site and the abundance and richness of birds within of sites to identify the spatial extent (local landscape size) within which forest cover best predicted bird diversity. We found that the strength of the relationship between forest cover and both the abundance and richness of forest specialist and habitat generalist birds increased with buffer size, reaching an asymptote in the 115 ha landscape (600 m radius) (Fig. S5). Hence, because local landscapes above 115 ha start overlapping in space, we selected this landscape size to avoid potential problems of independence among sites (see Eigenbrod, Hecnar & Fahrig 2011).

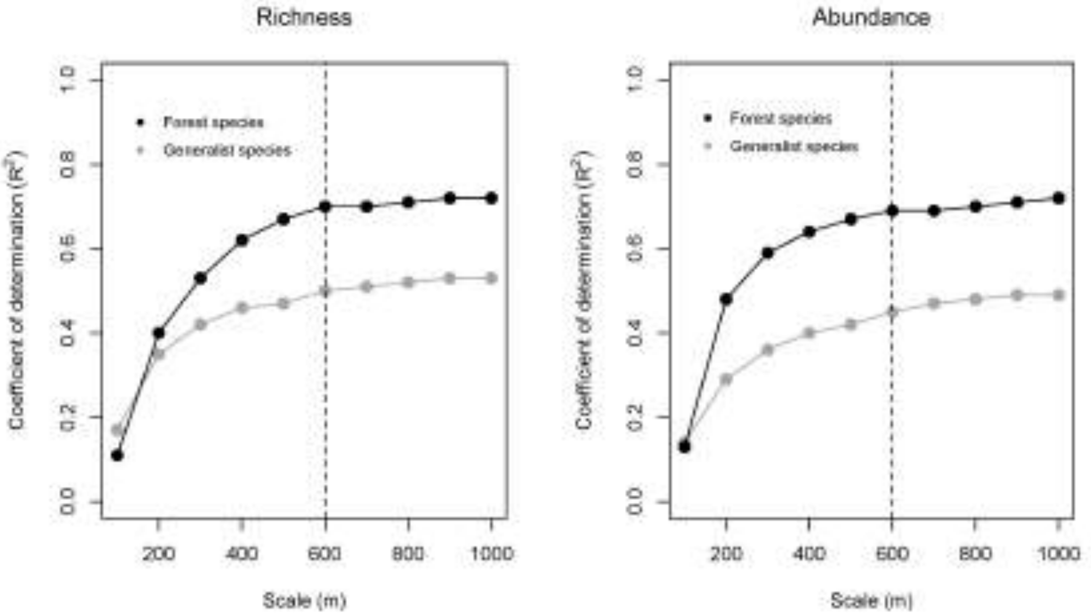

Fig. S4. Association between landscape size (x-axis) and the strength of the relationship (R^2, y-axis) between forest cover surrounding each site and the species richness and relative abundance of forest specialist and habitat generalist birds in the Brazilian Atlantic forest. The landscape size used in this study is indicated with a dashed line.

Appendix S4 Effect of alpha diversity and sample size (abundance of birds) on beta diversity.

Jost (2007, 2010) shows that alpha and beta diversities calculated with Hill numbers are independent, as “the value of one of these components does not put mathematical constraints on the value of the other (i.e., they would form a Cartesian product space)”. This is the case when we decompose gamma diversity into independent alpha and beta components. “Knowing alpha (and only alpha, not gamma) tells us nothing at all about beta, and vice-versa” (Jost 2010). Barwell *et al.* (2015) also demonstrate that, in general, the beta diversity indexes proposed by Jost (2006, 2007) do not depend on alpha diversity and sample size (i.e., number of individuals), although they found that beta diversity can be slightly higher when alpha diversity and sample size are too small. This can be related to the fact that gamma, alpha, and of course, beta diversity, depend on sample coverage (or sampling completeness), which is particularly low in small samples (Chao & Jost 2012). The impact of sample coverage on these diversity metrics is particularly high when considering the order 0 (${}^{0}D_{\beta}$), as this metric is highly sensitive to the number of rare species (singletons and doubletons), which are frequent in small samples (Chao & Jost 2012). Yet, as described in the Method section, our bird inventories were reasonably accurate with our sampling effort (sample coverage ca. 0.90 in all cases), and more importantly, we did not find differences among sites and between landscapes in sample coverage. This suggests that our results are not biased by this potential confounding factor.

Nevertheless, to assess this important constraint, we tested the effect of mean alpha diversity and mean sample size on mean beta diversity within each spatial scale with Pearson correlations (Fig. S6). We found no significant correlations across all spatial scales ($P > 0.28$, in all cases). This finding is not surprising, as it support the idea that beta diversity is independent of alpha diversity and sample size (Jost 2006, 2007, 2010).

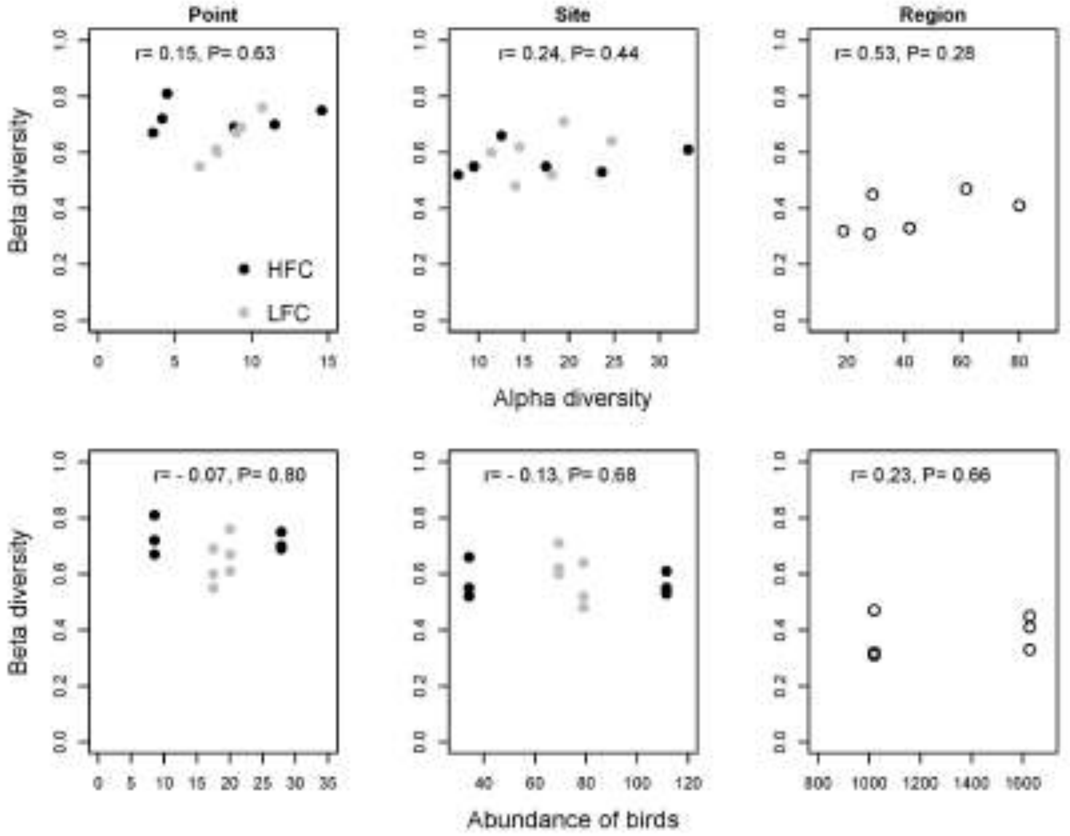

Fig. S5. Effect of alpha diversity and sample size (abundance of birds) on beta diversity across different spatial scales. With black and gray dots we indicate the sites and point counts sampled within a landscape with high forest cover (HFC) and a landscape with low forest cover (LFC), respectively.

Appendix S5 Differences between landscapes in local species richness.

Differences between landscapes in mean species richness per site were tested with generalised linear models (GLM), assuming a Quasipoisson error distribution to control for overdispersion problems in the models (Crawley 2012). We separately considered forest specialist and habitat generalist species. We found that the number of forest specialist birds was significantly higher in HFC than in LFC (GLM, *P* < 0.001), whereas generalist birds followed the opposite pattern (GLM, *P* < 0.001) (Fig. S7).

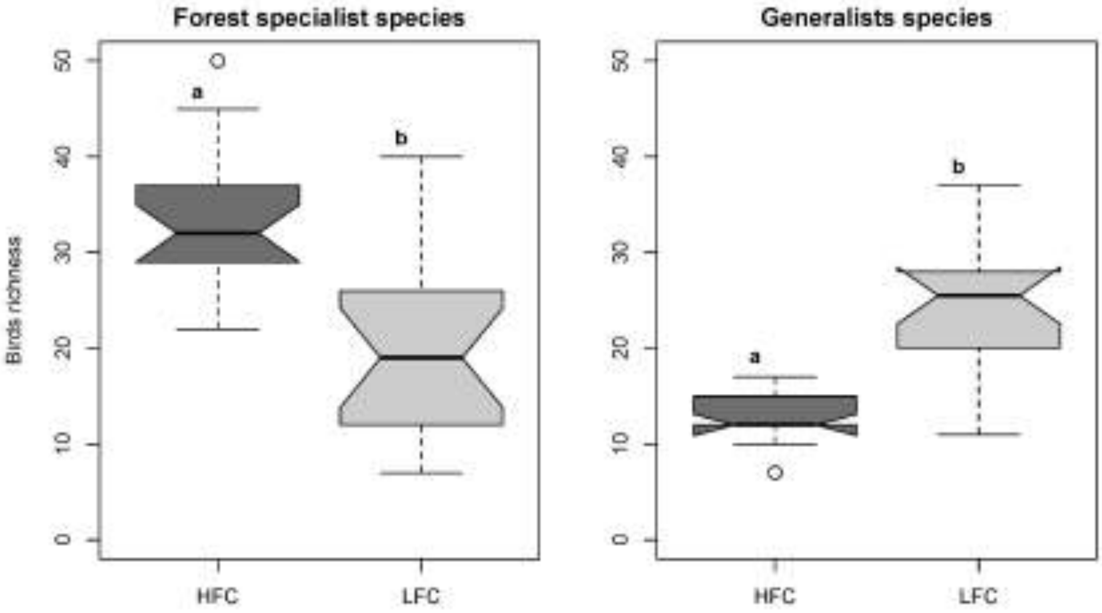

Fig. S6. Differences in bird species richness between a landscape with high forest cover (HFC) and a landscape with low forest cover (LFC) in southern Bahia State, Brazil. The median (solid line), 25th and 75th percentiles (boundaries of boxes), interquartile range (whiskers above and below box plots), and outlier points (value that lies more than one and a half times the length of the box from either end of the box) are indicated for each landscape. Different letters indicate significant differences (*P* < 0.01) between landscapes.

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Seção II

Influência das alterações ambientais sobre as funções ecológicas executadas pelas aves

Capítulo 3

Ecological functions perfomed by birds: current knowledge and way forward [#]

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Abstract. Birds perform several ecological roles that might help ecosystem functioning and generate great benefits for human population. However, natural landscape changes, mostly caused by anthropogenic action such as fragmentation, have caused a decrease in bird diversity that ultimately leads to the loss of their functions in the remaining habitats. In this context, I conducted a scientific literature review to understand the currently knowledge regarding of the effects of enviromnental changes on ecosystem functions performed by birds. In March 2014, I researched the Scopus and Web of Science databases using combinations of the words "bird", "ecosystem service", "trophic cascade", "top-down control", “land use”, “fragmentation”, and “landscapes”. The research returned 90 papers that targeted the importance of birds to the ecosystems’ maintenance. Among the studies that effectively assessed the ecological role of bird species (n=61), most were undertaken in natural habitats (n=37), and the most evaluated ecological function was invertebrate population control (n=49). Yet, only eight studies valued the ecosystem services provided by birds. About 49% of the publications related some environmental characteristic to the ecological function, but patch and landscape-scale factors were poorly investigated. Furthermore, 62% of the papers showed that the ecological function of birds could arise from a cascade effect on other trophic levels, though this may depend on the environmental characteristics. Despite the numerous studies in the ornithology field, the ecological roles of bird species in several ecosystems are poorly understood. Future research should evaluate a wider variety of ecological functions performed by birds, such as seed dispersal and polinization, and should account for differences in spatial scales, so that generalizations can be made based on ecosystem type and landscape composition variation. More research should quantify the economic value of provided services and generate information to justify the efforts for conservation of birds and their habitats in political decisions regarding land use.

Key-Words: Avian function, ecosystem services, human-altered landscape, top-down control, trophic cascade.

Introduction

Birds are an important and well-studied group of vertebrates due to their conspicuousness, morphological diversity, wide distribution and high local diversity (Wiens 1992, Stotz et al. 1996). In the last decades, many studies have assessed several ecosystem functions performed by birds, such as seed dispersal (Moran & Catterall 2014), control of insect populations (Sanz 2001, Van Bael et al. 2008) and diseases (Swaddle & Calos 2008) in different ecosystems throughout the world. Furthermore, it was found that the ecosystem functions of specific groups of birds can bring significant benefits to society (Whelan 2008, Wenny et al. 2011, Poch & Simonetti 2013a). For example, the predation of agricultural pests by insectivorous birds can increase crop productivity (Martin et al. 2013, Maas et al. 2013), a striking contribution of economical value. However, most of the biota is currently present in anthropogenic landscapes, in which historical deforestation has reduced large natural habitats that were once continuous into a myriad of small patches, often isolated from one another by other human-altered land uses (Farhrig 1997, Haddad et al. 2015). Consequently, a well-developed understanding exists of negative effects of loss habitat and fragmentation on biodiversity. Thus, if bird diversity declines because of such human-disturbance, functions performed by them is also likely to change or even lost.

Due to their high mobility, birds have large metabolic demands. Allied to this characteristic, the spacial and temporal variation in resource availability compels many species to move throughout landscapes (Whelan et al 2008). This process connects habitats in space and time and is crucial to the maintenance of functions and resilience of ecosystems (Lundberg & Moberg 2003, Sekercioglu 2006). However, fragmentation negatively affects ecosystem functions flows by interrupting movement of organisms across landscapes (Mitchell et al. 2015). This includes the daily movements of birds like pollinators and insect predators across human-altered landscapes. Futhermore, even when certain species are present in natural patches, their density may be so low that causes a functional extinction which precedes the own extinction of the species (Galetti et al. 2013, Tobias et al. 2013). The disappearance of frugivorous birds, for example, may change seed dispersal patterns and thus affect forest structure (Silva & Tabarelli 2000, Garcia et al. 2009); whereas the decrease of pollinating bird diversity may reduce the genetic diversity of plant community, which can become more susceptible to stochastic extinctions (Anderson et al. 2011).

In addition, the extirpation of bird species may exert a cascade effect on other trophic levels (Mäntylä et al. 2011). Trophic cascades result in inverse patterns of abundance or biomass across more than one trophic link in a food web. For a three-level food chain, abundant top predators result in lower abundances of midlevel consumers and higher abundance of basal producers (Pace et al. 1999). Several studies have examined the effect of bird predation on herbivores insect cascading down to plants (e.g. Marquis & Whelan 1994, Mäntylä et al. 2011), because the herbivory process may affect growth and survival of plant species (Duwyn & MacDougall 2015), possibly modifying plant community composition (Hulme 1996). However, landscape changes may result in the disruption of these ecological interactions, since insectivorous birds can reduce their diversity in anthropogenic landscapes (see Morante-Filho et al. 2015).

Despite the ecological importance of birds, the effects of species extinctions on ecosystem functioning and services provided by them are poorly understood (Sekercioglu 2006). It is necessary to quantify the ecosystem functions at different scales and investigate which features of landscape structure, fragmentation, and heterogeneity control the significantly improve our ability to manage landscapes for ecosystem services (Whittingham 2011, Mitchell et al. 2015). In this context, future research needs to move away from simply quantifying of ecological groups of birds and toward identifying locations of service demand and potential pathways of service flow (Bagstad et al. 2013). Moreover, it is essential to combine information from different ecosystem functions perfomed by birds and develop a metric to assess how services can be maximized in several land use contexts (Wenny et al. 2011, Geijzendorffer & Roche 2013). This information will be useful, among other things, to provide data on the economic valuation of environmental services, and are fundamental for the development of effective policy mechanisms.

Facing the growing need to understand how bird communities can contribute to natural and anthropic ecosystem functioning, in this paper I aimed to search for general trends established in the scientific literature on the ecosystem functions of birds. Therefore, I investigated which were the main functions and environments (natural and/or anthropic) studied so far, and what environmental factors, both at local and broad scales, are related to performed functions. I also wanted to quantify how many studies have evaluated the cascade effect of birds, and which environmental characteristics are commonly associated with the results. Overall, I wanted to understand if there is enough knowledge about the effects of enviromnental changes on ecosystem functions performed by birds. Thus, I intended to outline the gaps in knowledge and therefore guide future studies.

Methods

First, I searched in Scopus and ISI Web of Science databases using different combinations of the 8 keywords (bird, ecosystem service, trophic cascade, top-down control, land use, fragmentation, and landscapes) for dates prior to March 2014. Second, from the search results I considered only studies that focused on the bird community and those which, directly or indirectly, assessed the ecological role performed by this group. After selecting the publications that fitted the scope, I conducted exploratory analyses to identify general patterns of how birds' functional role is evaluated by the scientific community.

From each publication, I gathered informations on: (1) continent and climatic region of the study area, according to Köppen-Geiger's classification, (2) land use categories (natural, agroforestry or agricultural systems) and (3) the scale of explanatory variables (local, patch or landscape). I defined the variable scale as local when vegetation characteristics were measured to investigate their effect on bird ecological function. When metrics related to forest remnants, such as size or isolation, and characteristics of landscape structure and composition were analyzed, I classified the variables as patch and landscape scales, respectively.

Finally, I verified the studies that directly quantified the economic benefits of ecosystem services provided by birds and those that measured the trophic cascade effect. I considered Paine's (1980) definition of trophic cascade, which detects this process when changes in a species population's size lead to alterations in the populations of lower levels of the food chain. Although many studies used the term "trophic cascade", most have quantified only two levels of the food chain. For example, several authors only measured the top-down control exerted by birds on arthropod populations and, therefore, these studies were not classified here as trophic cascade ones.

Overview

I found 90 publications that reported the importance of birds as organisms that perform one or more ecological functions for ecosystem maintenance (Figure 1). However, 32% of the studies (n=29) did not directly measure bird ecological roles. For example, many studies only mention that a decrease in bird diversity cause a simplification of ecological roles, with eventual breakdown of interactions in cascade systems (Estes et al. 2011). This situation often occurs due to changes in natural habitats (Melo et al. 2013, Mendenhall et al. 2014), such as agricultural intensification throughout the world (Gavier-Pizarro et al. 2012, Sekercioglu 2012, Munoz et al. 2013). Other studies only focused on understanding what environmental conditions favor the maintenance of the guilds of birds that can perform important ecosystem services, such as control of agricultural pests (Jirinec et al. 2011).

From the total, 61 publications (68%) effectively assessed the ecological role of a species or a group of birds (Table 1). Empirical studies comprised 82% of all analyzed papers, and reviews and/or meta-analyzes comprised 18% (Table 1). Publication years ranged from 1995 to 2014, with a large increase in number of publications from 2005 (90% of the studies were published after this year) (Figure 2). This temporal trend may be a consequence of the influential United Nations report, the Millennium Ecosystem Assessment (2005), which not only compiled a significant proportion of existent informations, but also standardized and categorized the ecological functions of species in four classes of ecosystem services (Table 2): provisioning, regulating, cultural s and supporting. Birds may contribute in all four types of ecosystem services (see Whelan et al. 2008, Whelan et al. 2015). However, an ecological function is only considered an ecosystem service if it brings benefits to the human population (Whelan et al. 2008), for example, if pollination by birds results in an increasing crop yield. After the Millenium Ecosystem Assessment (2005), many debates were held to evaluate how birds' ecosystem services should be quantified and valued (Sekercioglu 2006, Whelan et al. 2008, Wenny et al. 2011).

The vast majority of the studies were conducted in the Americas (n=37), whereas only two were performed in Africa (Table 3). Studies were mainly from tropical and temperate climate zones, with 22 and 17 published papers, respectively. Furthermore, studies were mostly held in natural habitats (n=37), such as forests, and agricultural systems (n=16). Few studies were conducted in agroforestry systems (n=12), although these habitat contribute to biodiversity conservation in anthropogenic landscapes (Poch & Simonetti 2013a). Due to environmentaly-friendly conditions, agroforests may act as additional habitats for many bird species (Pardini et al. 2009). Thus, maintaining bird diversity and their ecological roles in agroforestry systems may contribute to the functioning of natural and anthropic habitats that compose the landscape (Beenhouwer et al. 2013).

The most analyzed ecological function was the control exerted by birds on invertebrate populations (n=49), mainly upon herbivorous insects (Peters & Greenberg 2013). Birds can perform this function on agricultural systems, controlling pest populations and, indirectly, reducing crop damages (Johnson et al. 2009, Mäntylä et al. 2011). Consequently, this service may result in an increase in the productivity of various crops (Kellermann et al. 2008). Nevertheless, other relevant functions, such as pollination and seed dispersal, have been scarcely investigated in the studies. Seed dispersal is arguably the most important ecosystem function provided by birds, especially in tropical forests (Sekercioglu 2006). Loss of avian seed dispersers can affect regeneration of natural habitats, ultimatly altering phenotypic and genetic characteristics of plants species (Sekercioglu 2006, Galetti et al. 2013). For example, compared with areas with more complete assemblages of vertebrates, defaunated areas for several decades in brazialian Atlantic Forest showed a phenotypic selection of smaller seeds of palm, *Euterpe Edulis*, due to the loss of wide-gaped avian frugivores, specially toucans and large cotingas (Galetti et al. 2013). Yet, only eight studies have economically valued the ecosystem services provided by birds. From these, five are empirical studies, being pest control in agricultural systems the most evaluated service. In a study conducted in coffee plantations in Jamaica, the predation by insectivorous birds on arthropods reduced the infestation of fruits by 1–14%, increasing the production value by US$44–$105/ha (Kellermann et al. 2008). Other study found that pest-control services by birds prevented $75–$310 ha-year^{-1} in damage in the coffee plantations of Costa Rica (Karp et al. 2013). Furthermore, the presence of birds of prey such as falcons in crop areas, thus removing avian pests, could potentially result in savings of $234/ha for the Sauvignon Blanc variety of grapes and $326/ha for Pinot Noir variety of grapes, according to a study conducted in the United States (Kross et al. 2011). Therefore, because of the economic benefits of birds to the society, more research should be conducted to value to the supllied services and generate informations to justify bird conservation allied to the preservation of their natural habitats (Wenny et al. 2011).

Nearly half (49%) of the studies evaluated the effect of environmental variables on ecological functions performed by birds. Factors at local scale (n=22), such as vegetation structure, were predominant, while patch and landscape features were poorly investigated (Table 3). This result highlights an important knowledge gap, since several studies demonstrate that processes operanting at large spacial scales are highly importance for biodiversity and ecosystem function maintenance (Östman et al. 2001, Jackson & Fahrig 2012). For example, loss and fragmentation due to logging exploitation, road construction, or agricultural and urban expansion can alter plant species composition and growth, negatively affecting animal species (Ewers & Didham 2006). Simultaneously, this process can improve forest access, increasing timber harvesting and hunting. Thus, thus by altering the arrangement and local structure of remaning patches, species composition changes, thus fragmentation can modify the functional role played by a species (Tscharntke et al. 2005, Skórka et al. 2013). To propose and achieve effective conservation practices for birds, their habitats, and especially their functions, it is necessary to understand how land use may interfere in the ecological role of species (Skórka et al. 2013, Maas et al. 2013). This approach can be used to estimate the economic value of native vegetation remnants within agricultural landscapes and provide estimates of ecosystem services under different land use scenarios (Wenny et al. 2011, Winqvist et al. 2012).

Trophic cascade effects

Most of the studies (n=38) found that the ecological function of birds can arise from a cascade effect on other trophic levels. For instance, the extinction of bird pollinators in New Zealand has reduced pollination, seed production, and density of the endemic shrub, *Rhabdothamnus solandri* (Anderson et al. 2011). Mainly, three levels of the food chain were evaluated, as in the interaction among birds, arthropods and plants (e.g. Marquis & Whelan 1994, Koh 2008). Several studies indicate that birds, in addition to reduce herbivorous insect populations, may also increase plants productivity and biomass (Barber & Marquis 2011, Mäntylä et al. 2011). However, the top-down control exerted by birds on other trophic levels may depend on the environmental characteristics (Barber & Wouk 2012, Giffard et al. 2012).

In 21 studies, the trophic cascade effect was related to some environmental variable. Most were categorical studies that evaluated cascades in two or more ecosystems (e.g. different forest types and comparisons between forests and agricultural systems) or studies that measured vegetation structure on sampling sites (Kellermann et al. 2008, Poch & Simonetti 2013b). On the other hand, only four studies have quantified landscape metrics and one study related the process of forest fragmentation to the cascade effect. These studies show that complex landscapes can facilitate the biological control performed by birds and indirectly contribute to an increase in crop productivity (Martin et al. 2013). Thus, agricultural areas with low land use intensity allied to natural habitats may sustain high bird diversity, facilitating the provision of services thus, comprising an important theoretical framework for large-scale conservation programs (Tscharntke et al. 2005). In a study conducted in Indonesia, Maas et al. (2013) found that cocoa productivity decreases in 31% with the reduction of shade tree cover and increase in distance between primary forests and crops. These factors increase the diversity of predatory birds and bats, which regulate the abundance of herbivorous insects (Maas et al. 2013). Similar result was found in study conducted in Costa Rica; borer-consuming birds increased in abundance and exerted stronger control on borer populations on coffee plantations with higher surrounding forest cover (Karp et al. 2013). By contrast, De La Vega et al. (2012) found that the functional role of insectivorous birds is not influenced by fragmentation process. According to the authors, bird density directly affects leaf damage in *Aristotelia chilensis* via insect control, but this process is similar between in patches and continuous forests.

The ecosystem functioning is dependent on the regional species' pool, which is closely related to the landscape characteristics (Whittingham 2011, Winqvist et al. 2012). Changes in landscapes composition and structure, such as reduced size and increased isolation of natural habitats, and decreased environmental heterogeneity may cause biodiversity decline and loss of different ecological functions (Tscharntke et al. 2005). Furthermore, changes in abiotic conditions and primarily changes in individuals density can modify trophic interactions by the exclusion of higher level species, which consequently affect basal level species (Taylor & Marriam 1995, Komonen et al. 2000).

Concluding remarks

Although birds are well studied organisms, the ecological roles performed by species in many ecosystems are still poorly understood. Of particular importance, future studies should analyze the relationship between biodiversity and ecological functions, and not only focus on the aspects of biodiversity *per se*. Thus, as the level of functional redundancy among bird species is not evident, it is necessary to understand the implications of bird diversity decline on the loss of ecological functions (Firbank et al. 2013). Furthermore, the loss of disturbance-sensitive species can be compensated for by the colonization of disturbance-adapted species (i.e. habitat generalist birds) in altered-human landscapes (see Morante-Filho et al. 2016). Hence this could result in functional homogenization (Olden et al. 2004), with serious implications for the ecological services performed by birds (Sekercioglu 2006).

This revision highlighted several gaps in the knowledge about the ecological functions performed by birds, indicating that further research should evaluate the role played by birds in other important ecosystem functions, such as seed dispersal and plant pollination. Moreover, it is necessary to understand the different benefits that the bird community may bring to the human population, such as diseases control. For instance, future studies should investigate scavenger bird ecology to assess the potential role of this guild in diseases control and nutrients transport within and between ecosystems (Sekercioglu 2006). This information are especially needed, since the extinction of this guild may lead to problems to human health (see Prakash et al. 2003). Another neglected function is the seed predation by seed-eating birds, an ecological process that affect the recruitment of several plant species (Marone et al. 2008). In addition, it is necessary more information about the importance of raptors on the population control of vertebrates that affect crop productivity (Gavier-Pizarro et al. 2012).

Furthermore, the ecological functions played by birds may depend on different spatial scales. Pollination is a good example, since it can be affected both by the local vegetation structure, which maintains the diversity of pollinating birds, but also on features at the landscape scale, such as the distance between habitats or the characteristics of the surrounding matrix. Therefore, research should account for different spatial scales (Tscharntke et al. 2005, Geijzendorffer & Roche 2013), so that generalizations can be made based in ecosystems type and landscape characteristics (Winqvist et al. 2012). This information may help to understand the influence of current landscapes dominated by human activities on the ecological role played by birds and, consequently, on the ecosystem functioning (Geijzendorffer & Roche 2013). Overall, it is necessary to evaluate the extent of provided services in the trophic cascades (Terborgh & Such 2010). Even the most assessed function, which is predation of invertebrates by birds, is scarcely addressed in a trophic cascade approach. Thus, it is necessary more information on how bird ecological roles can affect the interaction network existent in the ecosystems (Sekercioglu 2012). Finally, it is critical that future studies quantify the economic value of services provided by birds in different land use contexts (Wenny et al. 2011). There is a clear and dire need to use this information in political decisions of management and biodiversity conservation allied to agricultural system productivity.

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Table 1. Publications (n=61) from Web of Science and Scopus databases that evaluated some ecological function performed by birds.

Author	**Year**	**Reference**	**Study type**	**Study region**
Wootton	1995	Ecoscience 2: 321-328	Empirical	United States
Floyd	1996	Ecology 77: 1544-1555	Empirical	United States
Van Bael et al.	2003	PNAS 100: 830-8307	Empirical	Panama
Mazía et al.	2004	Ecography 27: 29-40	Empirical	Argentina
Brason	2005	Environ Entomol 34: 1114-1121	Empirical	United States
Van Bael & Brawn	2005	Oecologia 145: 658-668	Empirical	Panama
Mooney & Linhart	2006	J Anim Ecol 75: 350-357	Empirical	United States
Sekercioglu	2006	Trends Ecol Evol 21: 464-471	Review	Global
Gruner & Taylor	2006	Oecologia 147: 714-724	Empirical	United States
Boege & Marquis	2006	Oikos 115: 559-572	Empirical	Mexico
Fukami et al.	2006	Ecol Lett 9:1299-1307	Empirical	New Zealand
Mooney	2007	Ecology 88: 2005-2014	Empirical	United States
Skoczylas et al.	2007	Acta Oecol 32: 337-342	Empirical	United States
Dunham	2008	Oikos 117: 571-579	Empirical	Ivory Coast
Koh	2008	Ecol Appl 18: 821-825	Empirical	Island of Borneo
Whelan et al.	2008	Ann N Y Acad Sci 1134: 25-60	Review	Global
Van Bael et al.	2008	Ecology 89: 928-934	Meta-analysis	Central America
Marone et al.	2008	Oikos 117: 611-619	Empirical	Argentina
Kellermann et al.	2008	Conserv Biol 22: 1177-1185	Empirical	Jamaica
Johnson et al.	2009	Agroforest Syst 76:139-148	Empirical	Jamaica
Mazía et al.	2009	Austral Ecol 34: 59-367	Empirical	Argentina
Barber & Marquis	2009	Am. Midl. Nat. 162: 169-179	Empirical	United States
Philpott	2009	Ecol Appl 19: 1858-1867	Meta-analysis	Central America
Bridgeland	2010	Ecology 91: 73-84	Empirical	United States
Garcia et al.	2010	Conserv Biol 4: 1070-1079	Empirical	Spain, Argentina
Johnson et al.	2010	Anim Conserv 13:140-147	Empirical	Jamaica
Mooney et al.	2010	PNAS 107: 7335-7340	Meta-analysis	Global
Zenhder et al.	2010	Oecologia 164: 1017-1027	Empirical	United States
Bradbury et al.	2010	J Appl Ecol 47: 986-993	Review	England
Xiong et al.	2010	Wetlands 30:1203-1211	Empirical	China
Schuenk et al.	2010	J Avian Biol 41: 367-377	Empirical	United States

Garibaldi et al.	2010	Oikos 119: 337-349	Empirical	Argentina
Piñol et al.	2010	Ecol Entomol 35: 367–376	Empirical	Spain
Lenz et al.	2010	Proc R Soc Lond B Biol Sci 278: 2257-2264	Empirical	South Africa
Anderson et al.	2011	Science 331: 1068-1070	Empirical	New Zealand
Bohm et al.	2011	PLoS ONE 6: e17857	Empirical	Germany
Barber & Marquis	2011	Oecologia 166: 401-409	Empirical	United States
Kross et al.	2011	Conserv Biol 26:142-149	Empirical	New Zealand
Mäntylä et al.	2011	Oecologia 165: 143-151	Meta-analysis	Global
Wenny et al.	2011	The Auk 128: 1-14	Review	Global
Sekercioglu	2011	Science 331: 1019-1020	Review	Global
Jedlicka et al.	2011	PLoS ONE 6: e27347	Empirical	United States
Barber & Wouk	2012	Oecologia 170: 999-1007	Empirical/Meta-analysis	United States/Global
Bang et al.	2012	Ecol Monogr 82: 85-100	Empirical	United States
Singer et al.	2012	Am Nat 179: 363-74	Empirical	United States
De la Vega et al.	2012	Austral Ecol 37: 836-844	Empirical	Chile
Rogers et al.	2012	PLoS ONE 7: e43446	Empirical	United States
Garcia & Martinez	2012	Proc R Soc Lond B Biol Sci 279: 3106-3113	Empirical	Spain
Giffard et al.	2012	Oecologia 168:415–424	Empirical	France
Bergamino et al.	2012	Estuar Coasts 35:1571-1582	Empirical	Argentina, Uruguay
Ruiz Guerra et al.	2012	Biotropica 44: 228-236	Empirical	Mexico
Luck et al.	2012	J Anim Ecol 81: 1065-1076	Empirical	Australia
Winqvist et al.	2012	Ann N Y Acad Sci 1249: 191-203	Review	Global
Poch & Simonetti	2013	Agroforest Syst 87: 871-879	Meta-analysis	Global
Poch & Simonetti	2013	Forest Ecol Manag 304: 132-136	Empirical	Chile
Martin et al.	2013	PNAS 110: 5534-5539	Empirical	South Korea
Giffard et al.	2013	Ecol Entomol 38: 448-455	Empirical	France
Maas et al.	2013	Ecol Lett 16: 1480-1487	Empirical	Indonesyan
Peters & Greenberg	2013	Biotropica 45: 102-110	Empirical	Costa Rica

Karp et al.	2013	Ecology Letters 16: 1339-1347	Empirical	Costa Rica
Michel et al.	2014	J Trop Ecol 30:1-11	Empirical	Costa Rica

Table 2. Ecosystem services according to the Millennium Ecosystem Assessment (2005).

Ecosystem services	**Characteristics**
Provisioning	Services related to production of natural compounds involved in human needs, such as food production, fuel and water purification.
Regulating	Services obtained through ecosystem processes, such as regulation of agricultural pests, removal of carcasses, seed dispersal and diseases control.
Cultural	Services related to aesthetic, spiritual, recreational enrichment and inspiration for art and music.
Supporting	Services related to other processes that support ecosystem functioning, such as soil formation, nutrient cycling, biomass and atmospheric oxygen production.

Table 3. Attributes and categories used to classify papers (n=61) from Web of Science and Scopus databases that directly evaluated the ecological function of birds.

Attribute	Categories	Publication number
Continent	America	37
	Europa	7
	Oceania	5
	Asia	2
	Africa	2
	Do not apply[a]	8
Climatic Region	Tropical	22
	Temperate	17
	Dry	5
	Continental	4
	Polar	2
	Do not apply[a]	11
Ecosystem	Natural	37
	Agriculture	16
	Agroforestry	12
	Do not apply[a]	4
Ecological functional	Invertebrate predation	49
	Vertebrate predation	3
	Seed dispersion	3
	Polinization	2
	Seed predation	1
	Various[c]	5
Value of ecological functional	No	53
	Yes	8
Approach scale	Local	22
	Landscape	6
	Patch	2
	Not evaluated[b]	33
Trophic cascade	No	23
	Yes	38

[a] Review studies that do not fit any category.

[b] Studies that did not correlate any environmental variable with ecological function.

[c] Review studies that discussed several ecological functions.

Figure Legends

Figure 1. Examples of birds that perform different ecological functions. **A:** *Pteroglossus castanotis*, large frugivore that play a role in the dispersal of several tree species. **B:** *Trogon surrucura*, species considered an ecosystem engineer, since it builds cavities to nest in arboreal termite nests and abandoned hornet nests. The cavities are later used by other species of birds and small mammals. **C:** *Drymophila squamata,* insectivorous bird that consumes arthropods in the forest understory. **D:** *Phaethornis ruber* acts as pollinator of many plants. **E:** *Cathartes aura*, obligate scavenger that consumes carcasses and can assist in disease regulation. **F:** *Geranoaetus albicaudatus*, controls vertebrate populations, such as birds and small rodents. Photos: J.C. Morante Filho.

Figure 2. Accumulated number of publications (n=61) up to March 2014 that report the ecological functions performed by birds. Dashed line indicates the year of publication of the United Nations report.

Figure 1

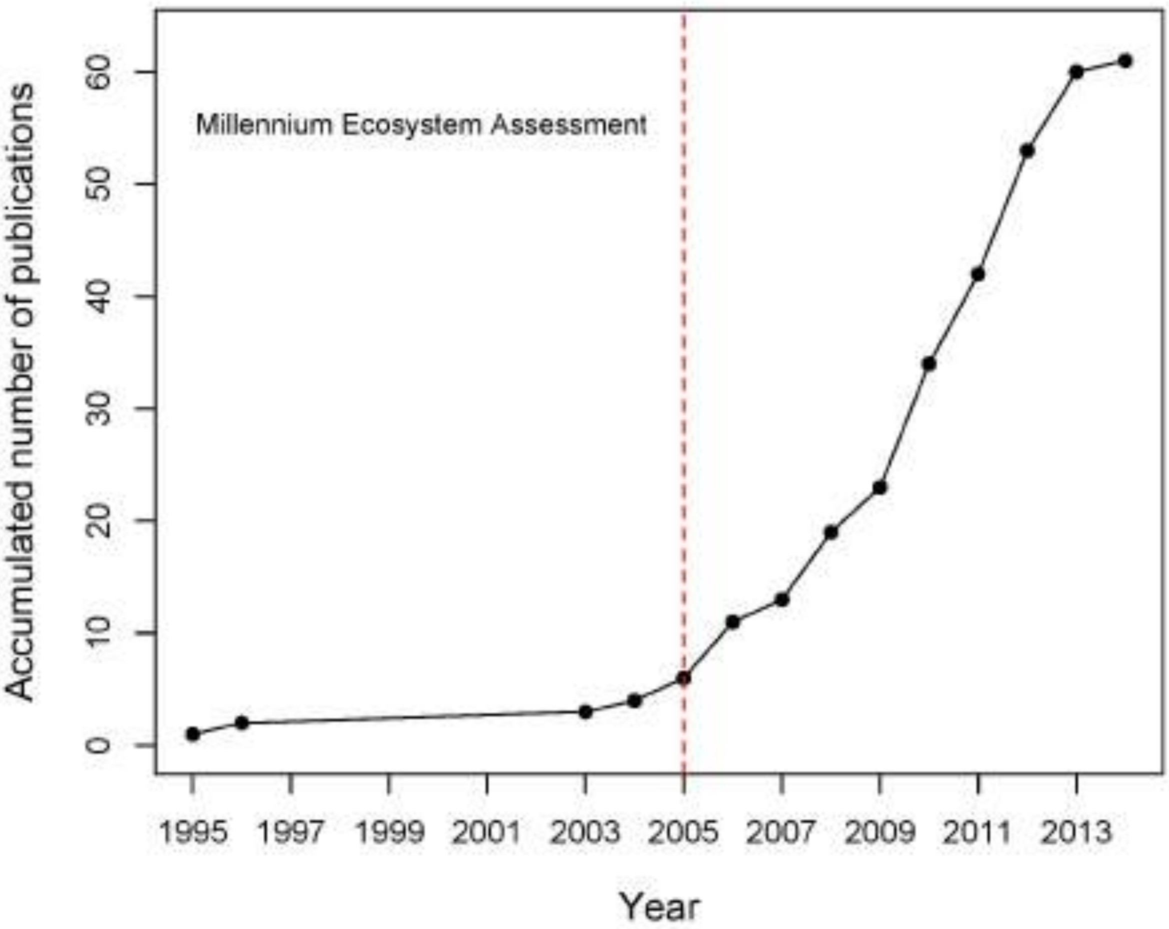
Millennium Ecosystem Assessment
Accumulated number of publications
0
10
20
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Figure 2

Capítulo 4

Running head: Forest loss effects on insect herbivory

Tropical forest loss and its multitrophic effects on insect herbivory[#]

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[#] **Article under review in the Ecology.**

Abstract. Forest loss threatens biodiversity, but its potential effects on multitrophic ecological interactions are poorly understood. Insect herbivory depends on complex bottom-up (e.g., resource availability and plant antiherbivore defenses) and top-down forces (e.g., abundance of predators and herbivorous), but its determinants in human-altered tropical landscapes are largely unknown. Using structural equation models, we assessed the direct and indirect effects of forest loss on insect herbivory in 40 landscapes (115 ha each) from two regions with contrasting land-use change trajectories in the Brazilian Atlantic rainforest. We considered landscape forest cover as an exogenous predictor, and (i) forest structure, (ii) abundance of predators (birds and insects), and (iii) abundance of herbivorous arthropods as endogenous predictors of insect leaf damage. From 12 predicted pathways, 11 were significant and showed that (i) leaf damage increases with forest loss (direct effect); (ii) leaf damage increases with forest loss through the simplification of vegetation structure and its associated dominance of herbivorous insects (indirect effect); and further demonstrate (iii) a lack of top-down control of herbivores by predators (birds and arthropods). We conclude that forest loss favors insect herbivory by undermining the bottom-up control (presumably reduced plant antiherbivore defense mechanisms) in forests dominated by fast-growing pioneer plant species, and by improving the conditions required for herbivores proliferation.

Key words: Atlantic rainforest; bottom-up control; defaunation; deforestation; forest fragmentation; leaf damage; top-down control.

INTRODUCTION

Tropical forests are threatened by agricultural expansion and land-use intensification (Malhi et al. 2014). The conversion of large tracts of tropical forests to human-altered landscapes leads to the extirpation of species (Fahrig 2013), loss of ecological assemblages (Clavel et al. 2011, Tabarelli et al. 2012, Morante-Filho et al. 2015), and can also alter complex ecological relationships through top-down and bottom-up multitrophic effects (Terborgh et al. 2001, Leal et al. 2014). Nevertheless, our knowledge on the cascading effects of forest loss on biodiversity maintenance and ecosystem functioning is far from being complete (Tscharntke et al. 2005, Mitchell et al. 2015), as most studies in human-altered landscapes focus on effects on selected species and communities, overlooking the effects on ecological processes and regulation of terrestrial ecosystems (but see Tscharntke et al. 2005, Mitchell et al. 2015).

Insect herbivory is a dominant animal-plant interaction in tropical forests (Coley and Barone 1996). Herbivores have substantial impact on terrestrial ecosystems, with estimates of herbivores, especially insects, consuming 18% of the biomass produced annually (Cyr and Pace 1993), and this effect may even be stronger in tropical regions (Coley and Barone 1996). Thus, this ecological process is a key driver of forest ecosystem functioning, once leaf consumption by herbivores affects tree growth, it will start negatively affecting tree health and fecundity, inhibiting regeneration and modifying ecosystem composition (Wirth et al. 2008, Allan and Crawley 2011), thereby influencing carbon stocks and forest productivity (Allan and Crawley 2011, Arroyo-Rodríguez et al. 2016). Habitat loss and fragmentation are known to affect herbivory levels in many ways though the outcomes are variable, as increases (Guimarães et al. 2014, Peter et al. 2015), decreases (Fáveri et al. 2008, Ruiz-Guerra et al. 2010), and no changes (De La Vega et al. 2012, Souza et al. 2013, Peter et al. 2014) in herbivory levels have been documented in human-altered landscapes. Such contradictory findings can be attributed to a large number of confounding factors in these emerging landscapes (Didham et al. 2012). For example, insect herbivory is determined by a complex set of bottom-up (e.g., resource availability and plant antiherbivore defenses; Coley and Barone 1996) and top-down (e.g., abundance of predators and herbivorous; Guimarães et al. 2014) controls, that are expected to vary across sites depending on the landscape structure (Didham et al. 2012, Arroyo-Rodríguez et al. 2016).

Forest loss is known to alter the composition and structure of remaining plant assemblages (Malhi et al. 2014, Arroyo-Rodríguez et al. 2016). Landscapes with lower forest cover are principally composed of small and edge-dominated forest patches (Didham et al. 2012) and have altered environmental conditions (e.g., higher light incidence, wind exposure, and temperature) (Laurance et al. 2007). This can increase the mortality of large shade-tolerant trees, and promote the proliferation of fast-growing light-demanding plant species (Laurance et al. 2006, Arroyo-

Rodríguez et al. 2016). The replacement of shade-tolerant with light-demanding species has direct consequences for insect herbivory, as light-demanding species are characterized by cheap-to-construct, fast-growing and short-lived leaves that offer little protection against herbivores (Coley and Barone 1996, Schuldt et al. 2012). Furthermore, forest loss and the consequent homogenization of forest structure can have a negative impact on forest specialist birds, most probably because of dispersal limitation associated with habitat specialization (Julliard et al. 2006, Morante-Filho et al. 2016) and a high sensitivity to habitat alteration (Şekercioḡlu et al. 2002, Powell et al. 2015). Therefore, the population decline and potential extirpation of forest birds in the remaining forest patches is expected to increase insect herbivory through the reduction of insect predation (Maas et al. 2013, Mitchell et al. 2015). In fact, the proliferation of light-demanding plant species in these landscapes can increase the abundance of herbivorous insects and insect herbivory (Guimarães et al. 2014, Leal et al. 2014), not only because of the increased abundance of food resources, but also because of reduced natural enemies of insects (e.g., predatory arthropods, birds, bats and terrestrial mammals; Karp and Daily 2014). Altogether this may lead to a reduced natural control of insects in human-altered landscapes (Guimarães et al. 2014, Leal et al. 2014), with large consequences for ecosystem functioning, including agricultural systems that may exhibit increases in crop damages by pests given the lack of natural enemies (Maas et al. 2013, Karp and Daily 2014). To mechanistically understand the complex nature of these multitrophic interactions we need comprehensive models, such as structural equation models (see Ruffell et al. 2016), that are able to unravel not only the direct effects of forest loss on herbivory, but also the indirect impact of pathways mediated by vegetation composition and structure, and by the abundance of both predators and herbivorous in landscapes with different amount of forest cover.

Here, we tested the direct and indirect effects of forest loss on leaf damage by herbivorous insects in the Brazilian Atlantic rainforest. We studied 40 landscapes (115 ha each) distributed along a gradient of forest loss (7-98% of remaining forest cover). Our conceptual model considers the direct effect that forest loss may have on forest structure, and on the abundance of forest specialist birds and predatory arthropods, which together may determine the abundance of herbivorous insects (Fig. 1). In particular, we predicted that leaf damage would be lower in landscapes with higher forest cover because such landscapes will be composed of large forest patches and core habitats (Fahrig 2013), dominated by shade-tolerant tree species (Laurance et al. 2006) with higher antiherbivore defenses (i.e., bottom-up control; Coley and Barone 1996). In fact, the proliferation of pioneer plants in landscapes with lower forest cover can favor generalist herbivores, such as leaf-cutting ants (Leal et al. 2014), thus increasing herbivory levels (Guimarães et al. 2014, Leal et al. 2014). At the same time, we can also expect a positive secondary effect of forest structure on the abundance of herbivorous insects through the negative effect of predatory birds on predatory arthropods (intraguild control; Karp and Daily 2014) (Fig. 1). We further predicted that the abundance of forest birds would be higher in landscapes with higher forest cover (Maas et al. 2013, Karp and Daily 2014, Morante-Filho et al. 2015 2016, Peter et al. 2015), thereby reducing the abundance of herbivorous insects and leaf damage levels. We also expected a positive effect of forest cover on the forest structure (e.g., increment of tree density and tree diameter at breast height; Arroyo-Rodríguez and Mandujano 2006), which would increase the abundance of forest birds, and in turn asserts control of the abundance of herbivorous insects (Fig. 1).

METHODS

Study area

The study area is located in the south-eastern Bahia State, Brazil (Fig. 2). Mean annual temperature is 24 °C, and annual rainfall average is 2000 mm year $^{-1}$, without a defined dry season (Pardini et al. 2009). The area was originally covered by lowland tropical wet forest (Thomas et al. 1998), but anthropogenic changes during the last 30 decades have transformed the native forest into a mosaic of land uses, including old-growth and secondary forest, shade cacao plantations, rubber tree and *Eucalyptus* sp. plantations, cattle pasture and human settlements (Pardini et al. 2009; Fig. 2).

We assessed two regions that have exhibited contrasting land-use change trajectories, but with similar soil, topography, and floristic characteristics (Fig. 2). We mapped the two regions using recent satellite images (QuickBird and WorldView, from 2011; RapidEye, from 2009-2010), and created maps by manually digitizing the land-use features visually interpreted at scale of 1:10000, which is adequate for classifying land cover patches in different vegetation types, as cropland, pasture and forest, based on the visual inspection. The remaining natural patches were classified in different habitat types (mangrove, sandbank vegetation and forest) following the typologies provided by IBGE (2006).

There are open areas within both regions, but most of the large and continuous forests are concentrated in the northern region, mainly around the Una Biological Reserve and the Una Wildlife Refugee, two federally protected conservation units that have a total area of 34,804 ha. In contrast, the southern region is clearly more deforested than the northern region, but there are still some large forest tracts (> 3000 ha) in this region. The northern region occupies 101900 ha, 50% of which corresponds to old-growth and secondary forests. The matrix in this region is very heterogeneous but is dominated by shade cacao plantations (22% of the matrix) and rubber trees (10%) (Fig. 2). Yet, the southern region occupies 201910 ha, 30% of which corresponds to old-growth and secondary forests. Being dominated by open areas (cattle pastures occupy 86% of the matrix) and *Eucalyptus* sp. plantations (7%), the matrix in the southern region is notably more homogeneous (see Morante-Filho et al. 2016).

Landscape forest cover

Within each region, we randomly selected 20 landscapes (Fig. 2). Using a sample site-landscape approach (sensu Fahrig 2013), we calculated the percent of natural forest (i.e., old-growth and secondary forest) within each landscape. In particular, we considered a 600-m radius (buffer, 115 ha) from the center of each landscape, as it is large enough to include a large variation in the explanatory variable (i.e., forest cover ranging from 7% to 98%); a necessary characteristic to provide confidence in landscape predictive models (Eigenbrod et al. 2011). Also, with this buffer size we avoided spatial overlap, which is needed to make accurate landscape-scale inferences (Eigenbrod et al. 2011). Finally, in a recent multi-scale analysis we demonstrated that this spatial scale is relevant for forest specialist birds (Morante-Filho et al. 2016).

Vegetation survey

In each landscape, we characterized the vegetation structure in four 20 x 4-m plots randomly located in the interior of one forest patch and separated by at least 150 m. Within each plot, we recorded all woody plants in the understory (50 to 200 cm in height), and all trees above the understory layer (i.e., with a diameter at breast height, DBH ≥ 5 cm). We then estimated the density of all stems, and the mean DBH of all stems ≥ 5 cm (i.e., mean DBH per tree hereafter).

Bird survey

We surveyed the birds in each landscape during three field campaigns (January to April 2013, May to September 2013, and October 2013 to April 2014), thus including the September-January bird-breeding season in the region. In forest patch interior in each landscape we randomly established four points (*sensu* Bibby et al. 1992), separated by 150 to 550 m, and placed at a minimum distance of 100 m from the nearest forest edge. In these points, visual and audio detection of birds took place for a period of 15 minutes, during times of greatest bird activity (between 0600 and 0900 hr, and between 1500 and 1700 hr). In each campaign, we randomly chose the points before the sampling to avoid any bias. The total sampling effort per landscape was 6 hours (3 field campaigns x 4 points x 2 periods x 15 min).

We classified birds into forest specialists and habitat generalists based on the scientific literature (Stotz et al. 1996, Bregman et al. 2014). For this study we only considered forest specialist birds because they are expected to be strongly influenced by forest cover loss (Martensen et al. 2012, Morante-Filho et al. 2015, 2016), which is the main focus of this study, and may strongly affect insect herbivory (Karp and Daily 2014, Peter et al. 2015). We expect that the loss of birds (especially of forest birds) has a positive effect on insect populations (Julliard et al. 2006). We included birds with different diets because also omnivorous birds may contribute to predation of insects or modify the foraging activity of herbivores (Bucher et al. 2015).

Arthropod surveys

Within each point-count we sampled arthropods in five randomly selected understory plants (50-200 cm in height). Since our aim was to evaluate the insects herbivory in understory plants, we randomly selected plants for measuring arthropods abundance, regardless of the species (Ruiz-Guerra et al. 2010, Souza et al. 2013). In total, we sampled 60 plants per landscape (3 field campaigns x 4 points x 5 plants). To select a plant we randomly selected a cardinal (north, south, east, and west) or collateral (northeast, southeast, northwest and southwest) direction from each point-count, as well as a random distance (from 1 to 50 m), after which we identified the nearest understory plant. We then used visual searches to quantify the abundance of all arthropods found in all branches and leaves of selected plant (Van Bael et al. 2003). We conducted surveys between 0930 and 1130 hr while avoiding rainy and windy days that reduce arthropods activity and detectability. We collected the specimens manually for further identification by specialists at the lower taxonomic level to classify them into predators and herbivores. We classified the orders Araneae, Pseudoscorpiones, Neuroptera, Mantodea, and ant species of genus *Crematogaster* and *Ectatomma* as predators. We considered ant abundance separately from arthropod abundance because ants are considered important predators, mainly in the tropics, due to their high abundance (Maas et al. 2013). Based on the morphology of buccal apparatus we categorized herbivorous arthropods into leaf-chewing insects (mainly the orders Lepidoptera, Orthoptera, Phasmatodea and Coleoptera) or plant-sucking insects (mainly the orders Hemiptera and Thysanoptera).

Leaf damage assessment

The plants selected for the arthropod survey were also assessed for leaf damage. For this, we estimated the area of leaf damage in 3 leaves per plant (3 leaves x 60 plants = 180 leaves per landscape), randomly selected by assigning a number to each leaf and randomly choosing three numbers (Ruiz-Guerra et al. 2010). We photographed leaves with a scale and against a white board, and the black-and-white photos were analyzed on Image Tools 3.0 to estimate leaf area. We quantified leaf damage caused by herbivorous insects (and not by fungi, virus or sunburn) as a percentage of leaf area lost, calculated by dividing the difference between the potential leaf area and the actual leaf area by the potential leaf area. When the leaf borders were damaged, we estimated the potential leaf area by drawing the leaf perimeter based on leaf symmetry. Mean leaf area loss per landscape is used as a direct measurement for insects herbivory. Yet, our herbivory estimates reflect the accumulated damage to a plant throughout its lifetime and not during the period of this specific study. This approach however was successfully applied in a variety of studies that tested the effects of ecological factors on insects herbivory at the landscape scale (Van Bael et al. 2003, Souza et al. 2013, Peter et al. 2015).

Finally, although plant traits (chemical, physical and physiological) are important predictors of interspecific variation to herbivores pressure (Schuldt et al. 2012) our study did not assess such differential responses, as we did not account for species identification. However, even considering differences in species composition, the idiosyncratic response to herbivory levels can also occur within single species populations (Cárdenas et al. 2014), as it depends on a variety of local conditions that are unlikely to be adequately controlled under field conditions (e.g., variation in co-specific density, available nutrients and light conditions).

Statistical analyses

We used structural equation models (SEM) to assess direct and indirect predictors of leaf damage. SEM is ideal for studying complex systems because it allows rigorous estimation of direct and indirect effects and tests for the overall fit of a complex network of influence (Grace 2006). We considered the percent forest cover within each landscape as an exogenous predictor. Subsequently, (i) forest structure, (ii) the abundance of vertebrate (only forest specialist birds) and invertebrate predators, and (iii) the abundance of invertebrate herbivores (Fig. 1) served as endogenous predictors. Forest complexity is a compound variable that was estimated using Principal Component Analysis (PCA), based on a series of parameters commonly used to describe forest structure (i.e., the density of plants in the understory, the density of trees above understory and mean DBH per tree). This produced a forest complexity axis (axis 1 from PCA) that explained 53% of the variation in vegetation structure. Forest complexity was positively related to tree and understory plant density and mean DBH per tree (see Appendix S1). We considered the abundance of forest birds and predatory arthropods (not their richness) as the driver of insect control, as insect control is expected to depend more strongly on the number of individuals than on the number of species present within each landscape. Similarly, we used the abundance of herbivorous insect, and not their species richness, as a driver of leaf damage because it is the individual that consumes leaves.

We first developed an “a priori” hypothetical model based on theoretical and empirical evidence. Using directional separation (d-separation) tests, we identified all conditional independence claims present in our model, and test whether the hypothesized pathways reflected variation present in the data (Shipley 2000). Based on this analysis we optimized our conceptual model (Fig. 1) and found that forest complexity only affected leaf damage indirectly through the abundance of vertebrates and invertebrates.

SEM assumes a multivariate normal distribution in the data, which was tested using Mardia's multivariate normality test. To meet normality assumptions a number of transformations were applied: the logarithmic transformation to mean DBH per tree, abundance of all herbivorous arthropods, abundance of all predatory arthropods, abundance of predatory arthropods (excluding ants), abundance of predatory ants and abundance of sucking herbivorous; and the arcsine transformation to the percent forest cover. We tested alternative models to select those variables that optimized the overall model performance since our sample size limited us to simple model structures (with few variables). The alternative models always included forest cover, abundance of forest birds and leaf damage, besides of combinations of variables related to forest structure (i.e., density of plants in the understory, density of trees above understory, mean DBH per tree, and forest complexity), abundance of invertebrate predators (i.e., all predatory arthropods, predatory arthropods (except ants), and predatory ants), and abundance of invertebrate herbivores (i.e., all herbivorous arthropods, chewing herbivorous, and sucking herbivorous) (see Fig. 1 and Appendix S2). Therefore, each model was composed of six variables and 40 observations, while considering that the observations were nested in two regions using the lavaan.survey package (Oberski 2014) that allows creating nested SEM. Subsequently, we selected the best-fitting model based on the lowest AIC (we present test results for all models in Table S2). We evaluated the fit of all models using a χ^2 goodness-of-fit test of the difference between the observed data and hypothesized model, Tucker-Lewis Fit Index (TLI), the Comparative Fit Index (CFI), and the Root Mean Square Error of Approximation (RMSEA). A satisfactory model fit was indicated by: (i) a non-significant χ^2 goodness-of-fit test ($P > 0.05$), (ii) CFI and LTI > 0.9, and (iii) lower 90% confidence intervals of RMSEA < 0.05 (Zhang et al. 2013). We present the standardized path coefficients (see Table S3) for each causal path in the final model. All the statistical analyses and graphs were carried out in R software (R Development Core Team 2013).

RESULTS

Forest loss at landscape scale directly increases the leaf damage ($R^2 = 0.19$, $P = 0.005$). Overall, 73% of the sampled leaves ($n = 7200$ leaves) showed signs of damage, with an average of 7.4 ± 1.9% of area loss per leaf. The results of d-separation test indicated that only forest cover and abundance of herbivorous arthropods directly affected leaf damage. In contrast, we found that forest complexity indirectly affected leaf damage through the decline in the abundance of forest birds, and the associated increase in the abundance of predatory arthropods and herbivores (Fig. 3).

All models showed a reasonably good fit (see Appendix S3), suggesting that our conceptual model adequately describes the data. The model with the lowest AIC was composed of forest cover, forest complexity, abundance of forest birds, abundance of predatory arthropods (excluding ants), abundance of all herbivorous arthropods and leaf damage (see Appendix S2, S3 and S4). Forest cover was positively related to forest complexity (see Appendix S1) represented as tree density having DBH > 5 cm (69.3 ± 18.5 trees/320 m^2, mean ± SD), density of woody plants in the understory (197.0 ± 55.7 plants/320 m^2), and mean DBH per tree (35.8 ± 4.6 cm). We recorded 3552 forest birds (88.9 ± 37.2 individuals/landscape), 1515 predatory arthropods (excluding ants) (36.0 ± 10.6 individuals/landscape), and 863 herbivorous arthropods (20.5 ± 8.7 individuals/landscape).

From the 12 pathways present in the best model, 11 were significant and 7 were consistent with our predictions (Fig. 3). Overall, this model explained 55% of forest complexity, 41% of forest bird abundance, 21% predatory arthropod abundance, 11% of herbivore abundance and 29% of leaf damage. Forest loss leads to forest structural simplification (β = 0.74), which causes different effects on predator and herbivore abundance. The abundance of forest birds was positively related to forest cover (β = 0.47) and forest complexity (β = 0.21). In contrast, the abundance of predatory arthropods was negatively related to forest cover (β = -0.54), and positively to forest complexity (β = 0.56) and abundance of forest birds (β = 0.25). Furthermore, the abundance of herbivorous arthropods was negatively related to forest complexity (β = -0.23). However, contrary to our predictions, herbivores were positively related to the abundance of forest birds (β = 0.23) and predatory arthropods (β = 0.30). Finally, leaf damage was positively related to the abundance of herbivores (β = 0.32) and negatively to forest cover (β = -0.40) (Fig. 3).

DISCUSSION

Our findings reveal that landscape-scale forest loss increases insect herbivory in understory plants in the fragmented Brazilian Atlantic rainforest. Three general patterns emerged. First, there is an increase of leaf damage in more deforested landscapes. Second, there is an indirect increase of leaf damage with forest loss through the cascading simplification of vegetation structure and the associated increase in the abundance of herbivorous insects. Third, there is a lack of top-down control of herbivores by birds and predatory arthropods. Therefore, this study demonstrates that leaf damage in human-altered landscapes is a complex ecological process that can be promoted by landscape-scale forest loss through bottom-up effects across trophic levels (Coley and Barone 1996, Wirth et al. 2008, Souza et al. 2013, Guimarães et al. 2014, Leal et al. 2014).

Direct effect of forest loss on leaf damage

We propose two alternative and mutually non-exclusive hypotheses to explain how forest loss increase insect herbivory. First, in agreement with the Resource Dilution Hypothesis (Moreira et al. 2016), the density of understory plants decreased in landscapes with lower forest cover (Appendix S5), and this may limit the availability of plant items, 'forcing' herbivores to concentrate on the few available items and cause more damage. Second, the bottom-up control associated with antiherbivore defense may be undermined in landscapes with lower forest cover. Although we do not have data on plant species composition and their functional strategies, there is ample evidence (including a research that is being conducted in our study region; M. Benchimol and colleagues, unpublished data) indicating that the percentage of fast-growing pioneer species increases in landscapes with lower forest cover (Arroyo-Rodríguez and Mandujano 2006, Laurance et al. 2006, Tabarelli et al. 2012). This is related to the increasing forest canopy openness in more deforested landscapes (Rocha-Santos et al. 2016), which promotes microclimatic changes (e.g., increased light incidence and decreased humidity) that prevent seed germination, recruitment and establishment of shade-tolerant species, while favoring light-demanding pioneers (Laurance et al. 2006). Pioneer plants tend to be poorly defended against herbivores (Coley and Barone 1996) and this lack of bottom-up control may drive increased herbivory rates in human-altered landscapes (Coley and Barone 1996, Wirth et al. 2008, Leal et al. 2014).

Multitrophic effect of forest loss on leaf damage

Our findings showed that forest loss exerted an indirect effect on herbivory, via the simplification of vegetation structure (e.g., lower density of plants and of smaller size) and the associated increase of herbivore abundance. The simplification of vegetation structure in deforested and fragmented landscapes is relatively well known (Arroyo-Rodríguez and Mandujano 2006, Laurance et al. 2006, Tabarelli et al. 2012), also in the study region, where forest cover is negatively related to stem density, diameter, and basal area (Rocha-Santos et al. 2016). The indirect effect that vegetation structure has on leaf damage was also found (Bereczki et al. 2014), but in studies performed in temperate forests at the local scale. Our novel contribution is that we demonstrated in a large-scale study that such increased damage is mediated by the proliferation of herbivorous insects in tropical forests with early successional forest attributes. The proliferation of herbivores may be associated with the increased abundance and richness of generalist insects (e.g., leaf-cutting ants), which found a higher availability of resources with higher palatability in disturbed forests (Guimarães et al. 2014, Leal et al. 2014). Furthermore, release from predation pressure due to the loss of potential predators can contribute to the proliferation of herbivorous insects (Wirth et al. 2008, Guimarães et al. 2014, Leal et al. 2014). Our results partially support this idea, as the abundance of both birds and predatory arthropods were significantly and positively associated with our index of forest complexity, but we do not find evidence supporting a top-down control of birds and predatory arthropods on herbivores (we discuss this issue in the following section).

Absence of the top-down control

Our study supports the idea that forest specialist birds are negatively affected by forest loss (Martensen et al. 2012, Morante-Filho et al. 2015, 2016), indeed most tropical forest bird are rare and specialized species that require large forest patches to forage and disperse (Martensen et al. 2012). Our results suggest that the simplification of vegetation structure is an important mechanism by which forest cover reduces forest birds. The reason is probably that simplification reduces favorable microclimatic conditions and availability of resources (Şekercioḡlu et al. 2002, Powell et al. 2015). In a similar way did forest structure simplification reduce the abundance of predatory arthropods (see Bolger et al. 2000, Prieto-Benítez and Méndez 2011), explained also by a reduction in refuges, favorable microclimatic conditions (Prieto-Benítez and Méndez 2011) and resources (e.g., generalist insects). This is shown especially to be true for spiders (Bolger et al. 2000) that represented 90% of our sample. The spread of predatory arthropods in more deforested landscapes can also be related to forest loss-induced extirpation of their natural enemies, especially birds and bats (Rogers et al. 2012, Karp and Daily 2014).

Surprisingly, the abundance of forest birds and predatory arthropods was positively related to the abundance of herbivorous insects, not negatively related as predicted by ‘green world’ theories (Polis and Strong 1996). These theories propose that the world is green because predators control herbivore populations and the damage these animals do to vegetation (Terborgh et al. 2001). Yet, many studies have questioned this idea because it is usually based on simplified webs with a few linear relationships, and often do not incorporate the effect of resource defenses (bottom-up control), pathogens, trophic symbioses, animal behavior, and other components of real-world food webs, which may cause inconsistencies and results that are very difficult to explain (e.g., Polis and Strong 1996). In this sense, the positive relationship between predators and herbivores can be interpreted as a bottom-up control (Scherber et al. 2010), i.e., the abundance of predators is higher in landscapes with higher abundance of preys, and, predators are therefore regulated by preys simply because they move to landscapes with high abundance of resources. Yet, this positive relationship could indicate that herbivore abundances over time can be maintained in forests with low predator abundance. In contrast, landscapes with high herbivore abundances also had high predator abundances, possibly limiting herbivore population growth (Bereczki et al. 2014, Smith and Schmitz 2016). In any case, the combination of bird abundance, predatory arthropods, forest structure complexity and forest cover only explained 11% of the variation of herbivores, so further studies are required to better understand the main drivers of herbivore abundance in human-altered landscapes.

The lack of a negative association between predators and herbivores does not necessarily implies a lack of top-down control by predators on insect herbivory (i.e., density-mediated effects), as the presence of predators can influence the feeding activity of herbivores (i.e., trait-mediated effects; Bucher et al. 2015). This occurs when preys change characteristics such as physiology, morphology, reproductive strategy or behavior in response to predation risk (Bucher et al. 2015). For example, predation risk can change the feeding rate of herbivores if energy costs linked to vigilance or mobility increase due to predator presence. Some studies suggest that such effects can be as important as density-mediated effects in arthropod-herbaceous plant systems (Prasad and Snyder 2006, Van Veen et al. 2009, Steffan and Snyder 2010). Thus, the higher abundance of predators, especially birds, in landscapes with higher forest cover may indirectly influence herbivory even without depressing herbivore populations.

Conclusions

Despite the complexity involved on such ecological process, and the evident limitations for controlling the many specific variables predicting herbivory outcomes in natural patches under different local and landscape-scale context, this study demonstrates that forest loss in the Brazilian Atlantic rainforest increases insect herbivory both directly and indirectly, through the simplification of vegetation structure and the associated increase in the abundance of herbivores. Thus, our results suggest that forest loss favors insect herbivory by undermining the bottom-up control (antiherbivore defense) in forests dominated by fast-growing pioneer plant species, and by improving the conditions required for herbivores proliferation. This study reinforces the idea that habitat loss is a pervasive threat to biodiversity, not only because it threatens forest dependent species and assemblages (Clavel et al. 2011, Fahrig 2013, Morante-Filho et al. 2016), but also as it increases local pressure of herbivory by insects. Such changes can limit the recruitment and regeneration (i.e., resilience) of plant populations and assemblages (Arroyo-Rodríguez et al. 2016). In this sense, and in agreement with the ‘landscape-divergence hypothesis’ (Laurance et al. 2007, Tscharntke et al. 2012), we would expect that forest remnants in landscapes with different forest cover would have different successional trajectories, potentially leading to divergence in plant species composition (Arroyo-Rodríguez et al. 2016); this topic represents a very important avenue for future research.

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FIGURE LEGENDS

Fig. 1. Conceptual model used to test the link between forest cover amount at the landscape scale, and forest structure, vertebrate and invertebrate predators, invertebrate herbivores and leaf damage. Positive and negative hypothetical pathways are indicated by blue and red lines, respectively.

Fig. 2. Study area in southern Bahia, Brazil. We show the location and land cover classes of the northern region (a), with 50% of remaining forest cover, and the southern region (b), with 30% of remaining forest cover. We indicate the study forest sites within each region with black dots.

Fig. 3. Best-fitting (see Table S2 and S3) structural equation model. Positive and negative pathways are indicated by blue and red lines, respectively. Arrow thickness is scaled to illustrate the relative strength of effects, and significant coefficients are indicated with asterisks (*$P < 0.05$; **$P < 0.01$; ***$P < 0.001$). The determination coefficient (R^2) is shown in black circles for all response variables (i.e. forest complexity; abundance of forest specialist birds; abundance of predatory arthropods, except ants; abundance of herbivorous arthropods and leaf damage).

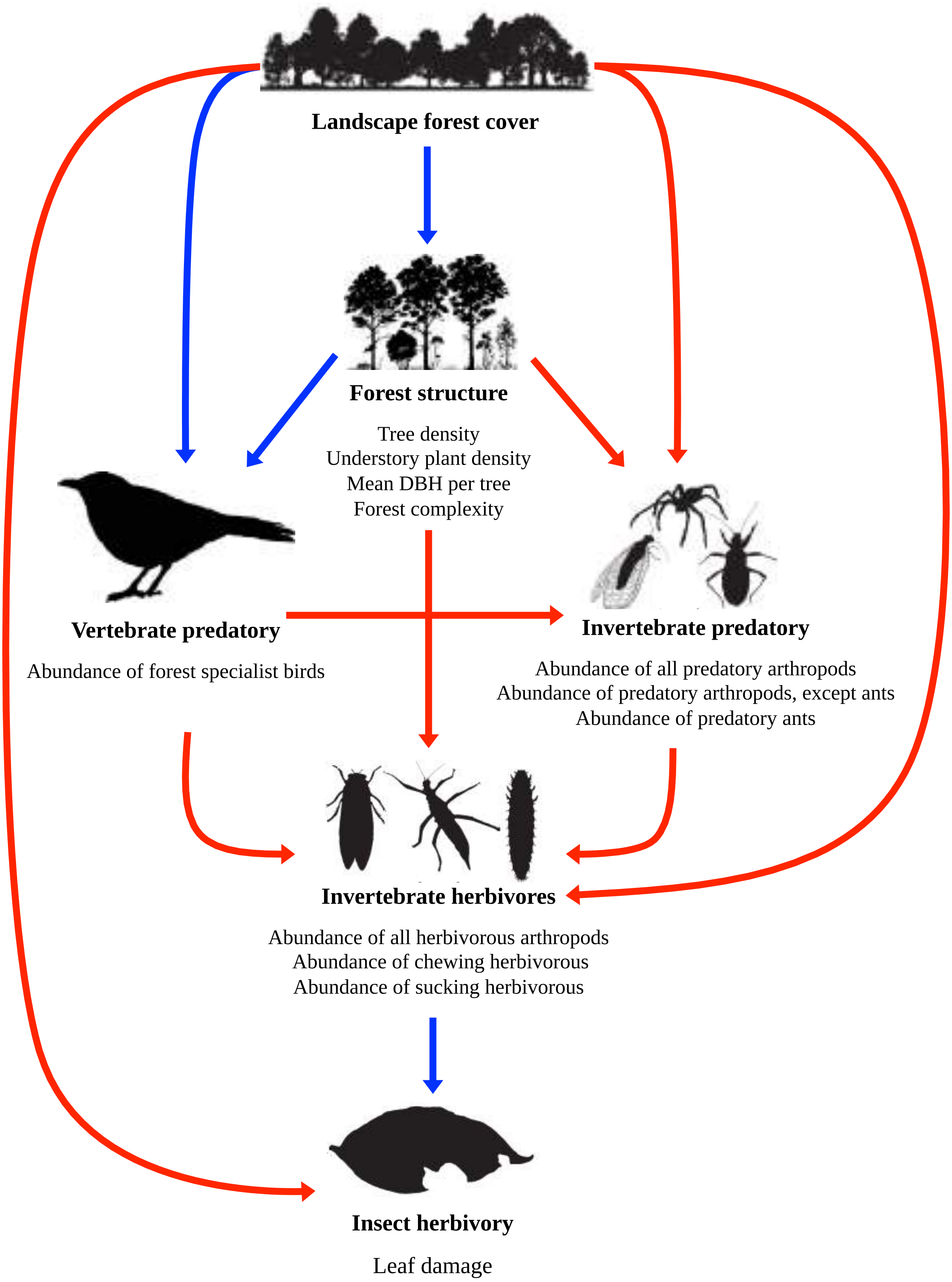

Landscape forest cover
Forest structure
Tree density
Understory plant density
Mean DBH per tree
Forest complexity
Vertebrate predatory
Abundance of forest specialist birds
Invertebrate predatory
Abundance of all predatory arthropods
Abundance of predatory arthropods, except ants
Abundance of predatory ants
Invertebrate herbivores
Abundance of all herbivorous arthropods
Abundance of chewing herbivorous
Abundance of sucking herbivorous
Insect herbivory
Leaf damage

Figure 1

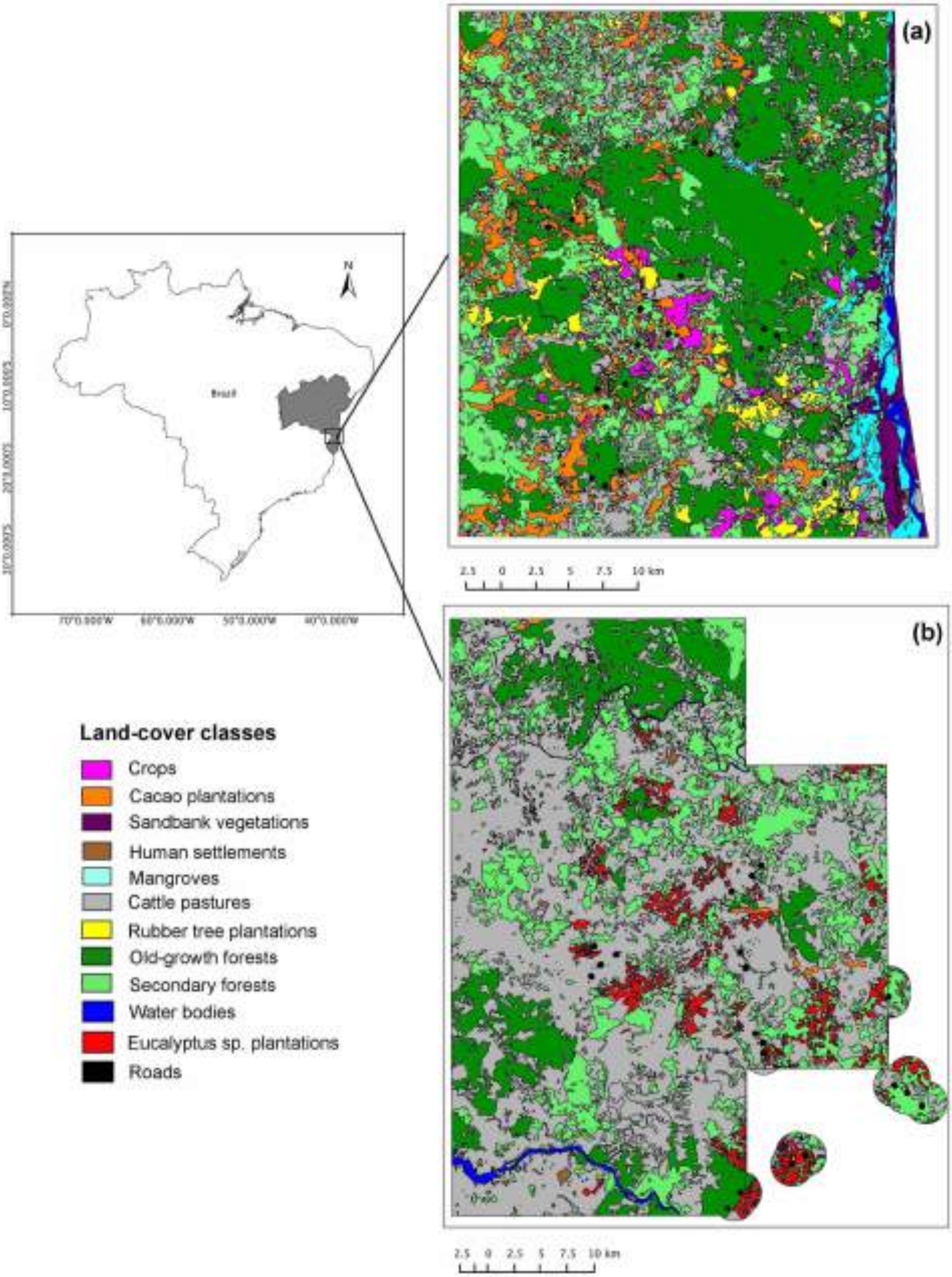

(a)
(b)
N
Brazil
70°0.000'W
60°0.000'W
50°0.000'W
40°0.000'W
2.5 0 2.5 5 7.5 10 km
2.5 0 2.5 5 7.5 10 km
Land-cover classes
Crops
Cacao plantations
Sandbank vegetations
Human settlements
Mangroves
Cattle pastures
Rubber tree plantations
Old-growth forests
Secondary forests
Water bodies
Eucalyptus sp. plantations
Roads

Figure 2

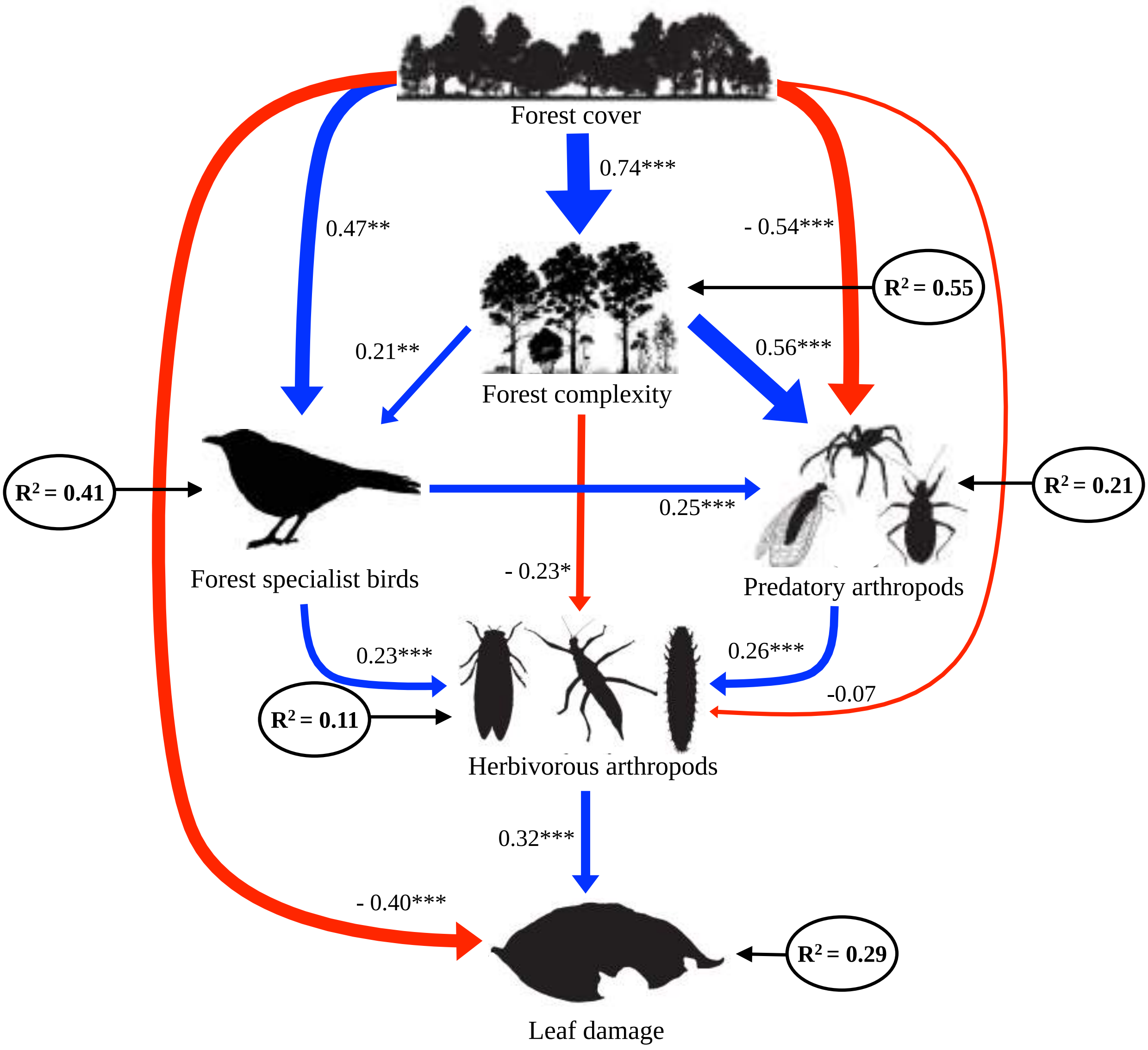
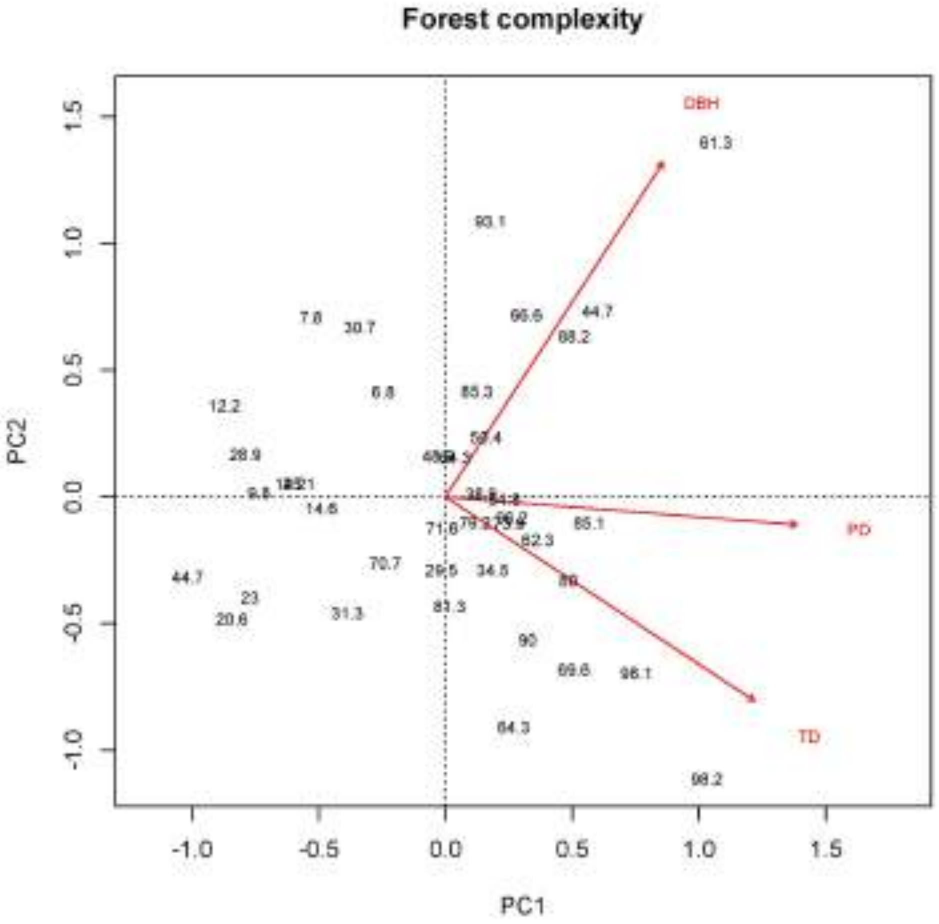

Forest cover
0.74***
0.47**
- 0.54***
R^2 = 0.55
0.21**
0.56***
Forest complexity
R^2 = 0.41
R^2 = 0.21
0.25***
- 0.23*
Forest specialist birds
Predatory arthropods
0.23***
0.26***
R^2 = 0.11
-0.07
Herbivorous arthropods
0.32***
- 0.40***
R^2 = 0.29
Leaf damage

Figure 3

SUPPORTING INFORMATION

Appendix S1. Biplot representation of the Principal Component Analysis to organize the study sites based on forest structure. The first two axes explained 84% of total variance in forest structure. Numbers indicate the percentage of forest cover surrounding each of the 40 forest sites, and red arrows show the predictors of forest structure: TD (density of trees with diameter at breast height, DBH > 5 cm), PD (density of plants in the understory) and DBH (mean DBH per tree).



Appendix S2. Path models constructed using different combinations of variables (see Fig 1). Each model was composed of six variables and 40 observations (sites) nested in two regions.

Model	Variables*
1	FC, PCA1, AFSB, AP, AH, LD
2	FC, PCA1, AFSB, AP, ACH, LD
3	FC, PCA1, AFSB, AP, ASH, LD
4	FC, PCA1, AFSB, AAP, AH, LD
5	FC, PCA1, AFSB, AAP, ACH, LD
6	FC, PCA1, AFSB, AAP, ASH, LD
7	FC, PCA1, AFSB, AP.NA, AH, LD
8	FC, PCA1, AFSB, AP.NA, ACH, LD
9	FC, PCA1, AFSB, AP.NA, ASH, LD
10	FC, TD, AFSB, AP, AH, LD
11	FC, TD, AFSB, AP, ACH, LD
12	FC, TD, AFSB, AP, ASH, LD
13	FC, TD, AFSB, AAP, AH, LD
14	FC, TD, AFSB, AAP, ACH, LD
15	FC, TD, AFSB, AAP, ASH, LD
16	FC, TD, AFSB, AP.NA, AH, LD
17	FC, TD, AFSB, AP.NA, ACH, LD
18	FC, TD, AFSB, AP.NA, ASH, LD
19	FC, PD, AFSB, AP, AH, LD
20	FC, PD, AFSB, AP, ACH, LD
21	FC, PD, AFSB, AP, ASH, LD
22	FC, PD, AFSB, AAP, AH, LD
23	FC, PD, AFSB, AAP, ACH, LD
24	FC, PD, AFSB, AAP, ASH, LD
25	FC, PD, AFSB, AP.NA, AH, LD
26	FC, PD, AFSB, AP.NA, ACH, LD
27	FC, PD, AFSB, AP.NA, ASH, LD
28	FC, DBH, AFSB, AP, AH, LD
29	FC, DBH, AFSB, AP, ACH, LD
30	FC, DBH, AFSB, AP, ASH, LD

31	FC, DBH, AFSB, AAP, AH, LD
32	FC, DBH, AFSB, AAP, ACH, LD
33	FC, DBH, AFSB, AAP, ASH, LD
34	FC, DBH, AFSB, AP.NA, AH, LD
35	FC, DBH, AFSB, AP.NA, ACH, LD
36	FC, DBH, AFSB, AP.NA, ASH, LD

*FC = Forest cover; PCA1 = first axis of the PCA to the data of vegetation; TD = Tree density with DBH > 5 cm, PD = Plant density in the understory, DBH = mean diameter at breast height per tree; AFSB = Abundance of forest specialist birds; AP = Abundance of predadory arthropods; AP.NA = Abundance of predadory arthropods, except ants; AAP = Abundance of predadory ants; AH = Abundance of herbivorous arthropods; ACH = Abundance of chewing herbivorous; ASH = Abundance of sucking herbivorous; LD = Leaf damage.

Appendix S3. Results of the adjustment coefficients of all models (Table S1). For each model we show the degrees of freedom (DF), test statistic (minimum function chi-square, χ^2), model p-value, comparative fit index (CFI), Tucker-Lewis fit index (TLI), Akaike Informaton Criterion (AIC), difference in AIC between the best model and the *i*-th model (ΔAIC), and root mean square error of approximation (RMSEA). Models are ranked by their AIC values, from the lowest to the largest.

Model*	**DF**	**χ^2**	**p-value**	**CFI**	**LTI**	**AIC**	**ΔAIC**	**RSMEA**
7	3	0.72	0.87	1	1.26	732.50	0.00	0
9	3	0.27	0.97	1	1.28	773.21	40.72	0
1	3	0.31	0.95	1	1.4	777.37	44.87	0
3	3	0.13	0.98	1	1.39	817.74	85.24	0
4	3	0.31	0.96	1	1.32	840.47	107.97	0
34	3	0.05	0.99	1	1.57	860.62	128.12	0
6	3	0.18	0.98	1	1.32	879.22	146.73	0
28	3	0.21	0.97	1	1.65	898.09	165.59	0
36	3	0.25	0.97	1	1.64	900.63	168.13	0
8	3	0.41	0.94	1	1.32	918.40	185.90	0
30	3	0.29	0.96	1	1.72	937.58	205.09	0
16	3	0.07	0.99	1	1.28	953.62	221.13	0
2	3	0.2	0.98	1	1.47	962.52	230.03	0
31	3	0.11	0.99	1	1.62	964.61	232.11	0
10	3	0.22	0.97	1	1.34	992.73	260.23	0
18	3	0.34	0.95	1	1.24	994.65	262.15	0
33	3	0.27	0.97	1	1.69	1002.55	270.05	0
5	3	0.28	0.96	1	1.34	1024.32	291.83	0
12	3	0.14	0.99	1	1.32	1033.51	301.01	0
35	3	0.18	0.98	1	1.76	1049.85	317.35	0
13	3	0.23	0.97	1	1.27	1053.74	321.24	0
25	3	0.14	0.98	1	1.32	1054.51	322.01	0
29	3	0.25	0.97	1	1.91	1087.19	354.69	0
15	3	0.25	0.97	1	1.24	1092.64	360.14	0
27	3	0.22	0.97	1	1.28	1094.86	362.37	0
19	3	0.35	0.95	1	1.42	1097.32	364.82	0
21	3	0.11	0.99	1	1.42	1136.76	404.26	0

17	3	0.34	0.95	1	1.31	1141.23	408.73	0
32	3	0.22	0.98	1	1.78	1153.78	421.28	0
22	3	0.57	0.9	1	1.29	1159.20	426.70	0
11	3	0.26	0.97	1	1.41	1180.12	447.62	0
24	3	0.2	0.97	1	1.31	1197.06	464.56	0
14	3	0.42	0.94	1	1.27	1240.04	507.54	0
26	3	0.34	0.95	1	1.39	1244.50	512.00	0
20	3	0.25	0.97	1	1.56	1285.47	552.97	0
23	3	0.39	0.94	1	1.37	1346.42	613.92	0

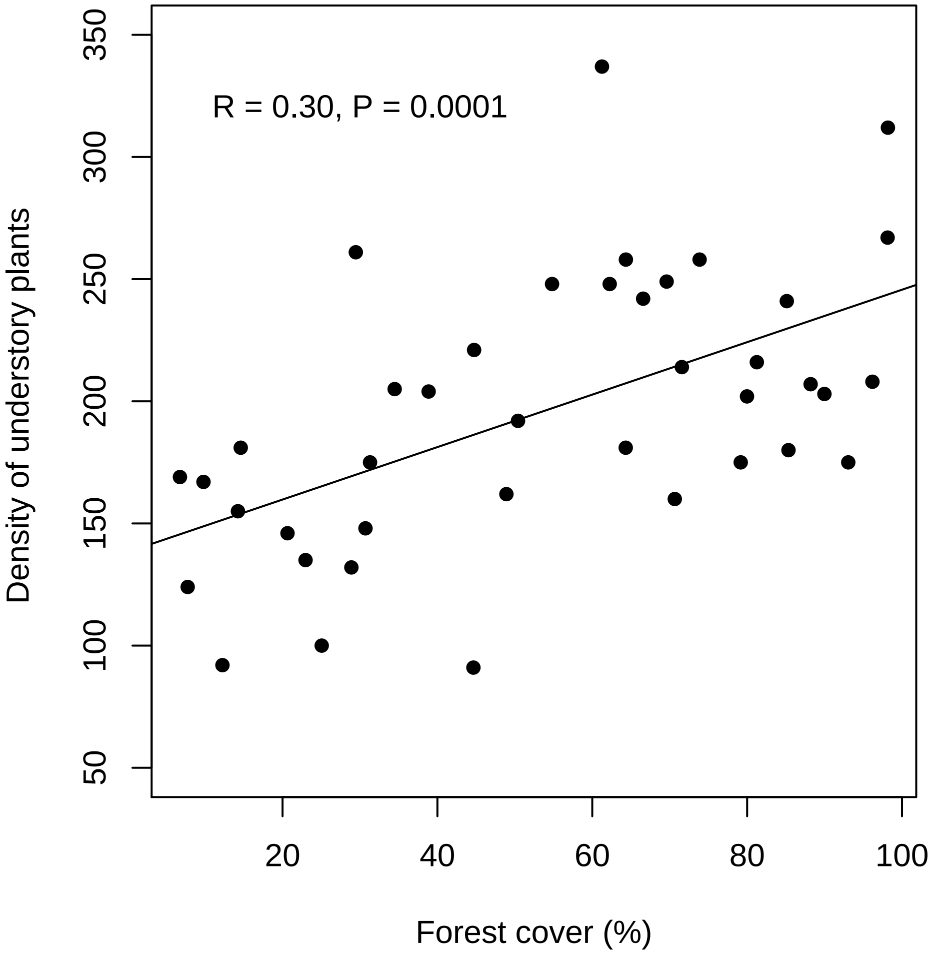
*The variables that compose each model are showed in Table S1.

Appendix S4. Test statistic for the best model. We show the unstandardized path coefficients (Coef.), the related standard error (SE), Z-value, p-value and standardized path coefficients (SEst). The significant paths are highlighted in bold.

Regressions	**Coef**	**SE**	**Z**	**p**	**SEst**
Forest complexity ~ Forest cover	**2.79**	**0.42**	**6.63**	**0.00**	**0.74**
Abundance of forest specialist birds ~					
Forest cover	**52.29**	**18.61**	**2.81**	**0.005**	**0.47**
Forest complexity	**6.06**	**1.88**	**3.22**	**0.001**	**0.21**
*Abundance of predatory arthropods ~					
Forest cover	**-0.42**	**0.03**	**-12.85**	**0.00**	**-0.54**
Forest complexity	**0.12**	**0.01**	**10.02**	**0.00**	**0.57**
Abundance of forest specialist birds	**0.002**	**0.001**	**5.64**	**0.00**	**0.25**
Abundance of herbivorous arthopods ~					
Forest cover	-0.09	0.22	-0.39	0.69	-0.07
Forest complexity	**-0.08**	**0.03**	**-2.49**	**0.01**	**-0.24**
Abundance of forest specialist birds	**0.003**	**0.001**	**4.58**	**0.00**	**0.23**
*Abundance of predatory arthropods	**0.42**	**0.05**	**8.79**	**0.00**	**0.26**
Leaf damage ~					
Forest cover	**-2.26**	**0.21**	**-10.96**	**0.00**	**-0.40**
Abundance of herbivorous arthopods	**1.42**	**0.29**	**4.97**	**0.00**	**0.32**

* In this datasets, we did not consider predatory ants.

Appendix S5. Association between density of understory plants and percentage of landscape forest cover in the Brazilian Atlantic forest.



Conclusões gerais

De maneira geral, os resultados obtidos nessa tese contribuíram para melhor compreensão da influência das mudanças na cobertura do solo, especialmente a redução de cobertura florestal, sobre a estrutura das comunidades de aves em paisagens antrópicas. Além disso, foi evidenciado que alterações ambientais podem impactar importantes processos ecológicos desempenhados pelas aves. As principais conclusões obtidas neste estudo foram:

1. A redução de cobertura florestal na escala de paisagem afeta negativamente a diversidade de aves, porém essa relação somente é evidente quando as análises são realizadas para grupos ecológicos específicos. Nas paisagens estudadas, a perda de floresta não afeta a riqueza e abundância total de aves devido a uma dinâmica compensatória existente entre aves especialistas florestais e generalistas de hábitat, ou seja, quando a quantidade de cobertura florestal diminui em torno de 50% ocorre uma redução abrupta da diversidade de aves florestais com um concomitante aumento de aves generalistas. Desta forma, a substituição dos grupos ecológicos permite a manutenção da diversidade de aves nas paisagens antrópicas.
2. A diversidade das guildas tróficas de aves (insetívoras e frugívoras) apresenta resposta similar para redução de quantidade de floresta, destacando uma relação não-linear e com uma diminuição drástica na riqueza e abundância em paisagens com menos de 50% de cobertura florestal. Além disso, a perda de floresta age como um filtro ambiental, alterando a composição de espécies de todos os grupos ecológicos de aves.
3. A diversidade gama de aves pode ser mantida pelo câmbio de espécies (diversidade beta) entre localidades, porém isso depende do grupo ecológico, da escala espacial e da heterogeneidade da paisagem. Por exemplo, aves florestais mostram maior diferenciação na composição de espécies (alta diversidade beta) entre fragmentos inseridos em paisagens com baixa cobertura florestal e dominadas por pastagem. Em contrapartida, aves generalistas apresentam maior diferenciação de espécies entre fragmentos inseridos em paisagens com grande quantidade de floresta e com uma matriz heterogênea. Dentro dos fragmentos florestais, ambos os grupos ecológicos apresentam uma homogeneização (baixa diversidade beta) na composição de espécies em paisagens com alto nível de desmatamento.
4. Fragmentos florestais com alta diferenciação na composição de aves também apresentam grandes diferenças nas características ambientais (estrutura da vegetação local e composição

da paisagem), indicando que alterações ambientais são importantes preditores da estrutura das assembleias de aves em paisagens fragmentadas.

5. Muitos estudos apenas reportam como ambientes perturbados podem afetar a diversidade de grupos ecológicos de aves, porém sem executar uma avaliação direta de tais efeitos sobre as funções desenvolvidas pelas aves. Além disso, distúrbios na escala local, como na estrutura da vegetação, são os principais fatores relacionadas a função ecológica, enquanto o efeito de mudanças ambientais na escala de paisagem sobre as funções executadas pelas aves são pobremente avaliadas pelos estudos.
6. No geral, o controle de populações de artrópodes efetuado especialmente por aves insetívoras é o principal papel ecológico avaliado pelos estudos, enquanto outras importantes funções, como a dispersão de sementes, polinização e controle de doenças, carecem de mais informações. Além disso, é necessário desenvolver mais pesquisadas com objetivo de valorar os serviços ecossistêmicos prestados pelas aves para a população humana, além de gerar mais informações sobre o efeito em cascata da perda de funções ecológicas sobre o funcionamento do ecossistema.
7. Por fim, nessa tese foi possível constatar que a redução da quantidade de floresta além de afetar negativamente a diversidade de espécies pode também acarretar efeitos significativos sobre processos ecológicos. Especificamente, a perda de floresta aumenta o nível de herbivoria foliar em plantas no subosque de fragmentos florestais. Diretamente, essa perturbação na escala de paisagem aumenta a proporção de espécies de plantas pioneiras que são mais suscetíveis ao dano foliar por possuir menor concentração de defesas químicas nas suas folhas. Por outro lado, a redução na quantidade de floresta exerce um efeito em cascata sobre a herbivoria, via simplificação da estrutura da vegetação e consequente aumento da abundância de insetos herbívoros.

Diante do exposto acima, futuros estudos devem buscar entender como a substituição de grupos ecológicos de aves podem impactar o funcionamento dos fragmentos florestais remanescentes, uma vez que não sabemos se as funções ecológicas executadas por aves especialistas florestas por ser mantidas pelas aves generalistas. Além disso, é necessário que novos estudos abordem como mudanças na cobertura do solo podem impactar outras importantes funções efetuadas pelas aves, como a dispersão de sementes que tem um papel fundamental na regeneração das florestas em paisagens antrópicas.