

Area and edge effects are mediated by adjacent land use in fragmented tropical forest

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. Our findings revealed that both area and edge effects are more pronounced in forest patches bordering pasture matrix, while patches bordering *Eucalyptus* plantation maintained compositionally similar bird communities between the edge and the interior, in addition to exhibiting reduced effects of patch size. These results suggest that 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.

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 (Brocknerhoff 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 (Prugh et al. 2008) in a permeable matrix because of rescue effects or weaker edge effects? Answering these questions is crucial if we are to manage matrix land uses to reduce biodiversity loss (Driscoll et al. 2013).

With the growing recognition that some matrix types are more permeable and hospitable to some species than others (Brocknerhoff 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 was highly permeable (e.g. semi-natural habitats), while area and isolation were strong predictors of biodiversity in more hostile types of matrix. This is logical as 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. On the other hand, Prevedello and Vieira (2010) argued 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 matrix habitats approximate to the physiognomy of native habitats, reducing the impact of biotic and abiotic gradients at edges (Banks-Leite & Ewers 2009). For example, Amazonian tree mortality appears to be higher at edges bordering cattle pastures than those bordering secondary forests (Mesquita et al. 1999). Shade coffee plantations have also been found to dampen edge effects in tropical montane forest when compared to corn plantations (Santos-Barrera & Urbina-Cardona 2011). Other effects such as spill-over of matrix species into forest patches may create an influx of disturbance-tolerant species, with 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 homogenisation, involving the proliferation of generalist species and the decline or local extinction 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 four temporal replicates spanning seasonal variation, stratifying 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 analysed 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 with forest species being more commonly associated with fragments bordered by plantation forest. We also expected that a *Eucalyptus* plantation matrix, which bears higher structural similarity to Atlantic Forest, would show reduced edge and area effects when compared to an open pasture 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 is composed of sub-montane 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% with mean total forest cover being 40% and altitude varying between 600 and 1130 m (Appendix S1). Continuous forest sites were located within the largest remaining well-connected forest patch network comprising over one million ha (Ribeiro et al. 2009). We surveyed a total of 49 sites, including 15 near continuous reference sites and 34 fragmented forest sites. At each site, we sampled three transects with three point count stations each. Points within transects were approximately 75 m apart (where terrain and landscape configuration allowed) and the three 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 three 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 six different transect types surveyed across the fragmented forest sites, representing the six 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 conducted in areas of the patch that bordered the chosen matrix type. Surveyed fragments were selected to sample the full range of fragment area and connectivity found in the study region and were part of the *name removed for review* project (Appendix S1). The 15 reference sites were chosen to encompass one land use each, and we thus sampled five large areas of forest (CF), five large areas of cattle pasture (CP), and five large *Eucalyptus* plantations (CE). Continuous sites were designed with the same grid configuration as explained above, but with all transects conducted in the same land use type.

Avifaunal surveys

Bird surveys were conducted between December 2015 and February 2017 using point counts. Each count was 15 minutes in duration, during which we recorded all birds identified within a 25 m radius of the point, with four temporal replicates (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 the species was detected at a site, a measure that ranged between 0 and 12, thus providing a proxy for abundance (Solar et al. 2015). This minimised 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 using 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 conducted on the dissimilarity matrix. For fragmented sites we used community integrity rather than community composition to allow comparison to continuous forest. Community integrity used the raw distances extracted from the Bray-Curtis dissimilarity matrix calculating 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

Forest cover (%) was measured for each site using radii of 600 m, 800 m, 1,500 m, and 3,000 m from the centre of the site and for the 10,000-ha landscape (5 by 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 modelled together due to high levels of collinearity (Appendix S2). We also measured size and proximity index (800 m search distance) for focal fragments with both being \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 ESRI ArcGIS v.10. (Environmental Systems Research Institute, Redlands, California, USA) and Fragstats v.4. (McGarigal et al. 2012). For more details see Appendix S1.

Data analysis

All analysis was conducted in R v.3.3.2 (R Core Team 2016). We examined the effect of transect type (the combination of position and matrix type) using mixed effect modelling in

lme4 (Schielzeth & Nakagawa 2013) with site as a random factor to account for spatial dependency between transects in the same landscape. For species richness, a generalised linear mixed model (Poisson error structure checked for over-dispersion (Appendix S1)) was used and community composition metrics used linear mixed models. The influence of transect type on the avifaunal community was only investigated for the 34 fragmented sites; with the position and matrix land use combination (e.g. Interior-Pasture) as a single fixed effect, conducting 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 one land use type surveyed at each of these sites, however, we analysed them separately to provide a baseline for comparison. The data was then partitioned into interior, edge and matrix to investigate the effects of landscape metrics using linear and generalised linear models. Landscape metric models were selected based on AICc (due to small sample size) or F tests in the case of overdispersion (Appendix S1). Due to small sample sizes, we were unable to fit all the interactions. We did however fit the interactions between matrix type and the other metrics as investigating the effect of matrix type is a major aim of this study. Plots from models containing multiple explanatory variables used partial residuals (Appendix S1).

We conducted analyses on the whole bird community as well as two subsets – termed 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 two groups we were able to reveal trends that are concealed by turnover when examining the community as a whole; for example, 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 categorisation is 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/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-zero 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 favoured this approach because previous classifications of species sensitivity or habitat use, such as Parker III et al. (1996), are not transparent regarding where data were obtained, the level of uncertainty associated with each classification, and do not separate between different stressors (e.g. a species may be sensitive to hunting but insensitive to the land use changes we investigated here)(Alexandrino et al. 2016). Our approach thus allowed us to identify the “winners” (i.e. disturbance-tolerant) and “losers” (i.e. forest-associated species) in our dataset. 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 III et al. (1996) – with taxonomic disagreement resolved following the checklist produced by BirdLife International (2017). *Estrilda astrild* was excluded from this comparison due to a lack of habitat usage information.

Site-scale analyses were conducted by aggregating the three transects at each site. This produced a frequency of occurrence for each species potentially ranging between 0 and 36 from which community integrity was calculated. Species richness and community integrity were modelled against percentage forest cover for the 10,000-ha landscape and matrix type surveyed using generalised 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. Using the weighted averages approach, the community was split

into 177 forest species and 90 disturbance adapted species. When compared to habitat usage information in Parker III et al. (1996), 72% of species that we assigned to the forest species group were found to be restricted to forest habitats based on the published information, compared with 2% of the species in disturbance-tolerant group. Although we do 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 three transect types were all significantly different from each other (Fig. 2b; CE – CF: $z = -14.24$, $p < 0.01$; CP – CF: $z = -26.07$, $p < 0.01$; CP – CE: $z = -11.83$, $p < 0.01$). 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 (Figure 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, while forest patches bordering *Eucalyptus* presented similar levels of integrity at edges and interiors (Fig. 2f), mirroring results

for continuous sites, where *Eucalyptus* transects had higher integrity than pasture transects (Fig. 2f).

The edge effects observed in patches bordering pastures was 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 the bordering matrix (Fig. 2g; $z = -5.31$, $p < 0.01$), but the richness of disturbance-tolerant species in patches bordering pasture was lower in forest interiors when compared to 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

Interior and edge transects showed a similar mediation of matrix type on community integrity responses to landscape configuration and habitat amount (Interior: $\text{adj-}R^2 = 0.57$; Edge: $\text{adj-}R^2 = 0.55$). In both cases, integrity was only positively affected by patch size in fragments bordering pasture (Fig. 3a and 4a; Interior: $t = 2.12$, $p = 0.04$; Edge: $t = 2.87$, $p < 0.01$). Landscape forest cover (10,000-ha) on the other hand 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 while the slope of this relationship was not affected by matrix type, the intercept was always higher in *Eucalyptus* bordering patches (Fig. 3b and 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 transects total species richness was found to decrease with forest cover 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 (Fig. 3c; $t = -2.14$, $p = 0.03$) and edge (Fig. 4c; $t = -2.29$, $p = 0.03$) transects was negatively correlated with patch size only in pasture

bordering patches. Richness of disturbance-tolerant species found in interior transects reduced with forest cover; the intercept was different between the matrix types, but the slope was the same ($z = -2.53$, $p = 0.01$).

Matrix

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

Forest species richness was positively correlated with forest patch area (Fig. 4f, $t = 2.57$, $p = 0.02$) 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, with pasture matrices having higher richness ($t = 9.25$, $p < 0.01$).

Site scale

At the site scale (Interior, edge and matrix transects combined; Fig. 5) community integrity was found to increase with forest cover ($t = 3.06$, $p < 0.01$) with fragments bordering pasture having lower integrity than those bordering plantations ($t = -3.10$, $p < 0.01$), yielding an adjusted- R^2 of 0.42. Species richness was only affected by matrix type with pasture bordering fragments having more species ($z = 5.90$, $p < 0.01$).

Discussion

We found that *Eucalyptus* plantation matrices were more beneficial for bird communities in the Atlantic Forest when compared to pasture matrices. Although pastures had higher species richness than *Eucalyptus* plantations, forest fragments bordering *Eucalyptus* have higher community similarity to continuous forest and weaker edge effects (Fig. 2, 3 and 4). We also show that the strengthening of edge and area effects in patches bordering pastures was mostly due to the increase in disturbance-specialists, rather than the loss of forest species.

Nonetheless, our findings suggest that spill-over 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, on the other hand, not only provide a habitat for different species (Moura et al. 2013; Lees et al. 2015), but also allow them to spill-over into native forest, as shown by the increase in the richness of disturbance-tolerant species in fragments (Fig. 2h and 3c). We also found evidence of reverse spill-over effects from the forest into the surrounding pasture (Tscharntke et al. 2012) in contrast to Boesing et al. (2018a) who found minimal spill-over of birds into cattle pasture in the Atlantic Forest. Our results suggest that community integrity in matrix transects increases with forest patch area (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 populations of forest-dependent bird species (Mayhew et al. 2019), thereby enriching the surrounding matrix via a spill-over of ecosystem services, such as pollination, pest control and seed dispersal. Spill-over of services has been widely documented for a range of taxa (Tscharntke et al. 2012) including insect and bird pollinators (Renjifo 2001; Ricketts et al. 2008) and bird spill-over 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 spill-over from large forest patches into the matrix may benefit crop productivity while also increasing 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

291 observed area effects on biodiversity in this fragmented landscape (Ewers et al. 2007; Fletcher
292 et al. 2007; Banks-Leite et al. 2010). Our results provide further corroboration of this
293 hypothesis as we only detected significant edge effects in patches bordering pasture matrices,
294 where patch area also had a significant influence on the interior bird community. Conversely,
295 for fragments with a plantation matrix, we found neither significant edge effects, nor significant
296 area effects.

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

308 Overall, this study supports the view that a shared border with *Eucalyptus* plantations
309 is less detrimental to forest bird communities than a shared border with pasture. *Eucalyptus*
310 plantations are likely able to buffer edge effects and reduce the infiltration of disturbance-
311 tolerant species into patch edges and interiors when compared to cattle pasture. They also
312 provide higher community integrity for a given level of native forest cover. From the
313 perspective of conservation, plantations therefore offer a management solution to reduce the
314 impact of fragmentation on biodiversity without requiring large increases in the area of native
315 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, as 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: while plantations consisting 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 harvesting. 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 have been found to be 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, as doing so may provide a key insight into practical conservation solutions for human modified tropical forest landscapes.

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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Figure 1 – (a): Map of sample site locations. Forest cover (all forest types) is shown in gray and represents areas with > 50% canopy closure in 2000 (Appendix S1: 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/>). (b) and (c): composite forest cover map and sampling points within transects for a fragmented site (b) and a continuous site (c), forest is shown in gray and non-forest in white. Point counts formed a regular (where terrain, patch size and edge shape allowed) nine-point grid spaced by 75m. Three points were situated in each position – interior, edge and matrix.

Figure 2 – Richness and composition measures for bird communities found at each site partitioned by transect type for continuous forest (CF), continuous plantation (CE), continuous pasture (CP), fragment interiors (I), fragments edges (E) and the surrounding matrix (M). Results are shown for control landscapes (top) and fragments (below) as well as for all species, forest species and disturbance adapted species. Letter labels show transect type groupings based on post-hoc significance tests. Fragments with pasture matrices are represented in white and plantation matrices in light gray. Continuous forest is indicated in dark gray.

Figure 3 – Partial residual values for community integrity and disturbance-tolerant species richness (DSR) against patch size in ha (a and c) and percentage forest cover (b and d) for interior transects. Plantation matrix fragments are shown in black, pasture in gray.

Figure 4 – Partial residual values for community integrity, species richness, disturbance-tolerant species richness (DSR) and forest species richness (FSR) against patch size in ha (b and d) and percentage forest cover (a, c, e and f) for edge (a – d) and matrix (e - f) transects. Plantation matrix fragments are shown in black, pasture in gray. d shows only a single line as matrix type was not found to be influential in this model.

Figure 5— Community integrity against forest cover percentage (a) and species richness (b) compared between the two matrix types - *Eucalyptus* plantation (Eu) and pasture (Pa). Gray is used for pasture matrix fragments with black representing plantation.

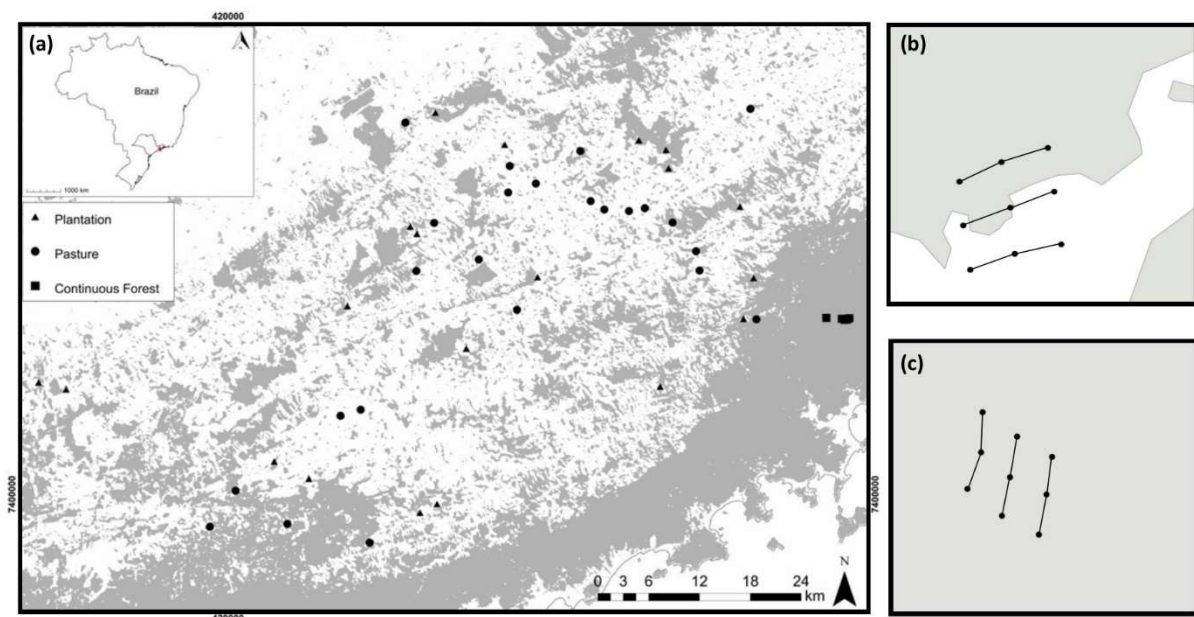


Figure 1 – (A): Map of sample site locations. Forest cover (all forest types) is shown in gray and represents areas with > 50% canopy closure in 2000 (Appendix S1: Hansen et al. (2013)/UMD/Google/USGS/NASA - Licensed under a Creative Commons Attribution 4.0 International License - <https://creativecommons.org/licenses/by/4.0/>). (B) and (C): composite forest cover map and sampling points within transects for a fragmented site (B) and a continuous site (C), forest is shown in gray and non-forest in white. Point counts formed a regular (where terrain, patch size and edge shape allowed) nine-point grid spaced by 75m. Three points were situated in each position – interior, edge and matrix.

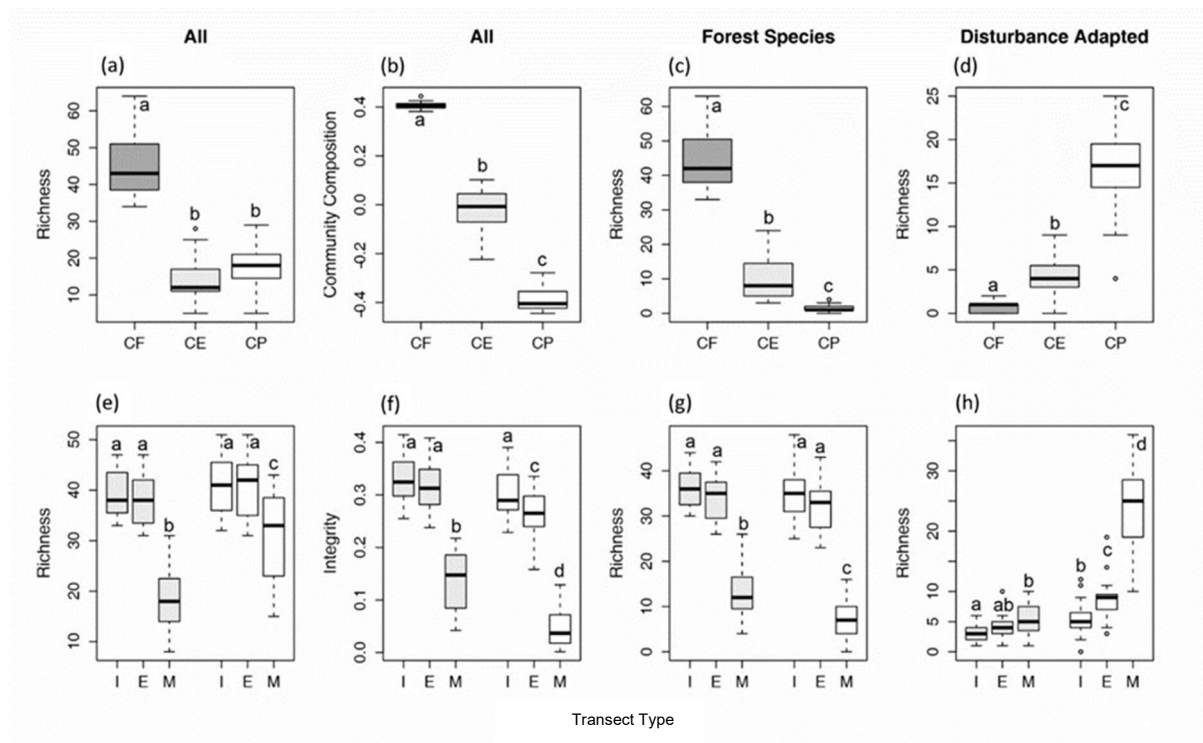


Figure 2 – Richness and composition measures for bird communities found at each site partitioned by transect type for control forest (CF), control plantation (CE), control pasture (CP), fragment interiors (I), fragments edges (E) and the surrounding matrix (M). Results are shown for control landscapes (top) and fragments (below) as well as for all species, forest species and disturbance adapted species. Letter labels show transect type groupings based on post-hoc significance tests. Fragments with pasture matrices are represented in white and plantation matrices in light gray. Control forest is indicated in dark gray.

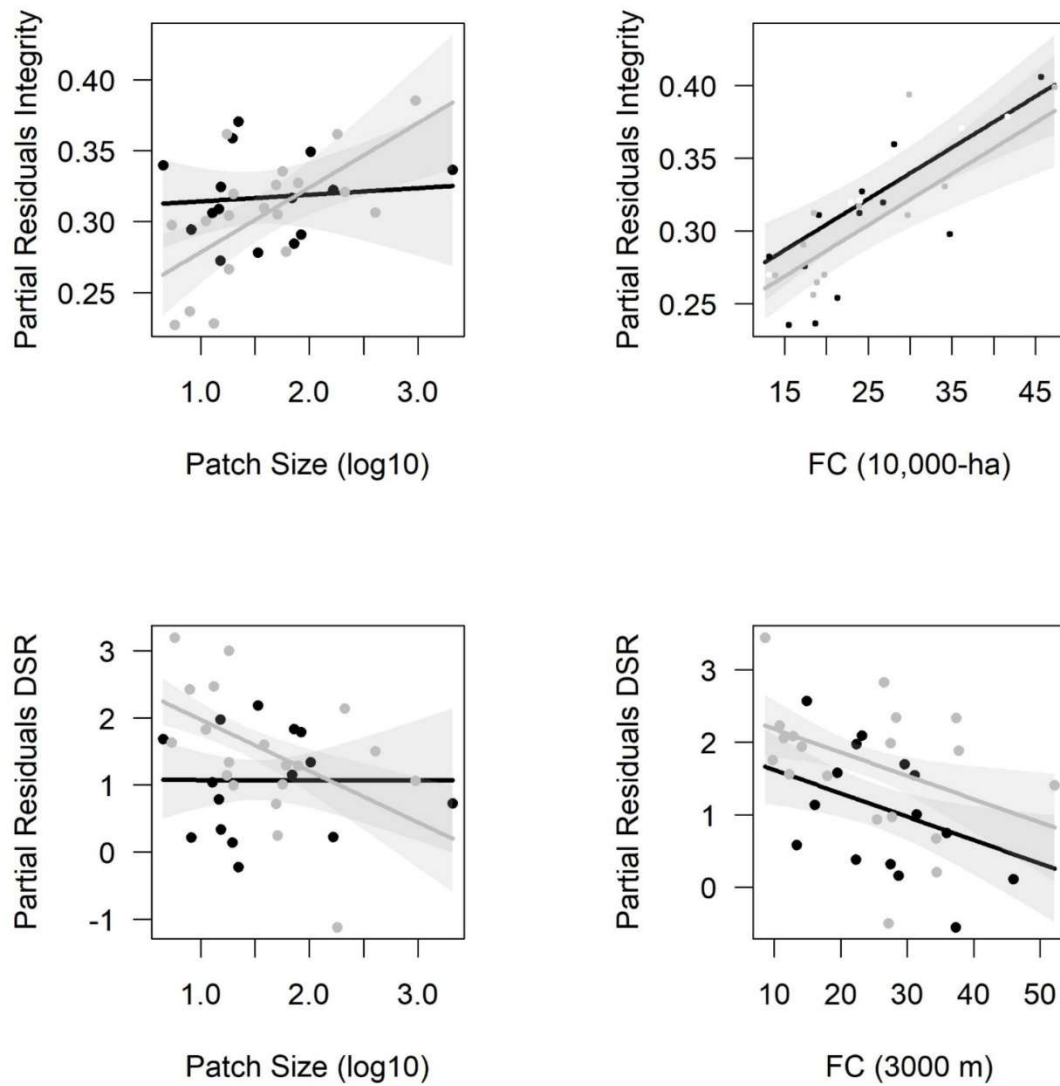
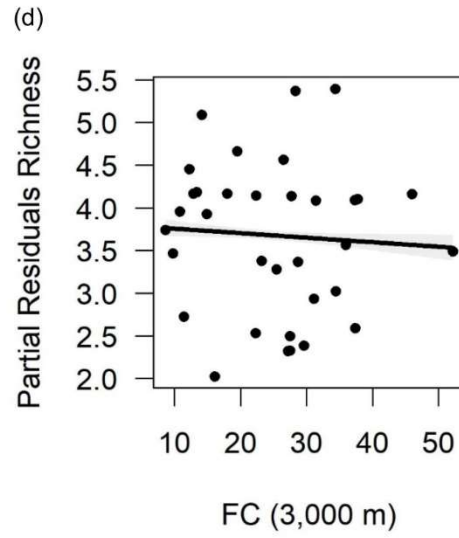
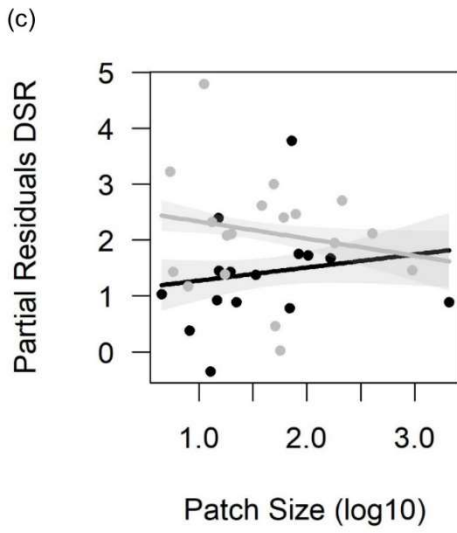
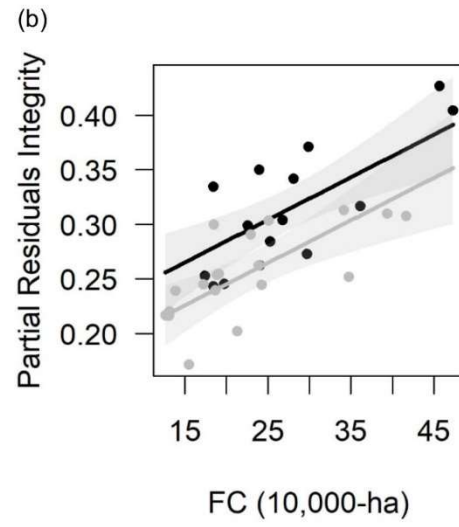
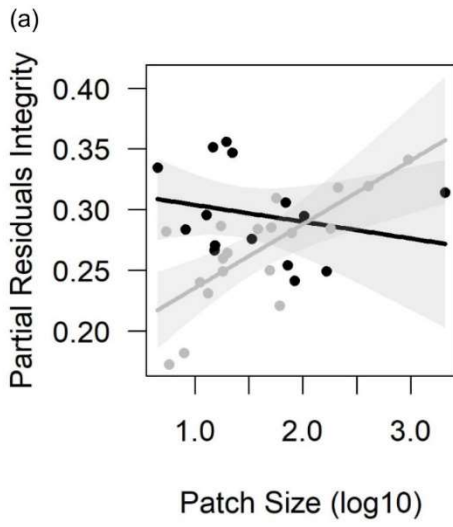


Figure 3 – Partial residual values for community integrity and disturbance-tolerant species richness (DSR) against patch size in ha (a and c) and percentage forest cover (b and d) for interior transects. Plantation matrix fragments are shown in black, pasture in gray.

Fragment Edge



Matrix

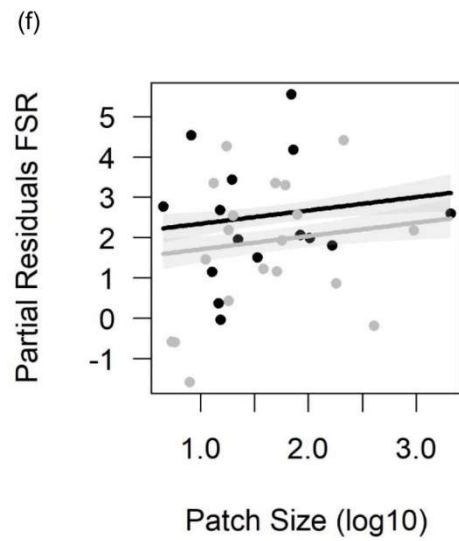
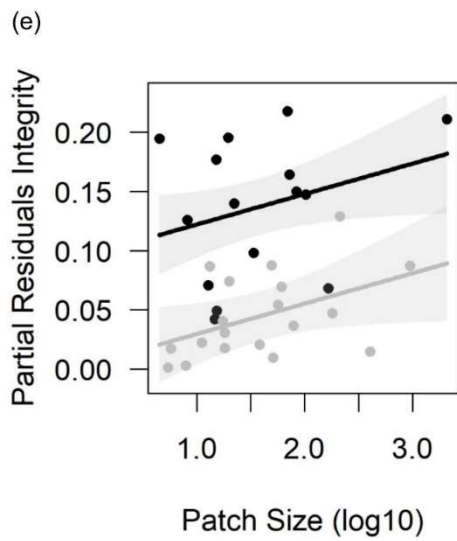


Figure 4 – Partial residual values for community integrity, species richness, disturbance tolerant species richness (DSR) and forest species richness (FSR) against patch size in ha (b and d) and percentage forest cover (a, c, e and f) for edge (a – d) and matrix (e - f) transects. Plantation matrix fragments are shown in black, pasture in gray. d shows only a single line as matrix type was not found to be influential in this model.

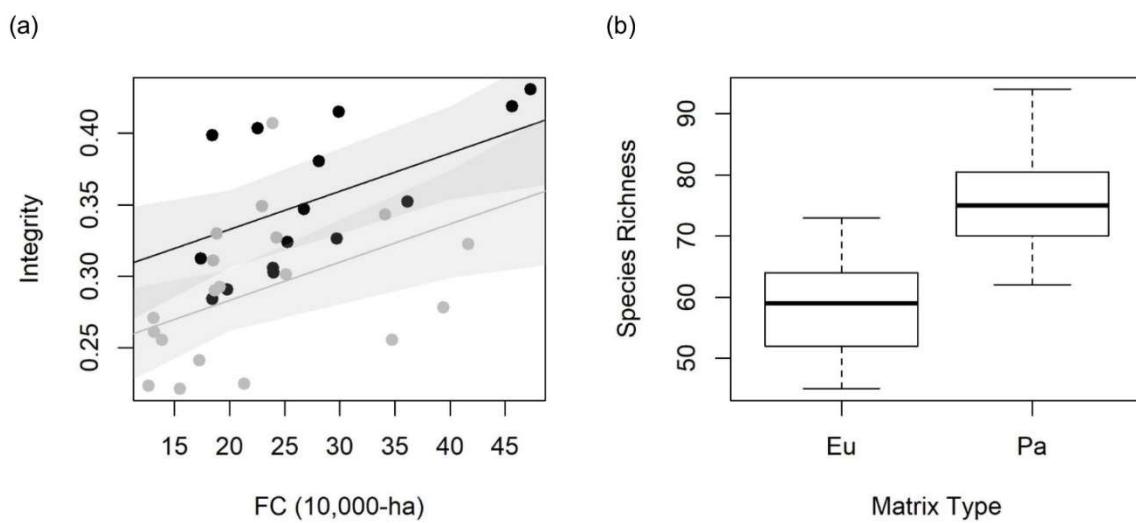


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