

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

2

3    **Abstract**

4    Habitat loss, fragmentation and degradation have pervasive detrimental effects on tropical  
5    forest biodiversity, but the role of the surrounding land use (i.e. matrix) in determining the  
6    severity of these impacts remains poorly understood. We surveyed bird species across an  
7    interior-edge-matrix gradient to assess the effects of matrix type on biodiversity at 49 different  
8    sites with varying levels of landscape fragmentation in the Brazilian Atlantic Forest – a highly  
9    threatened biodiversity hotspot. Our findings revealed that both area and edge effects are  
10   more pronounced in forest patches bordering pasture matrix, while patches bordering  
11   *Eucalyptus* plantation maintained compositionally similar bird communities between the edge  
12   and the interior, in addition to exhibiting reduced effects of patch size. These results suggest  
13   that the type of matrix in which forest fragments are situated can explain a substantial amount  
14   of the widely-reported variability in biodiversity responses to forest loss and fragmentation.

15

16    **Introduction**

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

26       With the growing recognition that some matrix types are more permeable and  
27   hospitable to some species than others (Brockerhoff et al. 2008; Felton et al. 2010), recent

28 research has increasingly focused on the interplay between matrix type and landscape  
29 composition (Driscoll et al. 2013). However, the extent to which matrix type can modulate  
30 biodiversity responses to area, edge and isolation remains controversial (Prugh et al. 2008;  
31 Prevedello & Vieira 2010; Watling et al. 2011). Prugh et al. (2008) found isolation and area to  
32 be poor predictors of species occupancy when matrix type was highly permeable (e.g. semi-  
33 natural habitats), while area and isolation were strong predictors of biodiversity in more hostile  
34 types of matrix. This is logical as any increase in structural similarity between the matrix and  
35 habitat patches can increase population connectivity among patches (Renjifo 2001;  
36 Prevedello & Vieira 2010), reducing local extinction by means of rescue effects. On the other  
37 hand, Prevedello and Vieira (2010) argued that these matrix effects are smaller and more  
38 species-specific than those of area and isolation.

39 The capacity of the matrix to buffer edge effects is expected to increase if matrix  
40 habitats approximate to the physiognomy of native habitats, reducing the impact of biotic and  
41 abiotic gradients at edges (Banks-Leite & Ewers 2009). For example, Amazonian tree mortality  
42 appears to be higher at edges bordering cattle pastures than those bordering secondary  
43 forests (Mesquita et al. 1999). Shade coffee plantations have also been found to dampen edge  
44 effects in tropical montane forest when compared to corn plantations (Santos-Barrera &  
45 Urbina-Cardona 2011). Other effects such as spill-over of matrix species into forest patches  
46 may create an influx of disturbance-tolerant species, with concomitant high species turnover  
47 (Banks-Leite et al. 2012, 2014) and changes to ecosystem function (De Coster et al. 2015).  
48 Changes in species composition can be problematic when they involve large-scale biotic  
49 homogenisation, involving the proliferation of generalist species and the decline or local  
50 extinction of many specialists (Solar et al. 2015). Given the likely complexity of the underlying  
51 mechanisms governing these changes in community assembly, a rigorous landscape-based  
52 approach (Fahrig 2003) is required to determine the propensity of the matrix to influence the  
53 effects of habitat loss and landscape configuration (i.e. isolation, patch area and edge effects).

54 To examine the ability of the matrix to mitigate the detrimental effects of landscape  
55 configuration on biodiversity, we considered bird communities in the highly fragmented and

56 biodiverse Brazilian Atlantic Forest (Myers et al. 2000; Ribeiro et al. 2009). To obtain a full  
57 picture of how bird communities change, we collected data with four temporal replicates  
58 spanning seasonal variation, stratifying sampling across fragment interiors, fragment edges  
59 and the surrounding matrix. Within this framework we examined both a habitat fragmentation  
60 gradient and different matrix types. To better understand how community composition  
61 changes, we analysed species richness, community integrity (compositional similarity to  
62 continuous forest) and richness of both forest-dependent and disturbance-tolerant species.  
63 Disturbance-tolerant species richness was expected to be higher in fragments surrounded by  
64 the open pasture matrix with forest species being more commonly associated with fragments  
65 bordered by plantation forest. We also expected that a *Eucalyptus* plantation matrix, which  
66 bears higher structural similarity to Atlantic Forest, would show reduced edge and area effects  
67 when compared to an open pasture matrix.

68

## 69 **Methods**

### 70 **Study Design**

71 The study area was located in the Vale do Paraíba and Serra do Mar regions in the state of  
72 São Paulo, Brazil. The area is composed of sub-montane forest of varying age surrounded by  
73 a range of matrix types. The mean native forest cover at the 10,000-ha scale across all sites  
74 was 30% with mean total forest cover being 40% and altitude varying between 600 and 1130  
75 m (Appendix S1). Continuous forest sites were located within the largest remaining well-  
76 connected forest patch network comprising over one million ha (Ribeiro et al. 2009). We  
77 surveyed a total of 49 sites, including 15 near continuous reference sites and 34 fragmented  
78 forest sites. At each site, we sampled three transects with three point count stations each.  
79 Points within transects were approximately 75 m apart (where terrain and landscape  
80 configuration allowed) and the three transects were also spaced by 75 m (Fig. 1). This design  
81 was chosen to ensure that even small forest fragments could be surveyed with equal effort. In  
82 fragmented forest sites, a single transect was conducted in each of three positions relative to

83 the focal forest patch; patch interior, patch edge and in the matrix bordering the focal patch  
84 (Fig. 1).

85 Fifteen patches were bordered by *Eucalyptus* plantation and 19 bordered pasture. The  
86 median patch size was 28 ha. There were six different transect types surveyed across the  
87 fragmented forest sites, representing the six unique combinations of position (interior, edge or  
88 matrix) and matrix land use (*Eucalyptus* plantation or cattle pasture). Due to availability and  
89 accessibility, as well as the mosaic nature of the landscape, patches were not surrounded by  
90 a uniform matrix; however, all transects were conducted in areas of the patch that bordered  
91 the chosen matrix type. Surveyed fragments were selected to sample the full range of  
92 fragment area and connectivity found in the study region and were part of the \*name removed  
93 for review\* project (Appendix S1). The 15 reference sites were chosen to encompass one land  
94 use each, and we thus sampled five large areas of forest (CF), five large areas of cattle pasture  
95 (CP), and five large *Eucalyptus* plantations (CE). Continuous sites were designed with the  
96 same grid configuration as explained above, but with all transects conducted in the same land  
97 use type.

98 Avifaunal surveys

99 Bird surveys were conducted between December 2015 and February 2017 using point counts.  
100 Each count was 15 minutes in duration, during which we recorded all birds identified within a  
101 25 m radius of the point, with four temporal replicates (equally split between wet and dry  
102 seasons) per point. The spatial and temporal replicate points for each of the 147 transects  
103 were then aggregated, providing a sampling effort of 12 point counts per transect. Species  
104 richness was calculated as the total number of species recorded at each transect. We also  
105 calculated a frequency of occurrence (i.e. an encounter rate) for each species in each transect.  
106 This was done by summing the number of times the species was detected at a site, a measure  
107 that ranged between 0 and 12, thus providing a proxy for abundance (Solar et al. 2015). This  
108 minimised the influence of single detections, which was especially useful for the matrix surveys

109 where some species may be transients infrequently recorded passing between forest patches.  
110 From the frequency of occurrence, we calculated community composition based on a Bray-  
111 Curtis dissimilarity matrix using the R package vegan (Oksanen et al. 2016). Values were then  
112 assigned based on the scores from the first axis of a Principal Coordinate Analysis conducted  
113 on the dissimilarity matrix. For fragmented sites we used community integrity rather than  
114 community composition to allow comparison to continuous forest. Community integrity used  
115 the raw distances extracted from the Bray-Curtis dissimilarity matrix calculating the mean  
116 distance between each transect and the continuous forest transects. This Bray-Curtis distance  
117 was then subtracted from 1 to provide a scale where 1 indicates a transect that highly  
118 resembles control forest and 0 indicates transects extremely dissimilar from continuous forest  
119 hence community integrity can be seen as a measure of similarity to the reference continuous  
120 forest (for a similar approach see De Coster et al. 2015).

121 Landscape metrics

122 Forest cover (%) was measured for each site using radii of 600 m, 800 m, 1,500 m, and 3,000  
123 m from the centre of the site and for the 10,000-ha landscape (5 by 5 km , hereafter: landscape  
124 forest cover). A single forest cover scale was chosen per model based on model fit because  
125 multiple scales could not be modelled together due to high levels of collinearity (Appendix S2).  
126 We also measured size and proximity index (800 m search distance) for focal fragments with  
127 both being  $\log_{10}$  transformed for analysis. Proximity index takes into account the area of  
128 surrounding patches and weights this by distance (Gustafson & Parker 1994). All  
129 measurements were conducted using ESRI ArcGIS v.10. (Environmental Systems Research  
130 Institute, Redlands, California, USA) and Fragstats v.4. (McGarigal et al. 2012). For more  
131 details see Appendix S1.

132 Data analysis

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

135 lme4 (Scheiplzeth & Nakagawa 2013) with site as a random factor to account for spatial  
136 dependency between transects in the same landscape. For species richness, a generalised  
137 linear mixed model (Poisson error structure checked for over-dispersion (Appendix S1)) was  
138 used and community composition metrics used linear mixed models. The influence of transect  
139 type on the avifaunal community was only investigated for the 34 fragmented sites; with the  
140 position and matrix land use combination (e.g. Interior-Pasture) as a single fixed effect,  
141 conducting post-hoc contrasts to assess significance. Although we do not include p-values  
142 from our main results, we provide them with the mixed effects models for factor level contrasts  
143 to aid in interpretation. The continuous sites were not included in the models because there  
144 was only one land use type surveyed at each of these sites, however, we analysed them  
145 separately to provide a baseline for comparison. The data was then partitioned into interior,  
146 edge and matrix to investigate the effects of landscape metrics using linear and generalised  
147 linear models. Landscape metric models were selected based on AICc (due to small sample  
148 size) or F tests in the case of overdispersion (Appendix S1). Due to small sample sizes, we  
149 were unable to fit all the interactions. We did however fit the interactions between matrix type  
150 and the other metrics as investigating the effect of matrix type is a major aim of this study.  
151 Plots from models containing multiple explanatory variables used partial residuals (Appendix  
152 S1).

153 We conducted analyses on the whole bird community as well as two subsets – termed  
154 forest species and disturbance-tolerant species owing to the high species turnover observed  
155 in Atlantic Forest bird communities (Banks-Leite et al. 2012, 2014). By dividing the community  
156 into two groups we were able to reveal trends that are concealed by turnover when examining  
157 the community as a whole; for example, whether compositional changes are governed by loss  
158 of forest species or gain of disturbance-tolerant species. These groups represented those  
159 species associated with the fragmented areas and those associated with the intact areas.  
160 Thus, this allowed us to individually consider those species responding negatively to  
161 disturbance and those that respond in a positive manner, but our categorisation is not intended

162 as a definitive classification. These distinctions were created using a species ranking system  
163 based on weighted averages ordination (Banks-Leite et al. 2014). Species presence/absence  
164 was first weighted by site scores taken from the first axis of a PCoA based on Bray-Curtis  
165 dissimilarity. The mean is then calculated from all non-zero weights. The division was made  
166 relative to the mean of the site scores (the value for a species that occurs at all sample  
167 locations).

168 Our method for partitioning the community into groups is a post-hoc approach based  
169 on observed species turnover across sites. We favoured this approach because previous  
170 classifications of species sensitivity or habitat use, such as Parker III et al. (1996), are not  
171 transparent regarding where data were obtained, the level of uncertainty associated with each  
172 classification, and do not separate between different stressors (e.g. a species may be sensitive  
173 to hunting but insensitive to the land use changes we investigated here)(Alexandrino et al.  
174 2016). Our approach thus allowed us to identify the “winners” (i.e. disturbance-tolerant) and  
175 “losers” (i.e. forest-associated species) in our dataset. We then used information on forest  
176 habitat restriction to better understand how our approach of community partitioning was  
177 related to the previous classification of Parker III et al. (1996) – with taxonomic disagreement  
178 resolved following the checklist produced by BirdLife International (2017). *Estrilda astrild* was  
179 excluded from this comparison due to a lack of habitat usage information.

180 Site-scale analyses were conducted by aggregating the three transects at each site.  
181 This produced a frequency of occurrence for each species potentially ranging between 0 and  
182 36 from which community integrity was calculated. Species richness and community integrity  
183 were modelled against percentage forest cover for the 10,000-ha landscape and matrix type  
184 surveyed using generalised linear and linear models, respectively.

185 **Results**

186 Overall we detected 267 species across the 49 landscapes. The first PCoA axis explained  
187 27.6% of the total variance. Using the weighted averages approach, the community was split

188 into 177 forest species and 90 disturbance adapted species. When compared to habitat usage  
189 information in Parker III et al. (1996), 72% of species that we assigned to the forest species  
190 group were found to be restricted to forest habitats based on the published information,  
191 compared with 2% of the species in disturbance-tolerant group. Although we do not examine  
192 this further, these comparisons demonstrate that our community split tallies well with published  
193 classifications.

194 Continuous sites

195 Analyses of the whole community revealed that both continuous plantation ( $z = -5.56$ ,  $p < 0.01$ )  
196 and continuous pasture ( $z = -6.82$ ,  $p < 0.01$ ) did not differ significantly from one another but  
197 both showed lower species richness than continuous forest transects (Fig. 2a). However, the  
198 community composition of three transect types were all significantly different from each other  
199 (Fig. 2b; CE – CF:  $z = -14.24$ ,  $p < 0.01$ ; CP – CF:  $z = -26.07$ ,  $p < 0.01$ ; CP – CE:  $z = -11.83$ ,  $p$   
200  $< 0.01$ ). Changes in community composition were driven by a decrease in forest species  
201 richness in both types of matrix, together with an increase in disturbance-tolerant species (Fig.  
202 2c, d). All continuous blocks were significantly different from each other in forest species (CE  
203 – CF:  $z = -7.79$ ,  $p < 0.01$ ; CP – CF:  $z = -12.38$ ,  $p < 0.01$ ; CP – CE:  $z = -6.63$ ,  $p < 0.01$ ) and  
204 disturbance-tolerant species richness (CE – CF:  $z = 4.94$ ,  $p < 0.01$ ; CP – CF:  $z = 9.21$ ,  $p <$   
205  $0.01$ ; CP – CE:  $z = 6.90$ ,  $p < 0.01$ ).

206 Fragmented forest sites

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

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

216 The edge effects observed in patches bordering pastures was mostly driven by an  
217 increase in disturbance-tolerant species rather than a reduction in forest species. The richness  
218 of forest species did not differ between edge and interior, regardless the bordering matrix (Fig.  
219 2g;  $z = -5.31$ ,  $p < 0.01$ ), but the richness of disturbance-tolerant species in patches bordering  
220 pasture was lower in forest interiors when compared to edges ( $z = -3.68$ ,  $p < 0.01$ ).  
221 Furthermore, the species richness of disturbance-tolerant species in the interior of patches  
222 bordering pasture was, on average, 1.9 times higher than fragment interiors bordering  
223 *Eucalyptus* ( $p = 0.02$ ), and similar to the number of species found in *Eucalyptus* matrix.

224 Landscape configuration

225 Interior and edge

226 Interior and edge transects showed a similar mediation of matrix type on community integrity  
227 responses to landscape configuration and habitat amount (Interior: adj- $R^2 = 0.57$ ; Edge: adj-  
228  $R^2 = 0.55$ ). In both cases, integrity was only positively affected by patch size in fragments  
229 bordering pasture (Fig. 3a and 4a; Interior:  $t = 2.12$ ,  $p = 0.04$ ; Edge:  $t = 2.87$ ,  $p < 0.01$ ).  
230 Landscape forest cover (10,000-ha) on the other hand positively influenced integrity both in  
231 pasture and *Eucalyptus* bordering fragments (Interior:  $t = 5.11$ ,  $p < 0.01$ ; Edge:  $t = 3.98$ ,  $p <$   
232 0.01), and while the slope of this relationship was not affected by matrix type, the intercept  
233 was always higher in *Eucalyptus* bordering patches (Fig. 3b and 4b). None of the landscape  
234 metrics (e.g. forest cover, patch size, proximity index) significantly correlated with species  
235 richness for interior transects whereas for edge transects total species richness was found to  
236 decrease with forest cover at the 3 km scale ( $z = -2.04$ ,  $p = 0.04$ ).

237 Forest species richness was not significantly affected by any landscape metric, but the  
238 richness of disturbance-tolerant species found at interior (Fig. 3c;  $t = -2.14$ ,  $p = 0.03$ ) and edge  
239 (Fig. 4c;  $t = -2.29$ ,  $p = 0.03$ ) transects was negatively correlated with patch size only in pasture

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

243 **Matrix**

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

248 Forest species richness was positively correlated with forest patch area (Fig. 4f,  $t =$   
249  $2.57$ ,  $p = 0.02$ ) and pasture matrices had lower forest species richness than plantation ( $t = -$   
250  $3.55$ ,  $p < 0.01$ ). Disturbance-tolerant species richness was only significantly affected by matrix  
251 type, with pasture matrices having higher richness ( $t = 9.25$ ,  $p < 0.01$ ).

252 **Site scale**

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

258 **Discussion**

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

265 Nonetheless, our findings suggest that spill-over of species can occur in both directions in  
266 fragmented tropical forests, from fragments to matrix and vice versa.

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

279 These results reinforce previous findings highlighting the value of extensive forest  
280 patches in providing source populations of forest-dependent bird species (Mayhew et al.  
281 2019), thereby enriching the surrounding matrix via a spill-over of ecosystem services, such  
282 as pollination, pest control and seed dispersal. Spill-over of services has been widely  
283 documented for a range of taxa (Tscharntke et al. 2012) including insect and bird pollinators  
284 (Renjifo 2001; Ricketts et al. 2008) and bird spill-over has been shown to be particularly  
285 important in coffee plantations (Boesing et al. 2018a), where birds control populations of pests  
286 (Johnson et al. 2010). Hence, species spill-over from large forest patches into the matrix may  
287 benefit crop productivity while also increasing seed dispersal of native trees which is key to  
288 natural reforestation and forest recovery (Bregman et al. 2016).

289 Edge effects are prominent in the Atlantic Forest bird community (Banks-Leite et al.  
290 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.

316 One of the important characteristics of plantations is their greater structural complexity  
317 compared with pastures. They are often structurally similar to native forest (Prevedello & Vieira  
318 2010), but variation in structural complexity of plantations is also important, as those with  
319 higher complexity (e.g. multiple vegetation strata) generally contain higher bird species  
320 richness and abundance (Nájera & Simonetti 2010; Millan et al. 2015). The plantation sites  
321 surveyed in this study often retained understory foliage, a practice that is not universal, but  
322 which matches the management practices in other studies that concluded that plantations  
323 have some utility for biodiversity (e.g. Barlow et al. 2007). Thus, it is likely that the detrimental  
324 impacts of plantations on native biodiversity are much stronger when plantation understory is  
325 cleared. The cyclic nature of plantations is another important consideration: while plantations  
326 consisting of adult trees may buffer edge effects, it is unlikely that young sapling trees will  
327 provide the same benefit, especially given the large reduction in structural complexity after  
328 harvesting. Future research should focus on extending the temporal span of data collection  
329 so that the effects of plantations can be assessed throughout the harvesting cycle. There is  
330 also scope to investigate the impacts of management, for example if certain management  
331 techniques or harvesting rotations provide a higher conservation benefit than others (Moreira  
332 et al. 2013).

333 In the wider context of expanding plantations worldwide and especially in the case of  
334 *Eucalyptus* in Brazil, the benefits may be more varied and depend on the land use plantations  
335 are replacing (Brokerhoff et al. 2013). Comparisons of plantations and pasturelands have  
336 been found to be highly contingent on the taxonomic focus and landscape specifics (Felton et  
337 al. 2010). Conversion of agricultural land to plantations has also received ample attention due  
338 to the other environmental benefits they may bring, such as climate change mitigation through  
339 carbon storage and sequestration (Jackson & Schlesinger 2004). However, other effects such  
340 as changes in soil organic carbon are less clear (Fialho & Zinn 2014).

341 Manipulation of the matrix can moderate species responses to habitat loss and  
342 fragmentation and the ongoing conversion of pasturelands to plantation may yet yield benefits

343 for bird biodiversity via improved connectivity among populations and the reduction of edge  
344 effects. As with secondary forests (Mayhew et al. 2019), the conservation value of plantations  
345 largely depends on the maintenance and extent of embedded native forest patches.  
346 Nonetheless, although intensive research has been conducted on the effects of management  
347 on biodiversity within plantations themselves (Nájera & Simonetti 2010; Millan et al. 2015),  
348 little is known about how plantation management and harvesting practices affect adjacent  
349 native forests. We recommend that future research investigates how management practices  
350 mediate effects of plantations on biodiversity in adjacent forest fragments, as doing so may  
351 provide a key insight into practical conservation solutions for human modified tropical forest  
352 landscapes.

353 **Supporting Information**

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

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509     **Figure 1 –**(a): Map of sample site locations. Forest cover (all forest types) is shown in gray  
510     and represents areas with > 50% canopy closure in 2000 (Appendix S1: Hansen et al.  
511     (2013)/UMD/Google/USGS/NASA - Licensed under a Creative Commons Attribution 4.0  
512     International License - <https://creativecommons.org/licenses/by/4.0/>). (b) and (c): composite  
513     forest cover map and sampling points within transects for a fragmented site (b) and a  
514     continuous site (c), forest is shown in gray and non-forest in white. Point counts formed a  
515     regular (where terrain, patch size and edge shape allowed) nine-point grid spaced by 75m.  
516     Three points were situated in each position – interior, edge and matrix.

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

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

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

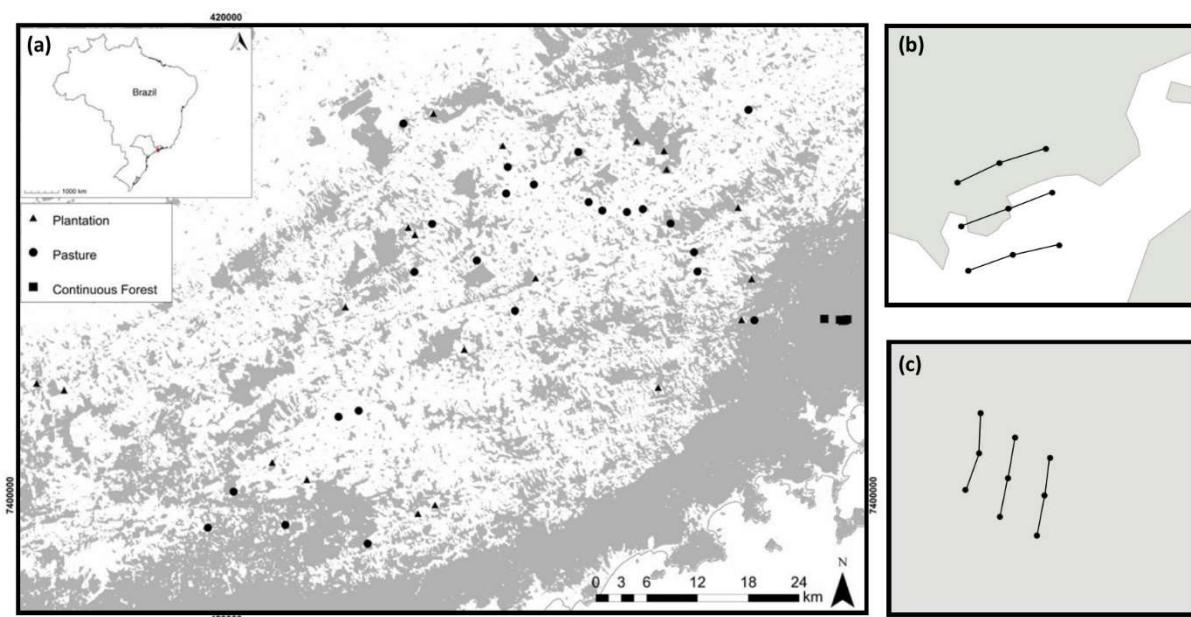
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534 **Figure 5**– Community integrity against forest cover percentage (a) and species richness (b)  
535 compared between the two matrix types - *Eucalyptus* plantation (Eu) and pasture (Pa). Gray  
536 is used for pasture matrix fragments with black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

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541 **Figure 1 – (A)**: Map of sample site locations. Forest cover (all forest types) is shown in gray  
542 and represents areas with > 50% canopy closure in 2000 (Appendix S1: Hansen et al.  
543 (2013)/UMD/Google/USGS/NASA - Licensed under a Creative Commons Attribution 4.0  
544 International License - <https://creativecommons.org/licenses/by/4.0/>). (B) and (C): composite  
545 forest cover map and sampling points within transects for a fragmented site (B) and a  
546 continuous site (C), forest is shown in gray and non-forest in white. Point counts formed a  
547 regular (where terrain, patch size and edge shape allowed) nine-point grid spaced by 75m.  
548 Three points were situated in each position – interior, edge and matrix.

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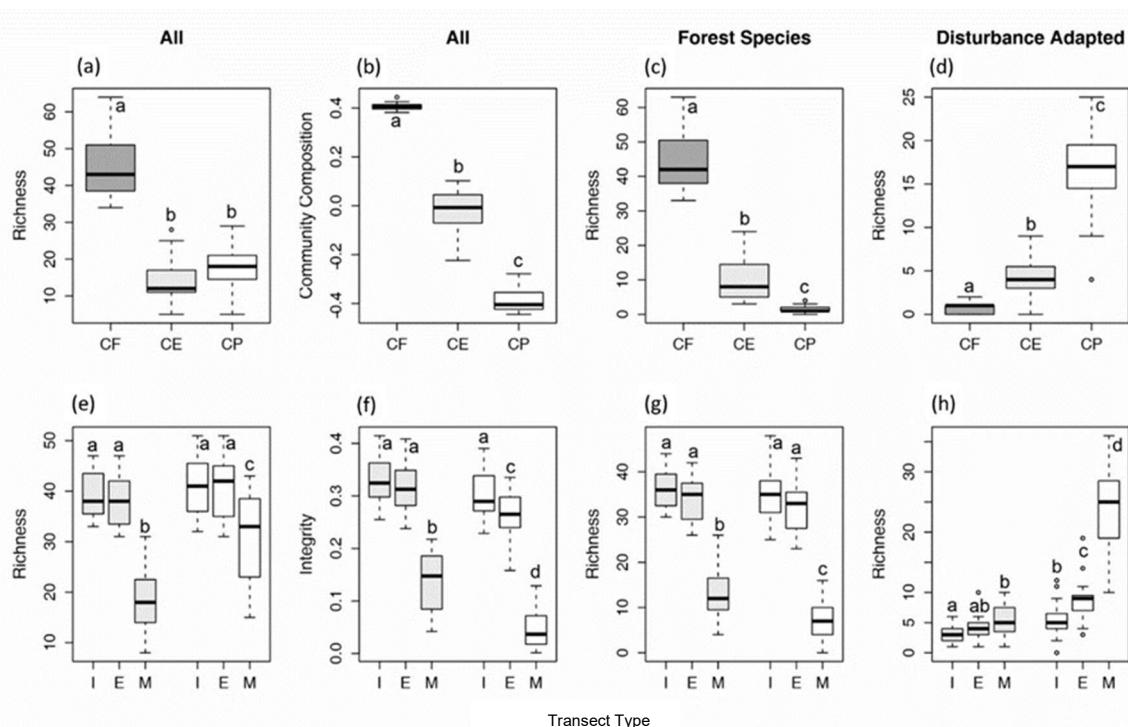
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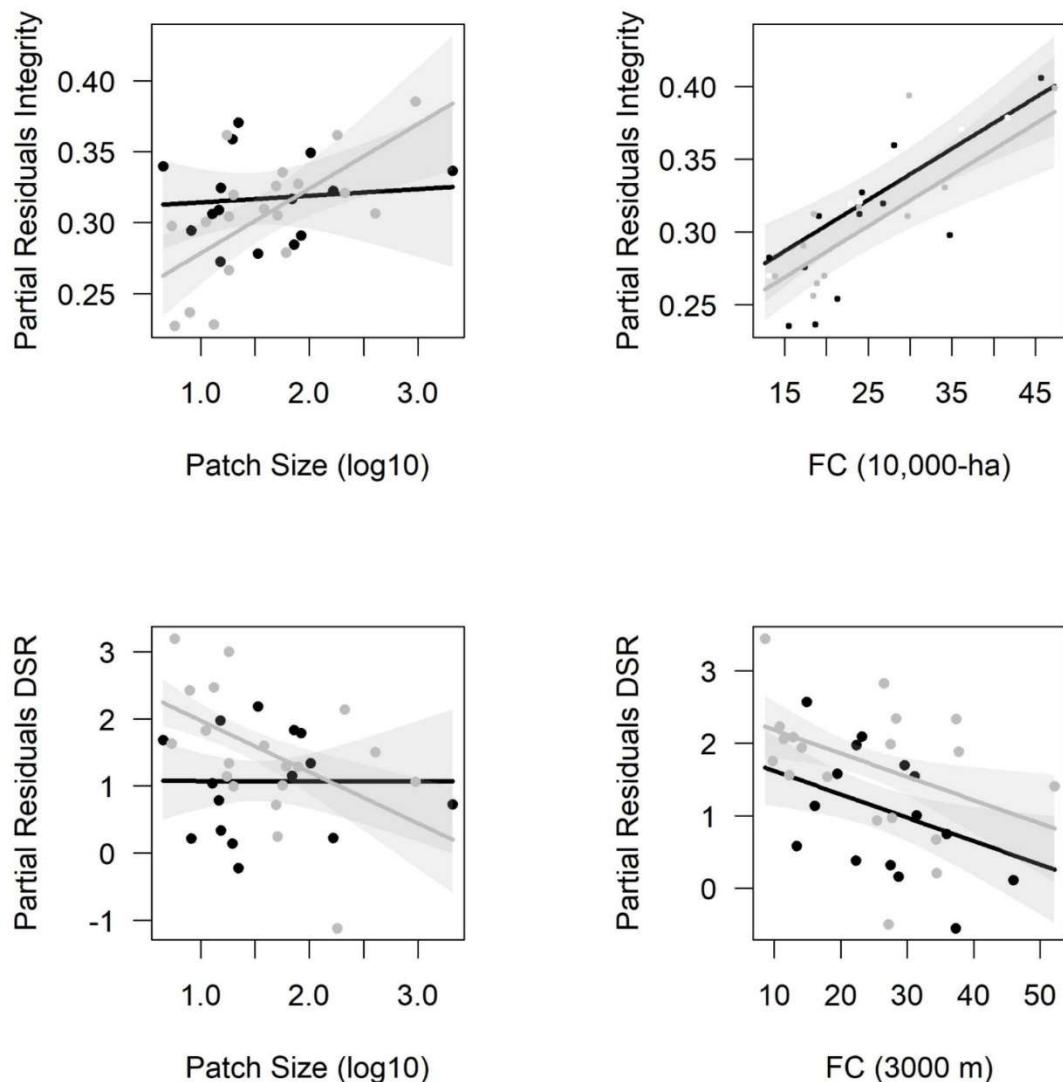


559

560 **Figure 2 – Richness and composition measures for bird communities found at each site**

561 partitioned by transect type for control forest (CF), control plantation (CE), control pasture  
 562 (CP), fragment interiors (I), fragments edges (E) and the surrounding matrix (M). Results are  
 563 shown for control landscapes (top) and fragments (below) as well as for all species, forest  
 564 species and disturbance adapted species. Letter labels show transect type groupings based  
 565 on post-hoc significance tests. Fragments with pasture matrices are represented in white  
 566 and plantation matrices in light gray. Control forest is indicated in dark gray.

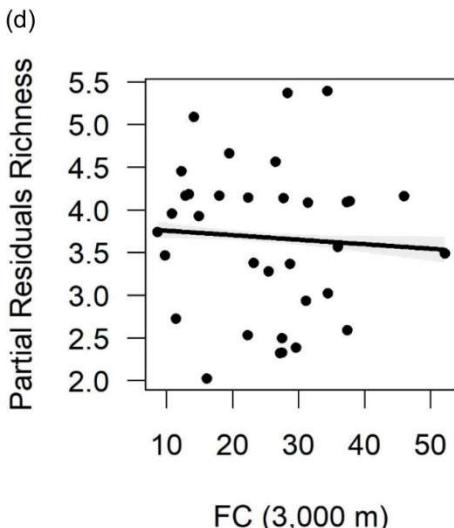
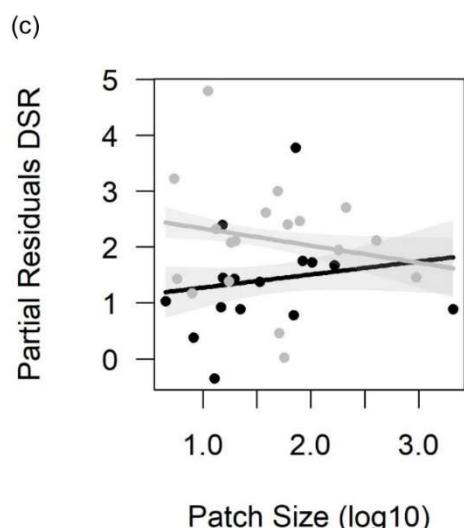
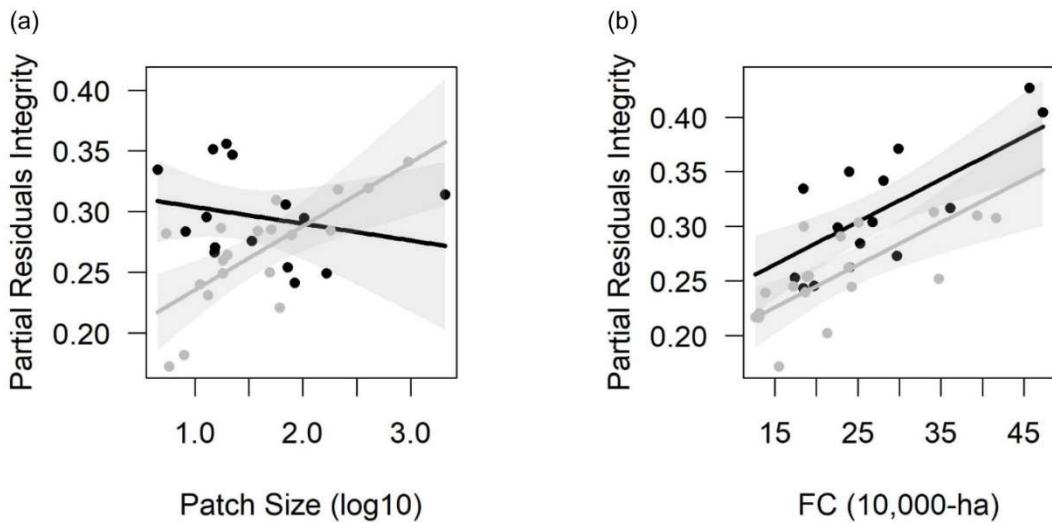
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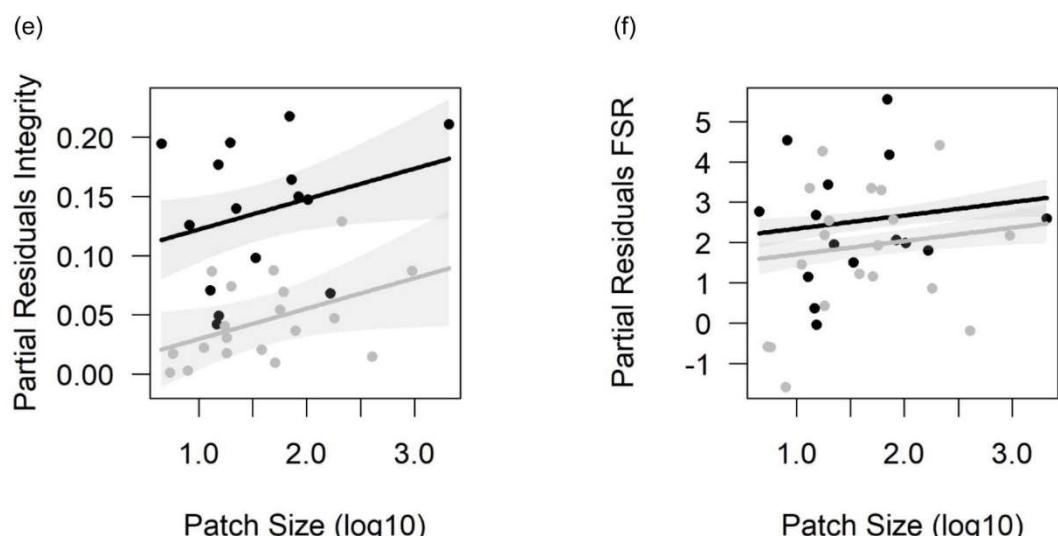
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569 **Figure 3 –** Partial residual values for community integrity and disturbance-tolerant species  
 570 richness (DSR) against patch size in ha (a and c) and percentage forest cover (b and d) for  
 571 interior transects. Plantation matrix fragments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

### Fragment Edge

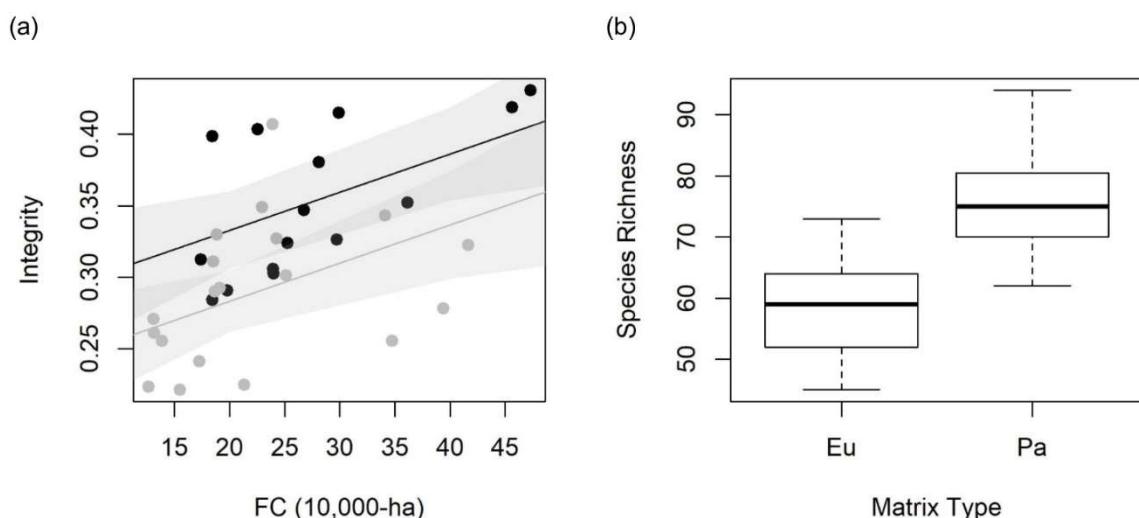


### Matrix



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

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579

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

583