



Mediation of area and edge effects in forest fragments by adjacent land use

Jack H. Hatfield ^{1,*}, Jos Barlow,² Carlos A. Joly ³, Alexander C. Lees ^{4,5},
Celso Henrique de Freitas Parruco,⁶ Joseph A. Tobias ¹, C. David L. Orme,¹
and Cristina Banks-Leite ^{1,7}

¹Grand Challenges in Ecosystems and the Environment, Department of Life Sciences, Imperial College London, Ascot, U.K.

²Lancaster Environment Centre, Lancaster University, Lancaster, U.K.

³Departamento de Biologia Vegetal, Instituto de Biologia, Universidade Estadual de Campinas, Campinas, São Paulo, Brazil

⁴School of Science and the Environment, Manchester Metropolitan University, Manchester, U.K.

⁵Cornell Lab of Ornithology, Cornell University, Ithaca, New York

⁶ES Consultoria Ambiental, Piracicaba, São Paulo, Brazil

⁷Department of Ecology, Biosciences Institute, University of São Paulo, São Paulo SP, Brazil

Abstract: Habitat loss, fragmentation, and degradation have pervasive detrimental effects on tropical forest biodiversity, but the role of the surrounding land use (i.e., matrix) in determining the severity of these impacts remains poorly understood. We surveyed bird species across an interior-edge-matrix gradient to assess the effects of matrix type on biodiversity at 49 different sites with varying levels of landscape fragmentation in the Brazilian Atlantic Forest—a highly threatened biodiversity hotspot. Both area and edge effects were more pronounced in forest patches bordering pasture matrix, whereas patches bordering *Eucalyptus* plantation maintained compositionally similar bird communities between the edge and the interior and exhibited reduced effects of patch size. These results suggest the type of matrix in which forest fragments are situated can explain a substantial amount of the widely reported variability in biodiversity responses to forest loss and fragmentation.

Keywords: Atlantic Forest, bird communities, forest cover, habitat fragmentation, pasture, plantations, patch size

Mediación de los Efectos de Área y de Borde sobre los Fragmentos de Bosque Causados por el Uso de Suelo Adyacente

Resumen: La pérdida del hábitat, la fragmentación y la degradación tienen efectos nocivos generalizados sobre la biodiversidad de los bosques tropicales. A pesar de esto, el papel del uso de suelo de los terrenos adyacentes (es decir, la matriz) en la determinación de la gravedad de estos impactos todavía está poco entendido. Censamos las especies de aves a lo largo de un gradiente de borde interno de matriz para evaluar los efectos del tipo de matriz sobre la biodiversidad en al menos 49 sitios con diferentes niveles de fragmentación del paisaje en el Bosque Atlántico Brasileño – un punto caliente de biodiversidad que se encuentra severamente amenazado. Tanto los efectos de área como los de borde estuvieron más pronunciados en los fragmentos de bosque que limitan con la matriz de pasturas, mientras que los fragmentos que limitan con plantaciones de *Eucalyptus* mantuvieron comunidades de aves similares en composición con aquellas entre el borde y el interior y mostraron efectos reducidos del tamaño de fragmento. Estos resultados sugieren que el tipo de matriz en el cual están situados los fragmentos de bosque puede explicar una cantidad sustancial de la ampliamente reportada variabilidad de respuestas a la pérdida del bosque y a la fragmentación.

Palabras Clave: Bosque Atlántico, cobertura forestal, comunidades de aves, fragmentación de hábitat, pasturas, plantaciones, tamaño del fragmento

*Address correspondence to Jack H. Hatfield, email jackbhatfield@gmail.com

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摘要: 生境丧失、破碎化和退化对热带森林生物多样性普遍具有负面影响,但周围的土地利用(即基质)在决定这些影响的严重性中的作用尚不明确。本研究通过沿内部-边缘-基质梯度的鸟类物种调查,评估了基质类型对巴西大西洋森林(一个高度受胁迫的生物多样性热点地区)49个景观破碎化程度不一的位点的生物多样性的影响。我们发现,与草地基质相邻的森林斑块的面积极效应和边缘效应更为显著,而与桉树种植林相邻的斑块边缘和内部鸟类群落组成相似,且斑块面积的影响较弱。以上结果表明,森林碎片所在基质的类型可以有力解释大量报道中的生物多样性对森林丧失和破碎化的响应变异性。**翻译: 胡怡思; 审核: 聂永刚**

关键词: 种植林, 草地, 生境破碎化, 森林覆盖, 斑块大小, 大西洋森林, 鸟类群落

Introduction

The type of matrix surrounding native forest patches in human-modified landscapes can modulate the responses of species and ecological communities to habitat loss and degradation (Brockerhoff et al. 2008; Prevedello & Vieira 2010). However, the mechanisms through which the matrix influences the effects of habitat change on biodiversity are still unclear. For instance, do inhospitable matrix types accelerate the local extinction of sensitive species in fragmented landscapes or promote the invasion of disturbance-tolerant species? Are patch area effects less pronounced in a permeable matrix because of rescue effects or weaker edge effects (Prugh et al. 2008)? Answering these questions is a crucial step toward effective management of matrix land uses to minimize biodiversity loss (Driscoll et al. 2013).

With the growing recognition that some matrix types are more permeable and hospitable to some species than others (Brockerhoff et al. 2008; Felton et al. 2010), recent research has increasingly focused on the interplay between matrix type and landscape composition (Driscoll et al. 2013). However, the extent to which matrix type can modulate biodiversity responses to area, edge, and isolation remains controversial (Prugh et al. 2008; Prevedello & Vieira 2010; Watling et al. 2011). Prugh et al. (2008) found isolation and area to be poor predictors of species occupancy when matrix type is highly permeable (e.g., seminatural habitats), whereas area and isolation are strong predictors of biodiversity in more hostile types of matrix. This is logical because any increase in structural similarity between the matrix and habitat patches can increase population connectivity among patches (Renjifo 2001; Prevedello & Vieira 2010), reducing local extinction by means of rescue effects. In contrast, Prevedello and Vieira (2010) argue that these matrix effects are smaller and more species specific than those of area and isolation.

The capacity of the matrix to buffer edge effects is expected to increase if the matrix approximates the physiognomy of native vegetation, which would reduce the impact of biotic and abiotic gradients at edges (Banks-Leite & Ewers 2009). For example, Amazonian tree mor-

talinity appears to be higher at edges bordering cattle pastures than edges bordering secondary forests (Mesquita et al. 1999). Shade coffee plantations also dampen edge effects in tropical montane forest relative to corn plantations (Santos-Barrera & Urbina-Cardona 2011). Other effects, such as spillover of matrix species into forest patches, may create an influx of disturbance-tolerant species and thus concomitant high species turnover (Banks-Leite et al. 2012, 2014) and changes to ecosystem function (De Coster et al. 2015). Changes in species composition can be problematic when they involve large-scale biotic homogenization, involving the proliferation of generalist species and the decline or extirpation of many specialists (Solar et al. 2015). Given the likely complexity of the underlying mechanisms governing these changes in community assembly, a rigorous landscape-based approach (Fahrig 2003) is required to determine the propensity of the matrix to influence the effects of habitat loss and landscape configuration (i.e., isolation, patch area, and edge effects).

To examine the ability of the matrix to mitigate the detrimental effects of landscape configuration on biodiversity, we considered bird communities in the highly fragmented and biodiverse Brazilian Atlantic Forest (Myers et al. 2000; Ribeiro et al. 2009). To obtain a full picture of how bird communities change, we collected data with 4 temporal replicates that spanned seasonal variation and stratified sampling across fragment interiors, fragment edges, and the surrounding matrix. Within this framework, we examined both a habitat-fragmentation gradient and different matrix types. To better understand how community composition changes, we analyzed species richness, community integrity (compositional similarity to continuous forest), and richness of both forest-dependent and disturbance-tolerant species. Disturbance-tolerant species richness was expected to be higher in fragments surrounded by the open-pasture matrix, and forest species are expected to be more commonly associated with fragments bordered by plantation forest. We also expected *Eucalyptus* plantation matrix, which bears higher structural similarity to Atlantic Forest, would show reduced edge and area effects relative to open-pasture matrix.

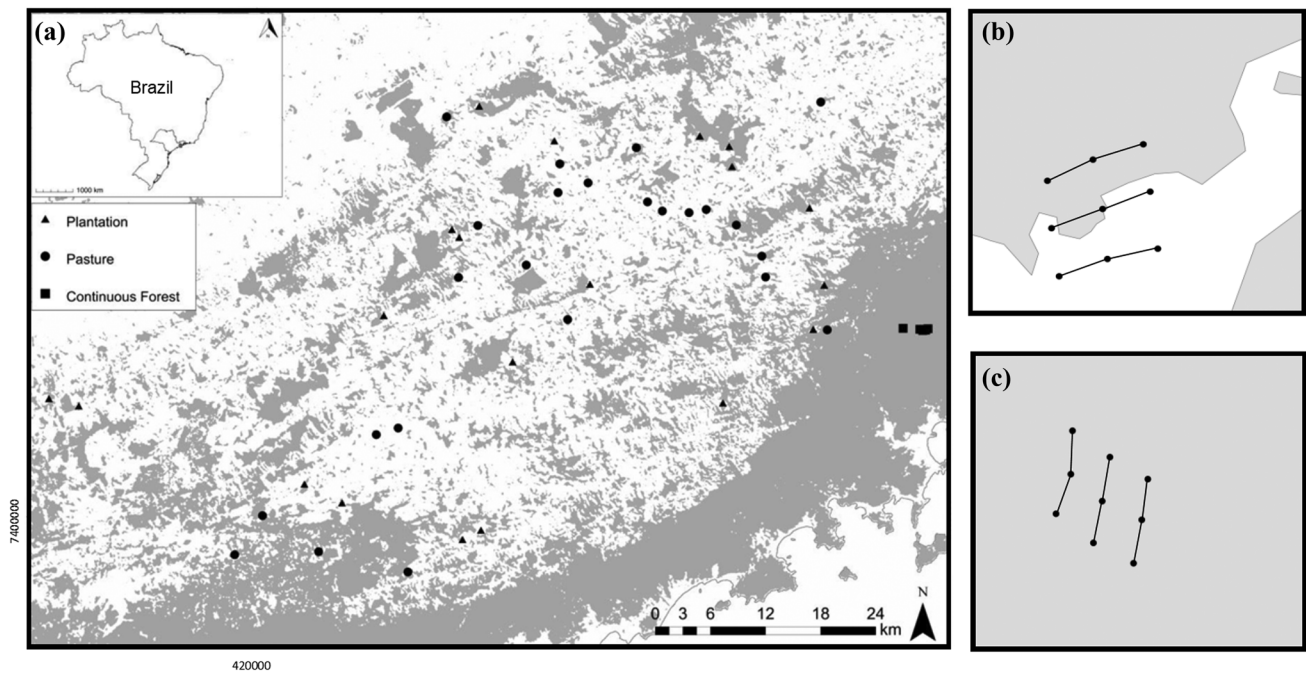


Figure 1. (a) Locations of bird survey sites (gray, all types of forest cover with >50% canopy closure in 2000) (Supporting Information and Hansen et al. [2013]) (/UMD/Google/USGS/NASA - Licensed under a Creative Commons Attribution 4.0 International License, <https://creativecommons.org/licenses/by/4.0/>). Composite forest cover maps and sampling points within transects for (b) a fragmented site and (c) a continuous site (gray, forest; white, nonforest). Point counts form a regular (where terrain, patch size, and edge shape allowed) 9-point grid with 75 m between points. Three points were situated in each position: interior, edge, and matrix.

Methods

Study Design

The study area was located in the Vale do Paraíba and Serra do Mar regions in the state of São Paulo, Brazil. The area was composed of submontane forest of varying age surrounded by a range of matrix types. The mean native forest cover at the 10,000-ha scale across all sites was 30%, mean total forest cover was 40%, and elevation ranged from 600 to 1130 m (Supporting Information). Continuous forest sites were in the largest remaining network of well-connected forest patches which comprised over 1 million ha (Ribeiro et al. 2009). We surveyed 49 sites, including 15 near continuous reference sites and 34 fragmented forest sites. At each site, we sampled 3 transects at 3 point-count stations each. Points within transects were approximately 75 m apart (where terrain and landscape configuration allowed), and the 3 transects were also spaced by 75 m (Fig. 1). This design was chosen to ensure that even small forest fragments could be surveyed with equal effort. In fragmented forest sites, a single transect was conducted in each of 3 positions relative to the focal forest patch: patch interior, patch edge, and in the matrix bordering the focal patch (Fig. 1).

Fifteen patches were bordered by *Eucalyptus* plantation and 19 bordered pasture. The median patch size was

28 ha. There were 6 different transect types surveyed across the fragmented forest sites, representing the 6 unique combinations of position (interior, edge, or matrix) and matrix land use (*Eucalyptus* plantation or cattle pasture). Due to availability and accessibility, as well as the mosaic nature of the landscape, patches were not surrounded by a uniform matrix; however, all transects were in sections of the patches that bordered the chosen matrix type. Surveyed fragments were selected to sample the full range of fragment area and connectivity in the study region and were part of the ECOFOR (Biodiversity and Ecosystem Functioning in Degraded and Recovering Amazonian and Atlantic Forests) project (Supporting Information). The 15 reference sites were chosen to encompass 1 land use each. Thus, we sampled 5 large areas of forest (CF), 5 large areas of cattle pasture (CP), and 5 large *Eucalyptus* plantations (CE). Continuous sites were designed with the same grid configuration as explained above, but all transect surveys were conducted in the same land-use type.

Avifaunal Surveys

Bird surveys were conducted from December 2015 to February 2017 with point counts. Each count was 15 minutes, during which time we recorded all birds

identified within a 25-m radius of the point. Four temporal replicates were equally split between wet and dry seasons per point. The spatial and temporal replicate points for each of the 147 transects were then aggregated, providing a sampling effort of 12 point counts per transect. Species richness was calculated as the total number of species recorded at each transect. We also calculated a frequency of occurrence (i.e., an encounter rate) for each species in each transect. This was done by summing the number of times (range 0–12) the species was detected at a site, which provided a proxy measure of abundance (Solar et al. 2015). This minimized the influence of single detections, which was especially useful for the matrix surveys, where some species may be transients infrequently recorded passing between forest patches. From the frequency of occurrence, we calculated community composition based on a Bray–Curtis dissimilarity matrix in the R package *vegan* (Oksanen et al. 2016). Values were then assigned based on the scores from the first axis of a principal coordinate analysis (PCoA) conducted on the dissimilarity matrix. For fragmented sites, we used community integrity rather than community composition to allow comparison to continuous forest. For community integrity, raw distances extracted from the Bray–Curtis dissimilarity matrix were used to calculate the mean distance between each transect and the continuous forest transects. This Bray–Curtis distance was then subtracted from 1 to provide a scale where 1 indicates a transect that highly resembles control forest and 0 indicates transects extremely dissimilar from continuous forest; hence, community integrity can be seen as a measure of similarity to the reference continuous forest (for a similar approach see De Coster et al. [2015]).

Landscape Metrics

Percent forest cover was measured for each site in radii of 600, 800, 1,500, and 3,000 m from the center of the site and for the 10,000-ha landscape (5×5 km, hereafter landscape forest cover). A single forest-cover scale was chosen per model based on model fit because multiple scales could not be modeled together due to high levels of collinearity (Supporting Information). We also measured size and calculated the proximity-index value (800-m search distance) for focal fragments; both were \log_{10} transformed for analysis. Proximity index takes into account the area of surrounding patches and weights this by distance (Gustafson & Parker 1994). All measurements were conducted using ArcGIS version 10 (Environmental Systems Research Institute, Redlands, CA, U.S.A.) and Fragstats version 4 (McGarigal et al. 2012) (Supporting Information).

Data Analyses

All analyses were conducted in R version 3.3.2 (R Core Team 2016). We examined the effect of transect type

(the combination of position and matrix type) with mixed-effect modeling in *lme4* (Bates et al. 2015); site was a random factor that accounted for spatial dependency between transects in the same landscape. For species richness, a generalized linear mixed model Poisson error structure checked for overdispersion (Supporting Information) was used and for community composition metrics linear mixed models were used. The influence of transect type on the avifaunal community was only investigated for the 34 fragmented sites. The position and matrix land-use combination (e.g., interior pasture) was a single fixed effect, and we conducted post hoc contrasts to assess significance. Although we do not include p values from our main results, we provide them with the mixed-effects models for factor-level contrasts to aid in interpretation. The continuous sites were not included in the models because there was only 1 land-use type surveyed at each of these sites; however, we analyzed them separately to provide a baseline for comparison. The data were then partitioned into interior, edge, and matrix to investigate the effects of landscape metrics with linear and generalized linear models. Landscape-metric models were selected based on the Akaike information criterion with correction for small sample size (AICc) or F tests in the case of overdispersion (Supporting Information). Because of small sample sizes, we were unable to fit all the interactions. We did however fit the interactions between matrix type and the other metrics because investigating the effect of matrix type was a major aim of the study. We used partial residuals in plots from models containing multiple explanatory variables (Supporting Information).

We conducted analyses on the whole bird community as well as 2 subsets (forest species and disturbance-tolerant species) owing to the high species turnover observed in Atlantic Forest bird communities (Banks-Leite et al. 2012, 2014). By dividing the community into 2 groups, we were able to reveal trends that are concealed by turnover when examining the community as a whole (e.g., whether compositional changes are governed by loss of forest species or gain of disturbance-tolerant species). These groups represented those species associated with the fragmented areas and those associated with the intact areas. Thus, this allowed us to individually consider those species responding negatively to disturbance and those that respond in a positive manner, but our categorization was not intended as a definitive classification. These distinctions were created using a species ranking system based on weighted averages ordination (Banks-Leite et al. 2014). Species presence or absence was first weighted by site scores taken from the first axis of a PCoA based on Bray–Curtis dissimilarity. The mean is then calculated from all non-0 weights. The division was made relative to the mean of the site scores (the value for a species that occurs at all sample locations).

Our method for partitioning the community into groups is a post hoc approach based on observed species turnover across sites. We favored this approach because previous classifications of species sensitivity or habitat use, such as Parker et al. (1996), were not transparent regarding where data were obtained and the level of uncertainty associated with each classification and do not differentiate among stressors (e.g., a species may be sensitive to hunting but insensitive to the land-use changes we investigated) (Alexandrino et al. 2016). We then used information on forest habitat restriction to better understand how our approach of community partitioning was related to the previous classification of Parker et al. (1996). We resolved taxonomic disagreement following the BirdLife International (2017) checklist. *Estrilda as-trild* was excluded from this comparison due to a lack of habitat-usage information.

Site-scale analyses were conducted by aggregating the 3 transects at each site. This produced a frequency of occurrence for each species potentially ranging from 0 to 36 from which community integrity was calculated. Species richness and community integrity were modeled against percent forest cover for the 10,000-ha landscape and matrix type surveyed with generalized linear and linear models, respectively.

Results

Overall, we detected 267 species across the 49 landscapes. The first PCoA axis explained 27.6% of the total variance. The community was split into 177 forest species and 90 disturbance-tolerant species. When compared with habitat usage information in Parker et al. (1996), 72% of species we assigned to the forest species group were restricted to forest based on published information, compared with 2% of the species in the disturbance-tolerant group. Although we did not examine this further, these comparisons demonstrate that our community split tallies well with published classifications.

Continuous Sites

Analyses of the whole community revealed that both continuous plantation ($z = -5.56, p < 0.01$) and continuous pasture ($z = -6.82, p < 0.01$) did not differ significantly from one another, but both showed lower species richness than continuous forest transects (Fig. 2a). However, the community composition of the 3 transect types were all significantly different from each other (CE - CF: $z = -14.24, p < 0.01$; CP - CF: $z = -26.07, p < 0.01$; CP - CE: $z = -11.83, p < 0.01$) (Fig. 2b). Changes in community composition were driven by a decrease in forest species richness in both types of matrix, together with an increase in disturbance-tolerant species (Fig. 2c, d). All continuous blocks were significantly different from each

other in forest species (CE - CF: $z = -7.79, p < 0.01$; CP - CF: $z = -12.38, p < 0.01$; CP - CE: $z = -6.63, p < 0.01$) and disturbance-tolerant species richness (CE - CF: $z = 4.94, p < 0.01$; CP - CF: $z = 9.21, p < 0.01$; CP - CE: $z = 6.90, p < 0.01$).

Fragmented Forest Sites

Transect type (i.e., position and matrix combination) influenced total species richness in the fragments ($F = 32.83$). Species richness in the matrix was significantly lower than both edge and interior (Fig. 2e), and pasture matrix transects had on average 39% more species than *Eucalyptus* ($z = 6.10, p < 0.01$). The results for community integrity however showed a different trend. Although transect type continued to have a significant influence ($F = 194.69$), edge effects were only observed in patches bordering pasture, whereas forest patches bordering *Eucalyptus* presented similar levels of integrity at edges and interiors (Fig. 2f), mirroring results for continuous sites, where *Eucalyptus* transects had greater integrity than pasture transects (Fig. 2f).

The edge effects observed in patches bordering pastures were mostly driven by an increase in disturbance-tolerant species rather than a reduction in forest species. The richness of forest species did not differ between edge and interior, regardless of the bordering matrix ($z = -5.31, p < 0.01$) (Fig. 2g), but the richness of disturbance-tolerant species in patches bordering pasture was lower in forest interiors when compared with edges ($z = -3.68, p < 0.01$). Furthermore, the species richness of disturbance-tolerant species in the interior of patches bordering pasture was, on average, 1.9 times higher than fragment interiors bordering *Eucalyptus* ($p = 0.02$) and similar to the number of species found in *Eucalyptus* matrix.

Landscape Configuration

Interior and edge transects showed a similar mediation of matrix type on community integrity responses to landscape configuration and habitat amount (interior: adjusted $R^2 = 0.57$; edge: adjusted $R^2 = 0.55$). In both cases, integrity was only positively affected by patch size in fragments bordering pasture (interior: $t = 2.12, p = 0.04$; edge: $t = 2.87, p < 0.01$) (Figs. 3a & 4a). Landscape forest cover (10,000-ha), in contrast, positively influenced integrity both in pasture and *Eucalyptus* bordering fragments (interior: $t = 5.11, p < 0.01$; edge: $t = 3.98, p < 0.01$), and although the slope of this relationship was not affected by matrix type, the intercept was always higher in *Eucalyptus* bordering patches (Figs. 3b & 4b). None of the landscape metrics (e.g., forest cover, patch size, proximity index) significantly correlated with species richness for interior transects, whereas for edge

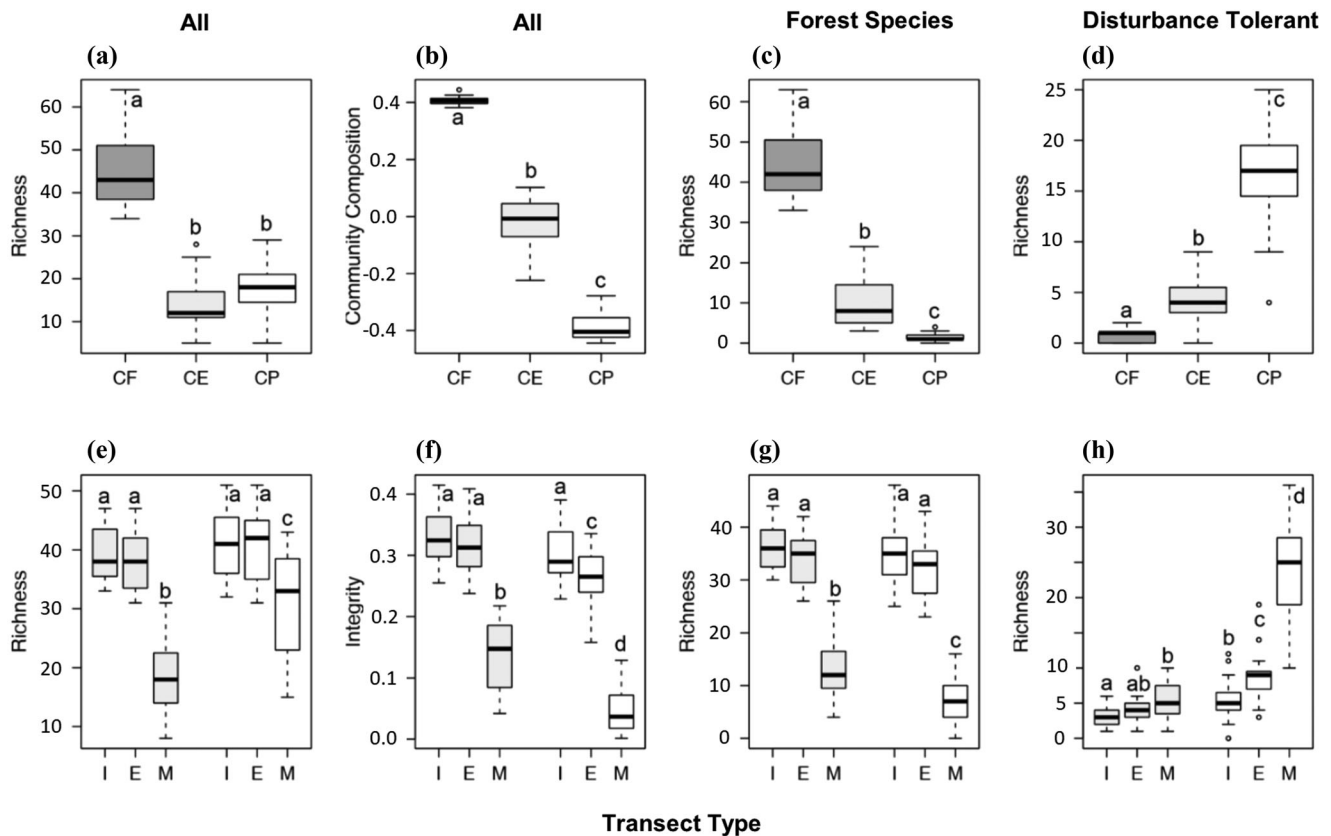


Figure 2. Species richness and composition measures for bird communities at each site partitioned by transect type for control forest (CF), control plantation (CE), control pasture (CP), fragment interiors (I), fragments edges (E), and surrounding matrix (M). Results for (a-d) control landscapes and (e-h) fragments for all species, forest species, and disturbance-tolerant species (bars, 1st and 3rd quartile; bold bar, median; whiskers, 1.5 times the interquartile range in length; letters above bars, transect-type groupings based on post hoc significance tests; white, fragments with pasture matrices; gray, plantation matrices; dark gray, control forest).

transects total species richness decreased as forest cover increased at the 3-km scale ($z = -2.04$, $p = 0.04$).

Forest species richness was not significantly affected by any landscape metric, but the richness of disturbance-tolerant species found at interior ($t = -2.14$, $p = 0.03$) (Fig. 3c) and edge ($t = -2.29$, $p = 0.03$) (Fig. 4c) transects was negatively correlated with patch size only in pasture bordering patches. Richness of disturbance-tolerant species in interior transects decreased as forest cover increased; the intercept was different between the matrix types, but the slope was the same ($z = -2.53$, $p = 0.01$).

Community integrity was lower for pasture matrices than plantation ($t = -5.95$, $p < 0.01$), and integrity was positively correlated with patch area ($t = 2.06$, $p = 0.05$, adjusted $R^2 = 0.53$) (Fig. 4e). Species richness was influenced by matrix type; pasture matrices had higher richness ($t = 4.10$, $p < 0.01$).

Forest species richness was positively correlated with forest patch area ($t = 2.57$, $p = 0.02$) (Fig. 4f), and pasture matrices had lower forest species richness than plantation ($t = -3.55$, $p < 0.01$). Disturbance-tolerant species richness was only significantly affected by matrix

type; pasture matrices had higher richness ($t = 9.25$, $p < 0.01$).

At the site scale (interior, edge, and matrix transects combined) (Fig. 5), community integrity increased as forest cover increased ($t = 3.06$, $p < 0.01$). Fragments bordering pasture had lower integrity than those bordering plantations ($t = -3.10$, $p < 0.01$; adjusted $R^2 = 0.42$). Species richness was affected only by matrix type; pasture bordering fragments had more species ($z = 5.90$, $p < 0.01$).

Discussion

Eucalyptus plantation matrices were more beneficial for bird communities in the Atlantic Forest relative to pasture matrices. Although pastures had higher species richness than *Eucalyptus* plantations, forest fragments bordering *Eucalyptus* had higher community similarity to continuous forest and weaker edge effects relative to pasture borders (Figs. 2–4). Strengthening of edge and area effects in patches bordering pastures was mostly due to

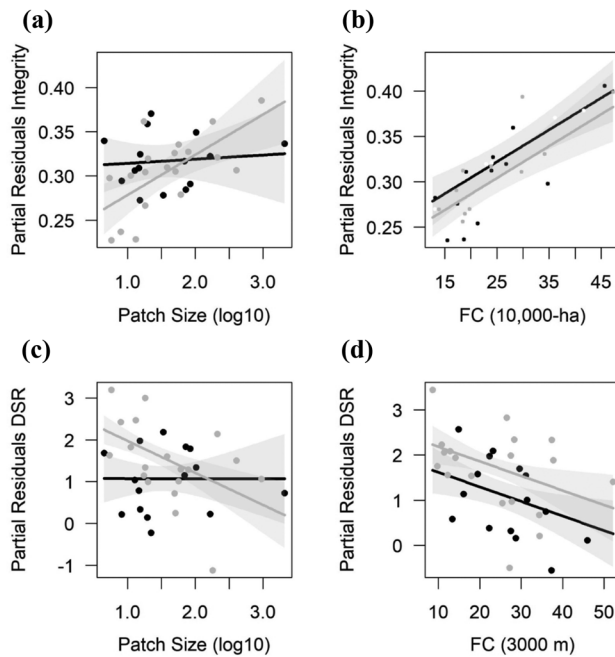


Figure 3. Partial residual values for bird community integrity and disturbance-tolerant species richness (DSR) against (a, c) patch size in hectares and (b, d) percent forest cover (FC) for interior transects (black, plantation matrix fragments; gray, pasture; shading, 95% confidence bands).

the increase in disturbance specialists, rather than the loss of forest species. Nonetheless, our findings suggest that spillover of species can occur in both directions in fragmented tropical forests, from fragments to matrix and vice versa.

In our study landscape, the *Eucalyptus* plantation matrix supported fewer bird species than pasture yet retained more forest species (Fig. 2). This aligns with previous studies showing that non-native plantations provide habitat for a small subset of tropical forest species (Barlow et al. 2007; Lees et al. 2015; Millan et al. 2015) without acting as a species source (Hawes et al. 2008). Pastures, in contrast, not only provide a habitat for different species (Moura et al. 2013; Lees et al. 2015), but also allow them to spillover into native forest, as shown by the increase in the richness of disturbance-tolerant species in fragments (Figs. 2h & 3c). We also found evidence of reverse spillover effects from the forest into the surrounding pasture (Tschardt et al. 2012), in contrast to Boesing et al. (2018a), who found minimal spillover of birds into cattle pasture in the Atlantic Forest. Our results suggest community integrity in matrix transects increases as forest patch area increases (Fig. 4e), indicating that large native forest patches help maintain community integrity in the surrounding matrix.

These results reinforce previous findings highlighting the value of extensive forest patches in providing source

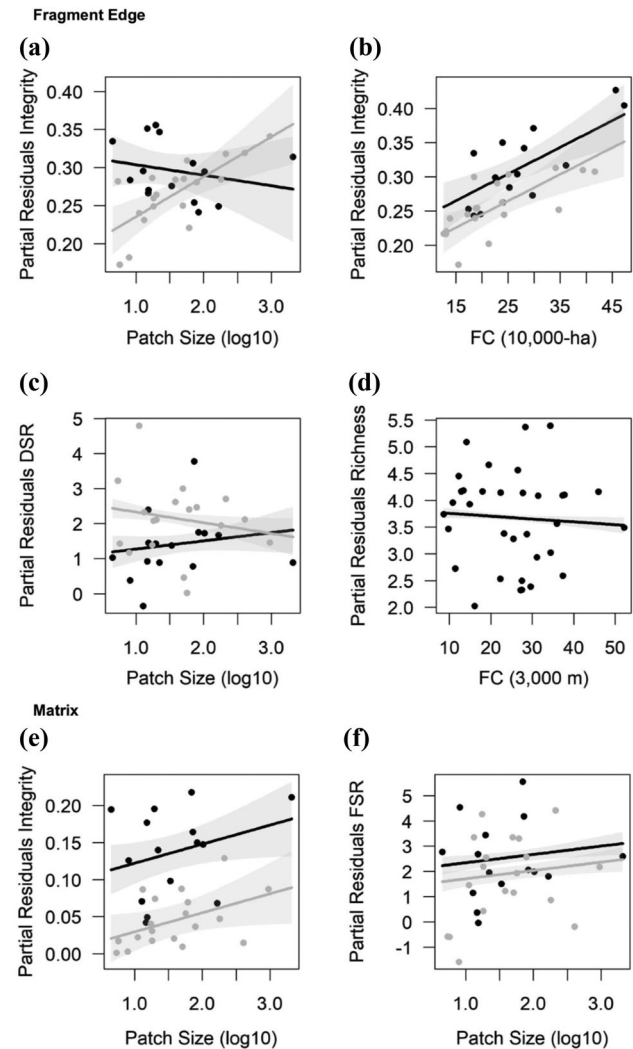


Figure 4. Partial residual values for bird community integrity, species richness, disturbance-tolerant species richness (DSR), and forest species richness (FSR) against (b, d) patch size (hectares) and (a, c, e, f) percent forest cover (FC) for (a–d) edge and (e and f) matrix transects (black, plantation matrix fragments; gray, pasture; gray shading, 95% confidence bands). In (d) there is only a single line because matrix type was not retained during model selection.

populations of forest-dependent bird species (Mayhew et al. 2019), thereby enriching the surrounding matrix via a spillover of ecosystem services, such as pollination, pest control, and seed dispersal. Spillover of services has been widely documented for a range of taxa (Tschardt et al. 2012), including insect and bird pollinators (Renjifo 2001; Ricketts et al. 2008), and bird spillover has been shown to be particularly important in coffee plantations (Boesing et al. 2018a), where birds control populations of pests (Johnson et al. 2010). Hence, species spillover from large forest patches into the matrix may benefit crop

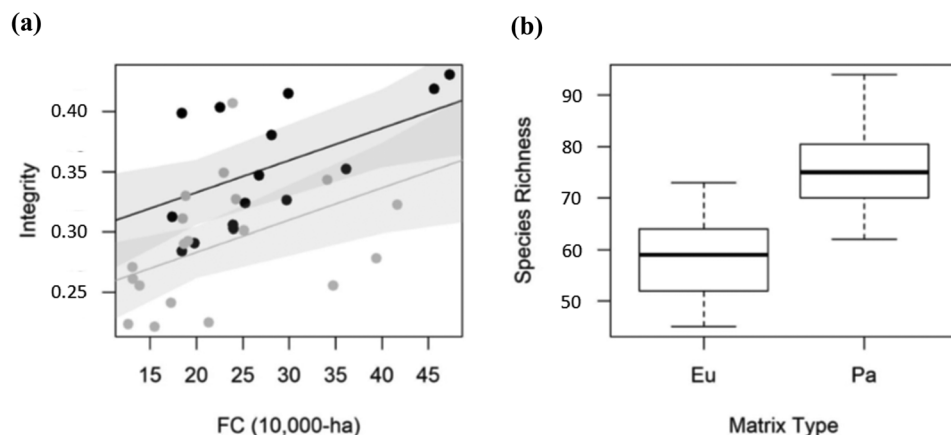


Figure 5. Bird community integrity against (a) percent forest cover (FC) and (b) species richness for 2 *Eucalyptus* plantation (Eu) and pasture (Pa) matrix types (gray, pasture matrix fragments; black, plantation).

productivity and increase seed dispersal of native trees, which is key to natural reforestation and forest recovery (Bregman et al. 2016).

Edge effects are prominent in the Atlantic Forest bird community (Banks-Leite et al. 2010; Ewers & Banks-Leite 2013; Pfeifer et al. 2017), where they are thought to drive the widely observed area effects on biodiversity in this fragmented landscape (Ewers et al. 2007; Fletcher et al. 2007; Banks-Leite et al. 2010). Our results provide further corroboration of this hypothesis because we detected significant edge effects only in patches bordering pasture matrices, where patch area also had a significant influence on the interior bird community. Conversely, for fragments with a plantation matrix, we found neither significant edge effects nor significant area effects.

The large difference in edge effects observed could be due to 2 main factors. First, plantations are known to harbor fewer open matrix species (Umetsu & Pardini 2007) limiting changes in community composition due to turnover. Second, plantations may contribute to the retention of forest species. Our results indicating that plantations may mitigate edge effects mirror those of Renjifo (2001), who found that exotic tree plantations had a buffering effect on the abundance of some forest species when compared with pasture. Ruffell et al. (2017) also found that the reduction in bird species richness with habitat loss was less severe when the matrix contained exotic tree plantations, even when plantations occupied as little as 10% of the matrix. In addition, Boesing et al. (2018b) found the extinction threshold for the bird community detected in fragments surrounded by coffee plantations is at 19% forest cover compared with 35% when the matrix is pasture.

Overall, our results support the view that a shared border with *Eucalyptus* plantations is less detrimental to forest bird communities than a shared border with pasture. *Eucalyptus* plantations are likely able to buffer edge effects and reduce the infiltration of disturbance-tolerant species into patch edges and interiors when compared with cattle pasture. They also provide higher community integrity for a given level of native forest cover. From the

perspective of conservation, plantations therefore offer a management solution to reduce the impact of fragmentation on biodiversity without requiring large increases in the area of native forest. However, these potential benefits carry several caveats.

One of the important characteristics of plantations is their greater structural complexity compared with pastures. They are often structurally similar to native forest (Prevedello & Vieira 2010), but variation in structural complexity of plantations is also important because those with higher complexity (e.g., multiple vegetation strata) generally contain higher bird species richness and abundance (Nájera & Simonetti 2010; Millan et al. 2015). The plantation sites surveyed in this study often retained understory foliage, a practice that is not universal, but which matches the management practices in other studies that concluded that plantations have some utility for biodiversity (e.g., Barlow et al. 2007). Thus, it is likely that the detrimental impacts of plantations on native biodiversity are much stronger when plantation understory is cleared. The cyclic nature of plantations is another important consideration. Although plantations of adult trees may buffer edge effects, it is unlikely that young sapling trees will provide the same benefit, especially given the large reduction in structural complexity after harvest. Future research should focus on extending the temporal span of data collection so that the effects of plantations can be assessed throughout the harvesting cycle. There is also scope to investigate the impacts of management, for example if certain management techniques or harvesting rotations provide a higher conservation benefit than others (Moreira et al. 2013).

In the wider context of expanding plantations worldwide and especially in the case of *Eucalyptus* in Brazil, the benefits may be more varied and depend on the land use plantations are replacing (Brockhoff et al. 2013). Comparisons of plantations and pasturelands are highly contingent on the taxonomic focus and landscape specifics (Felton et al. 2010). Conversion of agricultural land to plantations has also received ample attention due to the other environmental benefits they may bring, such

as climate-change mitigation through carbon storage and sequestration (Jackson & Schlesinger 2004). However, other effects, such as changes in soil organic carbon, are less clear (Fialho & Zinn 2014).

Manipulation of the matrix can moderate species responses to habitat loss and fragmentation, and the ongoing conversion of pasturelands to plantation may yet yield benefits for bird biodiversity via improved connectivity among populations and the reduction of edge effects. As with secondary forests (Mayhew et al. 2019), the conservation value of plantations largely depends on the maintenance and extent of embedded native forest patches. Nonetheless, although intensive research has been conducted on the effects of management on biodiversity within plantations themselves (Nájera & Simonetti 2010; Millan et al. 2015), little is known about how plantation management and harvesting practices affect adjacent native forests. We recommend that future research investigates how management practices mediate effects of plantations on biodiversity in adjacent forest fragments because doing so may provide a key insight into practical conservation solutions for human modified tropical forest landscapes.

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Supporting Information

Additional methods (Appendix S1), comparison of the different forest cover radii (Appendix S2), and information on species occurrence in the different land use types (Appendix S3) are available online. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

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