Manchester Metropolitan University

1 **Mediation of area and edge effects by adjacent land use**
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4 Jack H. Hatfield[1*], Jos Barlow[2], Carlos A. Joly[3], Alexander C. Lees[4,5], Celso H. de Freitas

5 Parruco[6], Joseph A. Tobias[1], C. David L. Orme[1], Cristina Banks-Leite[1,7]

6 [1]Grand Challenges in Ecosystems and the Environment, Department of Life Sciences,

7 Imperial College London, Silwood Park Campus, Ascot SL5 7PY, UK.

8 [2]Lancaster Environment Centre, Lancaster University, LA1 4YQ

9 [3]Departamento de Biologia Vegetal, Instituto de Biologia, Universidade Estadual de

10 Campinas, Rua Monteiro Lobato 255, 13083-862, Campinas, São Paulo, Brazil

11 [4]School of Science and the Environment, Manchester Metropolitan University, Manchester,

12 M1 5GD, UK

13 [5]Cornell Lab of Ornithology, Cornell University, Ithaca, NY 14850, USA

14 [6]ES - Ecological Solutions Consultoria Ambiental Ltda.

15
16 [7]Department of Ecology, Biosciences Institute, University of São Paulo, 05508-090 São Paulo

17 SP, Brazil.

18
19 * Corresponding author – jack.hatfield12@imperial.ac.uk

21 **Running head:** Matrix mediates fragmentation effects

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24

25 **Abstract**

26 Habitat loss, fragmentation and degradation have pervasive detrimental effects on tropical

27 forest biodiversity, but the role of the surrounding land use (i.e. matrix) in determining the

28 severity of these impacts remains poorly understood. We surveyed bird species across an

29 interior-edge-matrix gradient to assess the effects of matrix type on biodiversity at 49 different

30 sites with varying levels of landscape fragmentation in the Brazilian Atlantic Forest – a highly

31 threatened biodiversity hotspot. Our findings revealed that both area and edge effects are

32 more pronounced in forest patches bordering pasture matrix, while patches bordering

33 *Eucalyptus* plantation maintained compositionally similar bird communities between the edge

34 and the interior, in addition to exhibiting reduced effects of patch size. These results suggest

35 that the type of matrix in which forest fragments are situated can explain a substantial amount

36 of the widely-reported variability in biodiversity responses to forest loss and fragmentation.

37

38 **<u>Introduction</u>**

39 The type of matrix surrounding native forest patches in human-modified landscapes can

40 modulate the responses of species and ecological communities to habitat loss and

41 degradation (Brockerhoff et al., 2008; Prevedello & Vieira 2010). However, the mechanisms

42 through which the matrix influences the effects of habitat change on biodiversity are still

43 unclear. For instance, do inhospitable matrix types accelerate the local extinction of sensitive

44 species in fragmented landscapes or promote the invasion of disturbance-tolerant species?

45 Are patch area effects less pronounced (Prugh et al. 2008) in a permeable matrix because of

46 rescue effects or weaker edge effects? Answering these questions is crucial if we are to

47 manage matrix land uses to reduce biodiversity loss (Driscoll et al. 2013).

48   With the growing recognition that some matrix types are more permeable and

49 hospitable to some species than others (Brockerhoff et al. 2008; Felton et al. 2010), recent

50 research has increasingly focused on the interplay between matrix type and landscape

51 composition (Driscoll et al. 2013). However, the extent to which matrix type can modulate

52 biodiversity responses to area, edge and isolation remains controversial (Prugh et al. 2008;

53 Prevedello & Vieira 2010; Watling et al. 2011). Prugh et al. (2008) found isolation and area to

54 be poor predictors of species occupancy when matrix type was highly permeable (e.g. semi-

55 natural habitats), while area and isolation were strong predictors of biodiversity in more hostile

56 types of matrix. This is logical as any increase in structural similarity between the matrix and

57 habitat patches can increase population connectivity among patches (Renjifo 2001;

58 Prevedello & Vieira 2010), reducing local extinction by means of rescue effects. On the other

59 hand, Prevedello and Vieira (2010) argued that these matrix effects are smaller and more

60 species-specific than those of area and isolation.

61   The capacity of the matrix to buffer edge effects is expected to increase if matrix

62 habitats approximate to the physiognomy of native habitats, reducing the impact of biotic and

63 abiotic gradients at edges (Banks-Leite & Ewers 2009). For example, Amazonian tree mortality

64 appears to be higher at edges bordering cattle pastures than those bordering secondary

65 forests (Mesquita et al. 1999). Shade coffee plantations have also been found to dampen edge

66 effects in tropical montane forest when compared to corn plantations (Santos-Barrera &

67 Urbina-Cardona 2011). Other effects such as spill-over of matrix species into forest patches

68 may create an influx of disturbance-tolerant species, with concomitant high species turnover

69 (Banks-Leite et al. 2012, 2014) and changes to ecosystem function (De Coster et al. 2015).

70 Changes in species composition can be problematic when they involve large-scale biotic

71 homogenisation, involving the proliferation of generalist species and the decline or local

72 extinction of many specialists (Solar et al. 2015). Given the likely complexity of the underlying

73 mechanisms governing these changes in community assembly, a rigorous landscape-based

74 approach (Fahrig 2003) is required to determine the propensity of the matrix to influence the

75 effects of habitat loss and landscape configuration (i.e. isolation, patch area and edge effects).

76   To examine the ability of the matrix to mitigate the detrimental effects of landscape

77 configuration on biodiversity, we considered bird communities in the highly fragmented and

78 biodiverse Brazilian Atlantic Forest (Myers et al. 2000; Ribeiro et al. 2009). To obtain a full

79 picture of how bird communities change, we collected data with four temporal replicates

80 spanning seasonal variation, stratifying sampling across fragment interiors, fragment edges

81 and the surrounding matrix. Within this framework we examined both a habitat fragmentation

82 gradient and different matrix types. To better understand how community composition

83 changes, we analysed species richness, community integrity (compositional similarity to

84 continuous forest) and richness of both forest-dependent and disturbance-tolerant species.

85 Disturbance-tolerant species richness was expected to be higher in fragments surrounded by

86 the open pasture matrix with forest species being more commonly associated with fragments

87 bordered by plantation forest. We also expected that a *Eucalyptus* plantation matrix, which

88 bears higher structural similarity to Atlantic Forest, would show reduced edge and area effects

89 when compared to an open pasture matrix.

90

91 **Methods**

92 Study Design

93 The study area was located in the Vale do Paraíba and Serra do Mar regions in the state of

94 São Paulo, Brazil. The area is composed of sub-montane forest of varying age surrounded by

95 a range of matrix types. The mean native forest cover at the 10,000-ha scale across all sites

96 was 30% with mean total forest cover being 40% and altitude varying between 600 and 1130

97 m (Appendix S1). Continuous forest sites were located within the largest remaining well-

98 connected forest patch network comprising over one million ha (Ribeiro et al. 2009). We

99 surveyed a total of 49 sites, including 15 near continuous reference sites and 34 fragmented

100 forest sites. At each site, we sampled three transects with three point count stations each.

101 Points within transects were approximately 75 m apart (where terrain and landscape

102 configuration allowed) and the three transects were also spaced by 75 m (Fig. 1). This design

103 was chosen to ensure that even small forest fragments could be surveyed with equal effort. In

104 fragmented forest sites, a single transect was conducted in each of three positions relative to

105 the focal forest patch; patch interior, patch edge and in the matrix bordering the focal patch

106 (Fig. 1).

107   Fifteen patches were bordered by *Eucalyptus* plantation and 19 bordered pasture. The

108   median patch size was 28 ha. There were six different transect types surveyed across the

109   fragmented forest sites, representing the six unique combinations of position (interior, edge or

110   matrix) and matrix land use (*Eucalyptus* plantation or cattle pasture). Due to availability and

111   accessibility, as well as the mosaic nature of the landscape, patches were not surrounded by

112   a uniform matrix; however, all transects were conducted in areas of the patch that bordered

113   the chosen matrix type. Surveyed fragments were selected to sample the full range of

114   fragment area and connectivity found in the study region and were part of the *name removed

115   for review* project (Appendix S1). The 15 reference sites were chosen to encompass one land

116   use each, and we thus sampled five large areas of forest (CF), five large areas of cattle pasture

117   (CP), and five large *Eucalyptus* plantations (CE). Continuous sites were designed with the

118   same grid configuration as explained above, but with all transects conducted in the same land

119   use type.

120   <u>Avifaunal surveys</u>

121   Bird surveys were conducted between December 2015 and February 2017 using point counts.

122   Each count was 15 minutes in duration, during which we recorded all birds identified within a

123   25 m radius of the point, with four temporal replicates (equally split between wet and dry

124   seasons) per point. The spatial and temporal replicate points for each of the 147 transects

125   were then aggregated, providing a sampling effort of 12 point counts per transect. Species

126   richness was calculated as the total number of species recorded at each transect. We also

127   calculated a frequency of occurrence (i.e. an encounter rate) for each species in each transect.

128   This was done by summing the number of times the species was detected at a site, a measure

129   that ranged between 0 and 12, thus providing a proxy for abundance (Solar et al. 2015). This

130   minimised the influence of single detections, which was especially useful for the matrix surveys

131   where some species may be transients infrequently recorded passing between forest patches.

132   From the frequency of occurrence, we calculated community composition based on a Bray-

133   Curtis dissimilarity matrix using the R package vegan (Oksanen et al. 2016). Values were then

134   assigned based on the scores from the first axis of a Principal Coordinate Analysis conducted

135   on the dissimilarity matrix. For fragmented sites we used community integrity rather than

136   community composition to allow comparison to continuous forest. Community integrity used

137   the raw distances extracted from the Bray-Curtis dissimilarity matrix calculating the mean

138   distance between each transect and the continuous forest transects. This Bray-Curtis distance

139   was then subtracted from 1 to provide a scale where 1 indicates a transect that highly

140   resembles control forest and 0 indicates transects extremely dissimilar from continuous forest

141   hence community integrity can be seen as a measure of similarity to the reference continuous

142   forest (for a similar approach see De Coster et al. 2015).

143   <u>Landscape metrics</u>

144   Forest cover (%) was measured for each site using radii of 600 m, 800 m, 1,500 m, and 3,000

145   m from the centre of the site and for the 10,000-ha landscape (5 by 5 km , hereafter: landscape

146   forest cover). A single forest cover scale was chosen per model based on model fit because

147   multiple scales could not be modelled together due to high levels of collinearity (Appendix S2).

148   We also measured size and proximity index (800 m search distance) for focal fragments with

149   both being $\log_{10}$ transformed for analysis. Proximity index takes into account the area of

150   surrounding patches and weights this by distance (Gustafson & Parker 1994). All

151   measurements were conducted using ESRI ArcGIS v.10. (Environmental Systems Research

152   Institute, Redlands, California, USA) and Fragstats v.4. (McGarigal et al. 2012). For more

153   details see Appendix S1.

154   <u>Data analysis</u>

155   All analysis was conducted in R v.3.3.2 (R Core Team 2016). We examined the effect of

156   transect type (the combination of position and matrix type) using mixed effect modelling in

157   lme4 (Schielzeth & Nakagawa 2013) with site as a random factor to account for spatial

158   dependency between transects in the same landscape. For species richness, a generalised

159   linear mixed model (Poisson error structure checked for over-dispersion (Appendix S1)) was

160 used and community composition metrics used linear mixed models. The influence of transect

161 type on the avifaunal community was only investigated for the 34 fragmented sites; with the

162 position and matrix land use combination (e.g. Interior-Pasture) as a single fixed effect,

163 conducting post-hoc contrasts to assess significance. Although we do not include p-values

164 from our main results, we provide them with the mixed effects models for factor level contrasts

165 to aid in interpretation. The continuous sites were not included in the models because there

166 was only one land use type surveyed at each of these sites, however, we analysed them

167 separately to provide a baseline for comparison. The data was then partitioned into interior,

168 edge and matrix to investigate the effects of landscape metrics using linear and generalised

169 linear models. Landscape metric models were selected based on AICc (due to small sample

170 size) or F tests in the case of overdispersion (Appendix S1). Due to small sample sizes, we

171 were unable to fit all the interactions. We did however fit the interactions between matrix type

172 and the other metrics as investigating the effect of matrix type is a major aim of this study.

173 Plots from models containing multiple explanatory variables used partial residuals (Appendix

174 S1).

175   We conducted analyses on the whole bird community as well as two subsets – termed

176 forest species and disturbance-tolerant species owing to the high species turnover observed

177 in Atlantic Forest bird communities (Banks-Leite et al. 2012, 2014). By dividing the community

178 into two groups we were able to reveal trends that are concealed by turnover when examining

179 the community as a whole; for example, whether compositional changes are governed by loss

180 of forest species or gain of disturbance-tolerant species. These groups represented those

181 species associated with the fragmented areas and those associated with the intact areas.

182 Thus, this allowed us to individually consider those species responding negatively to

183 disturbance and those that respond in a positive manner, but our categorisation is not intended

184 as a definitive classification. These distinctions were created using a species ranking system

185 based on weighted averages ordination (Banks-Leite et al. 2014). Species presence/absence

186 was first weighted by site scores taken from the first axis of a PCoA based on Bray-Curtis

187 dissimilarity. The mean is then calculated from all non-zero weights. The division was made

188 relative to the mean of the site scores (the value for a species that occurs at all sample

189 locations).

190 Our method for partitioning the community into groups is a post-hoc approach based

191 on observed species turnover across sites. We favoured this approach because previous

192 classifications of species sensitivity or habitat use, such as Parker III et al. (1996), are not

193 transparent regarding where data were obtained, the level of uncertainty associated with each

194 classification, and do not separate between different stressors (e.g. a species may be sensitive

195 to hunting but insensitive to the land use changes we investigated here)(Alexandrino et al.

196 2016). Our approach thus allowed us to identify the "winners" (i.e. disturbance-tolerant) and

197 "losers" (i.e. forest-associated species) in our dataset. We then used information on forest

198 habitat restriction to better understand how our approach of community partitioning was

199 related to the previous classification of Parker III et al. (1996) – with taxonomic disagreement

200 resolved following the checklist produced by BirdLife International (2017). *Estrilda astrild* was

201 excluded from this comparison due to a lack of habitat usage information.

202 Site-scale analyses were conducted by aggregating the three transects at each site.

203 This produced a frequency of occurrence for each species potentially ranging between 0 and

204 36 from which community integrity was calculated. Species richness and community integrity

205 were modelled against percentage forest cover for the 10,000-ha landscape and matrix type

206 surveyed using generalised linear and linear models, respectively.

207 **Results**

208 Overall we detected 267 species across the 49 landscapes. The first PCoA axis explained

209 27.6% of the total variance. Using the weighted averages approach, the community was split

210 into 177 forest species and 90 disturbance adapted species. When compared to habitat usage

211 information in Parker III et al. (1996), 72% of species that we assigned to the forest species

212 group were found to be restricted to forest habitats based on the published information,

213   compared with 2% of the species in disturbance-tolerant group. Although we do not examine

214   this further, these comparisons demonstrate that our community split tallies well with published

215   classifications.

216   Continuous sites

217   Analyses of the whole community revealed that both continuous plantation ($z = -5.56$, $p < 0.01$)

218   and continuous pasture ($z = -6.82$, $p < 0.01$) did not differ significantly from one another but

219   both showed lower species richness than continuous forest transects (Fig. 2a). However, the

220   community composition of three transect types were all significantly different from each other

221   (Fig. 2b; CE – CF: $z = -14.24$, $p < 0.01$; CP – CF: $z = -26.07$, $p < 0.01$; CP – CE: $z = -11.83$, p

222   < 0.01). Changes in community composition were driven by a decrease in forest species

223   richness in both types of matrix, together with an increase in disturbance-tolerant species (Fig.

224   2c, d). All continuous blocks were significantly different from each other in forest species (CE

225   – CF: $z = -7.79$, $p < 0.01$; CP – CF: $z = -12.38$, $p < 0.01$; CP -CE: $z = - 6.63$, $p < 0.01$) and

226   disturbance-tolerant species richness (CE – CF: $z = 4.94$, $p < 0.01$; CP – CF: $z = 9.21$, $p <$

227   0.01; CP - CE: $z = 6.90$, $p < 0.01$).

228   Fragmented forest sites

229   Transect type (i.e. position and matrix combination) influenced total species richness in the

230   fragments ($F = 32.83$). Species richness in the matrix was significantly lower than both edge

231   and interior (Figure 2e), and pasture matrix transects had on average 39% more species than

232   *Eucalyptus* ($z = 6.10$, $p < 0.01$). The results for community integrity however showed a different

233   trend. Although transect type continued to have a significant influence ($F = 194.69$), edge

234   effects were only observed in patches bordering pasture, while forest patches bordering

235   *Eucalyptus* presented similar levels of integrity at edges and interiors (Fig. 2f), mirroring results

236   for continuous sites, where *Eucalyptus* transects had higher integrity than pasture transects

237   (Fig. 2f).

238   The edge effects observed in patches bordering pastures was mostly driven by an

239   increase in disturbance-tolerant species rather than a reduction in forest species. The richness

240   of forest species did not differ between edge and interior, regardless the bordering matrix (Fig.

241   2g; z = -5.31, p < 0.01), but the richness of disturbance-tolerant species in patches bordering

242   pasture was lower in forest interiors when compared to edges (z = -3.68, p < 0.01).

243   Furthermore, the species richness of disturbance-tolerant species in the interior of patches

244   bordering pasture was, on average, 1.9 times higher than fragment interiors bordering

245   *Eucalyptus* (p = 0.02), and similar to the number of species found in *Eucalyptus* matrix.

246   Landscape configuration

247   Interior and edge

248   Interior and edge transects showed a similar mediation of matrix type on community integrity

249   responses to landscape configuration and habitat amount (Interior: adj-R^2 = 0.57; Edge: adj-

250   R^2 = 0.55). In both cases, integrity was only positively affected by patch size in fragments

251   bordering pasture (Fig. 3a and 4a; Interior: t = 2.12, p = 0.04; Edge: t = 2.87, p < 0.01).

252   Landscape forest cover (10,000-ha) on the other hand positively influenced integrity both in

253   pasture and *Eucalyptus* bordering fragments (Interior: t = 5.11, p < 0.01; Edge: t = 3.98, p <

254   0.01), and while the slope of this relationship was not affected by matrix type, the intercept

255   was always higher in *Eucalyptus* bordering patches (Fig. 3b and 4b). None of the landscape

256   metrics (e.g. forest cover, patch size, proximity index) significantly correlated with species

257   richness for interior transects whereas for edge transects total species richness was found to

258   decrease with forest cover at the 3 km scale (z = -2.04, p = 0.04).

259   Forest species richness was not significantly affected by any landscape metric, but the

260   richness of disturbance-tolerant species found at interior (Fig. 3c; t = -2.14, p = 0.03) and edge

261   (Fig. 4c; t = -2.29, p = 0.03) transects was negatively correlated with patch size only in pasture

262   bordering patches. Richness of disturbance-tolerant species found in interior transects

263   reduced with forest cover; the intercept was different between the matrix types, but the slope

264   was the same (z = -2.53, p = 0.01).

265   <u>Matrix</u>

266   Community integrity was lower for pasture matrices than plantation (t = -5.95, p < 0.01), and

267   integrity was positively correlated with patch area (Fig. 4e, t = 2.06, p = 0.05, adj R^2 = 0.53).

268   Species richness was influenced by matrix type with pasture matrices having higher richness

269   (t = 4.10, p < 0.01).

270   Forest species richness was positively correlated with forest patch area (Fig. 4f, t =

271   2.57, p = 0.02) and pasture matrices had lower forest species richness than plantation (t = -

272   3.55, p < 0.01). Disturbance-tolerant species richness was only significantly affected by matrix

273   type, with pasture matrices having higher richness (t = 9.25, p < 0.01).

274   <u>Site scale</u>

275   At the site scale (Interior, edge and matrix transects combined; Fig. 5) community integrity

276   was found to increase with forest cover (t = 3.06, p < 0.01) with fragments bordering pasture

277   having lower integrity than those bordering plantations (t = -3.10, p < 0.01), yielding an

278   adjusted-R^2 of 0.42. Species richness was only affected by matrix type with pasture bordering

279   fragments having more species (z = 5.90, p < 0.01).

280   **Discussion**

281   We found that *Eucalyptus* plantation matrices were more beneficial for bird communities in the

282   Atlantic Forest when compared to pasture matrices. Although pastures had higher species

283   richness than *Eucalyptus* plantations, forest fragments bordering *Eucalyptus* have higher

284   community similarity to continuous forest and weaker edge effects (Fig. 2, 3 and 4). We also

285   show that the strengthening of edge and area effects in patches bordering pastures was

286   mostly due to the increase in disturbance-specialists, rather than the loss of forest species.

287 Nonetheless, our findings suggest that spill-over of species can occur in both directions in

288 fragmented tropical forests, from fragments to matrix and vice versa.

289 In our study landscape, the *Eucalyptus* plantation matrix supported fewer bird species

290 than pasture yet retained more forest species (Fig. 2). This aligns with previous studies

291 showing that non-native plantations provide habitat for a small subset of tropical forest species

292 (Barlow et al. 2007; Lees et al. 2015; Millan et al. 2015), without acting as a species source

293 (Hawes et al., 2008). Pastures, on the other hand, not only provide a habitat for different

294 species (Moura et al. 2013; Lees et al. 2015), but also allow them to spill-over into native

295 forest, as shown by the increase in the richness of disturbance-tolerant species in fragments

296 (Fig. 2h and 3c). We also found evidence of reverse spill-over effects from the forest into the

297 surrounding pasture (Tscharntke et al. 2012) in contrast to Boesing et al. (2018a) who found

298 minimal spill-over of birds into cattle pasture in the Atlantic Forest. Our results suggest that

299 community integrity in matrix transects increases with forest patch area (Fig. 4e), indicating

300 that large native forest patches help maintain community integrity in the surrounding matrix.

301 These results reinforce previous findings highlighting the value of extensive forest

302 patches in providing source populations of forest-dependent bird species (Mayhew et al.

303 2019), thereby enriching the surrounding matrix via a spill-over of ecosystem services, such

304 as pollination, pest control and seed dispersal. Spill-over of services has been widely

305 documented for a range of taxa (Tscharntke et al. 2012) including insect and bird pollinators

306 (Renjifo 2001; Ricketts et al. 2008) and bird spill-over has been shown to be particularly

307 important in coffee plantations (Boesing et al. 2018a), where birds control populations of pests

308 (Johnson et al. 2010). Hence, species spill-over from large forest patches into the matrix may

309 benefit crop productivity while also increasing seed dispersal of native trees which is key to

310 natural reforestation and forest recovery (Bregman et al. 2016).

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

312 2010; Ewers & Banks-Leite 2013; Pfeifer et al. 2017) where they are thought to drive the widely

313 observed area effects on biodiversity in this fragmented landscape (Ewers et al. 2007; Fletcher

314 et al. 2007; Banks-Leite et al. 2010). Our results provide further corroboration of this

315 hypothesis as we only detected significant edge effects in patches bordering pasture matrices,

316 where patch area also had a significant influence on the interior bird community. Conversely,

317 for fragments with a plantation matrix, we found neither significant edge effects, nor significant

318 area effects.

319 The large difference in edge effects observed could be due to two main factors. First,

320 plantations are known to harbour fewer open matrix species (Umetsu & Pardini 2007) limiting

321 changes in community composition due to turnover. Second, plantations may contribute to the

322 retention of forest species. Our results indicating that plantations may mitigate edge effects

323 mirror those of Renjifo (2001), who found that exotic tree plantations had a buffering effect on

324 the abundance of some forest species when compared to pasture. Ruffell et al. (2017) also

325 found that the reduction in bird species richness with habitat loss was less severe when the

326 matrix contained exotic tree plantations, even when plantations occupied as little as 10% of

327 the matrix. In addition, Boesing et al. (2018b) have shown that the extinction thresholds for

328 the bird community detected in fragments surrounded by coffee plantations was at 19% forest

329 cover compared to 35% when the matrix is pasture.

330 Overall, this study supports the view that a shared border with *Eucalyptus* plantations

331 is less detrimental to forest bird communities than a shared border with pasture. *Eucalyptus*

332 plantations are likely able to buffer edge effects and reduce the infiltration of disturbance-

333 tolerant species into patch edges and interiors when compared to cattle pasture. They also

334 provide higher community integrity for a given level of native forest cover. From the

335 perspective of conservation, plantations therefore offer a management solution to reduce the

336 impact of fragmentation on biodiversity without requiring large increases in the area of native

337 forest. However, these potential benefits carry several caveats.

338   One of the important characteristics of plantations is their greater structural complexity

339   compared with pastures. They are often structurally similar to native forest (Prevedello & Vieira

340   2010), but variation in structural complexity of plantations is also important, as those with

341   higher complexity (e.g. multiple vegetation strata) generally contain higher bird species

342   richness and abundance (Nájera & Simonetti 2010; Millan et al. 2015). The plantation sites

343   surveyed in this study often retained understory foliage, a practice that is not universal, but

344   which matches the management practices in other studies that concluded that plantations

345   have some utility for biodiversity (e.g. Barlow et al. 2007). Thus, it is likely that the detrimental

346   impacts of plantations on native biodiversity are much stronger when plantation understory is

347   cleared. The cyclic nature of plantations is another important consideration: while plantations

348   consisting of adult trees may buffer edge effects, it is unlikely that young sapling trees will

349   provide the same benefit, especially given the large reduction in structural complexity after

350   harvesting. Future research should focus on extending the temporal span of data collection

351   so that the effects of plantations can be assessed throughout the harvesting cycle. There is

352   also scope to investigate the impacts of management, for example if certain management

353   techniques or harvesting rotations provide a higher conservation benefit than others (Moreira

354   et al. 2013).

355   In the wider context of expanding plantations worldwide and especially in the case of

356   *Eucalyptus* in Brazil, the benefits may be more varied and depend on the land use plantations

357   are replacing (Brockerhoff et al. 2013). Comparisons of plantations and pasturelands have

358   been found to be highly contingent on the taxonomic focus and landscape specifics (Felton et

359   al. 2010). Conversion of agricultural land to plantations has also received ample attention due

360   to the other environmental benefits they may bring, such as climate change mitigation through

361   carbon storage and sequestration (Jackson & Schlesinger 2004). However, other effects such

362   as changes in soil organic carbon are less clear (Fialho & Zinn 2014).

363   Manipulation of the matrix can moderate species responses to habitat loss and

364   fragmentation and the ongoing conversion of pasturelands to plantation may yet yield benefits

365 for bird biodiversity via improved connectivity among populations and the reduction of edge

366 effects. As with secondary forests (Mayhew et al. 2019), the conservation value of plantations

367 largely depends on the maintenance and extent of embedded native forest patches.

368 Nonetheless, although intensive research has been conducted on the effects of management

369 on biodiversity within plantations themselves (Nájera & Simonetti 2010; Millan et al. 2015),

370 little is known about how plantation management and harvesting practices affect adjacent

371 native forests. We recommend that future research investigates how management practices

372 mediate effects of plantations on biodiversity in adjacent forest fragments, as doing so may

373 provide a key insight into practical conservation solutions for human modified tropical forest

374 landscapes.

375 **Supporting Information**

376 Additional methods (Appendix S1), comparison of the different forest cover radii (Appendix

377 S2) and information on species occurrence in the different land use types (Appendix S3) are

378 available online. The authors are solely responsible for the content and functionality of these

379 materials. Queries (other than absence of the material) should be directed to the

380 corresponding author.

381 **Literature Cited**

382 Alexandrino ER, Buechley ER, Piratelli AJ, Ferraz KMPMB, Moral RA, Sekercioglu CH, Silva

383 WR, Couto HTZ. 2016. Bird sensitivity to disturbance as an indicator of forest patch

384 conditions: An issue in environmental assessments. Ecological Indicators, **66:** 369-381.

385 Banks-Leite C, Ewers RM. 2009. Ecosystem Boundaries, in: Encyclopedia of Life Sciences

386 (ELS). John Wiley & Sons, Ltd.

387 Banks-Leite C, Ewers RM, Metzger JP. 2010. Edge effects as the principal cause of area

388 effects on birds in fragmented secondary forest. Oikos **119**: 918–926.

389   Banks-Leite C, Ewers RM, Metzger JP. 2012. Unravelling the drivers of community

390   dissimilarity and species extinction in fragmented landscapes. Ecology **93**: 2560–2569.

391   Banks-Leite C, Pardini R, Tambosi LR, Pearse WD, Bueno AA, Bruscagin RT, Condez TH,

392   Dixo M, Igari AT, Martensen AC, et al. 2014. Using ecological thresholds to evaluate the

393   costs and benefits of set-asides in a biodiversity hotspot. Science (80-.) **345**: 1041–1045.

394   Barlow J, Gardner TA, Araujo IS, Avila-Pires TC, Bonaldo AB, Costa JE, Esposito MC,

395   Ferreira L V, Hawes J, Hernandez MIM, et al. 2007. Quantifying the biodiversity value of

396   tropical primary, secondary, and plantation forests. Proceedings of the National Academy of

397   Sciences of the United States of America. **104**: 18555–18560.

398   BirdLife International. 2017. Handbook of the Birds of the World and BirdLife International

399   digital checklist of the birds of the world. Version 9.1. Available at:

400   http://datazone.birdlife.org/species/taxonomy

401   Boesing AL, Nichols E, Metzger JP. 2018a. Land use type, forest cover and forest edges

402   modulate avian cross-habitat spillover. Journal of Applied Ecology **55**:1252–1264.

403   Boesing AL, Nichols E, Metzger JP. 2018b. Biodiversity extinction thresholds are modulated

404   by matrix type. Ecography **41**: 1520–1533.

405   Bregman TP, Lees AC, MacGregor HEA, Darski B, de Moura NG, Aleixo A, Barlow J, Tobias

406   JA. 2016. Using avian functional traits to quantify the impact of land-cover change on

407   ecosystem processes linked to resilience in tropical forests. Proceedings of the Royal

408   Society B 283: 20161289.

409   Brockerhoff EG, Jactel H, Parrotta JA, Quine CP, Sayer J. 2008. Plantation forests and

410   biodiversity: oxymoron or opportunity? Biodiversity and Conservation **17**: 925–951.

411   Brockerhoff, EG, Jactel H, Parrotta J A, Ferraz SFB. 2013. Role of eucalypt and other

412   planted forests in biodiversity conservation and the provision of biodiversity-related

413   ecosystem services. Forest Ecology and Management **301**: 43–50.

414   De Coster G, Banks-Leite C, Metzger JP. 2015. Atlantic forest bird communities provide

415   different but not fewer functions after habitat loss. Proceedings of the Royal Society B

416   Biological Sciences **282**: 20142844.

417   Driscoll DA, Banks SC, Barton PS, Lindenmayer DB, Smith, AL. 2013. Conceptual domain of

418   the matrix in fragmented landscapes. Trends in Ecology and Evolution **28**: 605-613.

419   Ewers RM, Banks-Leite C. 2013. Fragmentation impairs the microclimate buffering effect of

420   tropical forests. PLoS One **8**: e58093.

421   Ewers RM, Thorpe S, Didham RK. 2007. Synergistic interactions between edge and area

422   effects in a heavily fragmented landscape. Ecology **88**: 96–106.

423   Fahrig L, 2003. Effects of Habitat Fragmentation on Biodiversity. Annual Review of Ecology,

424   Evolution, and Systematics **34**:487–515.

425   Felton A, Knight E, Wood J, Zammit C, Lindenmayer D. 2010. A meta-analysis of fauna and

426   flora species richness and abundance in plantations and pasture lands. Biological

427   Conservation **143**: 545–554.

428   Fialho RC, Zinn YL. 2014. Changes in soil organic carbon under Eucalyptus plantations in

429   Brazil: a comparative analysis. Land Degradation and Development **25**: 428–437.

430   Fletcher RJJ, Ries L, Battin J, Chalfoun AD. 2007. The role of habitat area and edge in

431   fragmented landscapes: definitively distinct or inevitably intertwined? Canadian Journal of

432   Zoology **85**: 1017–1030.

433   Gustafson EJ, Parker GR. 1994. Using an index of habitat patch proximity for landscape

434   design. Landscape and Urban Planning **29**: 117–130.

435   Hansen MC, Potapov PV, Moore R, Hancher M, Turubanova SA, Tyukavina A, Thau D,

436   Stehman SV, Goetz SJ, Loveland TR, et al. 2013 High-Resolution Global Maps of 21st-

437   Century Forest Cover Change. Science (80-) **342**: 850–853.

438   Hawes J, Barlow J, Gardner TA, Peres C.A. 2008. The value of forest strips for understorey

439   birds in an Amazonian plantation landscape. Biological Conservation **141**: 2262–2278.

440   Jackson RB, Schlesinger WH. 2004. Curbing the U.S. carbon deficit. Proceedings of the

441   National Academy of Sciences of the United States of America **101**: 15827–15829.

442   Johnson MD, Kellermann JL, Stercho AM. 2010. Pest reduction services by birds in shade

443   and sun coffee in Jamaica. Animal Conservation **13**: 140–147.

444   Lees AC, Moura NG, de Almeida AS, Vieira ICG. 2015. Poor prospects for avian biodiversity

445   in Amazonian oil palm. PLOS ONE **10**: e0122432.

446   Mayhew RJ, Tobias JA, Bunnefeld L, Dent DH. 2019. Connectivity with primary forest

447   determines the value of regenerating tropical forests for bird conservation. Biotropica **51**:

448   219– 233.

449   McGarigal K, Cushman S, Ene E. 2012. FRAGSTATS v4: Spatial pattern analysis program

450   for categorical and continuous maps. University of Massachusetts, Amherst.

451   http://www.umass.edu/landeco/research/fragstats/fragstats.html

452   Mesquita RCG, Delamônica P, Laurance WF. 1999. Effect of surrounding vegetation on

453   edge-related tree mortality in Amazonian forest fragments. Biological Conservation **91**: 129–

454   134.

455   Millan CH, Develey PF, Verdade LM. 2015. Stand-level management practices increase

456   occupancy by birds in exotic Eucalyptus plantations. Forest Ecology and Management **336**:

457   174–182.

458   Moreira, JMM, Rodriguez LCE, Caixeta-Filho JV. 2013. An optimization model to integrate

459   forest plantations and connecting corridors. Forest Science **59**:661–669.

460   Moura NG, Lees AC, Andretti CB, Davis BJW, Solar RRC, Aleixo A, Barlow J, Ferreira J,

461   Gardner TA. 2013. Avian biodiversity in multiple-use landscapes of the Brazilian Amazon.

462   Biological Conservation **167**: 339-348.

463   Myers N, Mittermeier RA, Mittermeier CG, da Fonseca GAB, Kent J. 2000. Biodiversity

464   hotspots for conservation priorities. Nature **403**: 853–858.

465   Nájera A, Simonetti JA. 2010. Enhancing avifauna in commercial plantations. Conservation

466   Biology **24**: 319–324.

467   Oksanen J, Blanchet G, Friendly M, Kindt R, Legendre P, McGlinn D, Minchin PR, O'Hara

468   RB, Simpson GL, Solymos P, et al. 2016. Vegan: community ecology package.

469   https://cran.r-project.org/package=vegan.

470   Parker III TA, Stotz DF, Fitzpatrick JW. 1996. Ecological and distributional databases. In: Stotz DF,

471   Fitzpatrick JW, Parker III TA, Moskovits DK (Eds.), Neotropical Birds: Ecology and Conservation. The

472   University of Chicago Press, Chicago, pp. 111–410.

473   Pfeifer M, Lefebvre V, Peres CA, Banks-Leite C, Wearn OR, Marsh CJ, Butchart SHM,

474   Arroyo-Rodríguez V, Barlow J, Cerezo A, et al. 2017. Creation of forest edges has a global

475   impact on forest vertebrates. Nature **551**: 187-191.

476   Prevedello JA, Vieira MV. 2010. Does the type of matrix matter? A quantitative review of the

477   evidence. Biodiversity and Conservation **19**: 1205–1223.

478   Prugh LR, Hodges KE, Sinclair ARE, Brashares JS. 2008. Effect of habitat area and isolation

479   on fragmented animal populations. Proceedings of the National Academy of Sciences of the

480   United States of America **105**: 20770–20775.

481   R Core Team, 2016. R: A language and environment for statistical computing. R Foundation

482   for Statistical Computing, Vienna, Austria. https://www.r-project.org/.

483   Renjifo LM. 2001. Effect of natural and anthropogenic landscape matrices on the abundance

484   of subandean bird species. Ecological Applications **11**: 14–31.

485   Ribeiro MC, Metzger JP, Martensen AC, Ponzoni FJ, Hirota MM. 2009. The Brazilian Atlantic

486   Forest: How much is left, and how is the remaining forest distributed? Implications for

487   conservation. Biological Conservation **142**: 1141–1153.

488   Ricketts TH, Regetz J, Steffan-Dewenter I, Cunningham SA, Kremen C, Bogdanski A,

489   Gemmill-Herren B, Greenleaf SS, Klein AM, Mayfield MM, et al. 2008. Landscape effects on

490   crop pollination services: are there general patterns? Ecology Letters **11**: 499–515.

491   Ruffell J, Clout MN, Didham RK. 2017. The matrix matters, but how should we manage it?

492   Estimating the amount of high-quality matrix required to maintain biodiversity in fragmented

493   landscapes. Ecography **40**: 171–178.

494   Santos-Barrera G, Urbina-Cardona JN. 2011. The role of the matrix edge dynamics of

495   amphibian conservation in tropical montane fragmented landscapes. Revista Mexicana de

496   Biodiversidad **82**: 679–687.

497   Schielzeth H, Nakagawa S. 2013. Nested by design: Model fitting and interpretation in a

498   mixed model era. Methods in Ecology and Evolution **4**: 14–24.

499   Solar RRC, Barlow J, Ferreira J, Berenguer E, Lees AC, Thomson JR, Louzada J, Maués M,

500   Moura NG, Oliveira VHF, et al. 2015. How pervasive is biotic homogenization in human

501   modified tropical forest landscapes? Ecology Letters **18**: 1108–1118.

502   Tscharntke T, Tylianakis JM, Rand TA, Didham RK, Fahrig L, Batáry P, Bengtsson J, Clough

503   Y, Crist TO, Dormann CF, et al. 2012. Landscape moderation of biodiversity patterns and

504   processes - eight hypotheses. Biological Reviews **87**: 661–685.

505 Umetsu F, Pardini R. 2007. Small mammals in a mosaic of forest remnants and

506 anthropogenic habitats - evaluating matrix quality in an Atlantic forest landscape. Landscape

507 Ecology **22**: 517–530.

508 Watling JI, Nowakowski AJ, Donnelly MA, Orrock JL. 2011. Meta-analysis reveals the

509 importance of matrix composition for animals in fragmented habitat. Global Ecology and

510 Biogeography **20**: 209–217.

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531   **Figure 1 –** (a): Map of sample site locations. Forest cover (all forest types) is shown in gray

532   and represents areas with > 50% canopy closure in 2000 (Appendix S1: Hansen et al.

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534   International License - https://creativecommons.org/licenses/by/4.0/). (b) and (c): composite

535   forest cover map and sampling points within transects for a fragmented site (b) and a

536   continuous site (c), forest is shown in gray and non-forest in white. Point counts formed a

537   regular (where terrain, patch size and edge shape allowed) nine-point grid spaced by 75m.

538   Three points were situated in each position – interior, edge and matrix.

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

540   partitioned by transect type for continuous forest (CF), continuous plantation (CE),

541   continuous pasture (CP), fragment interiors (I), fragments edges (E) and the surrounding

542   matrix (M). Results are shown for control landscapes (top) and fragments (below) as well as

543   for all species, forest species and disturbance adapted species. Letter labels show transect

544   type groupings based on post-hoc significance tests. Fragments with pasture matrices are

545   represented in white and plantation matrices in light gray. Continuous forest is indicated in

546   dark gray.

547   **Figure 3 –** Partial residual values for community integrity and disturbance-tolerant species

548   richness (DSR) against patch size in ha (a and c) and percentage forest cover (b and d) for

549   interior transects. Plantation matrix fragments are shown in black, pasture in gray.

550   **Figure 4 –** Partial residual values for community integrity, species richness, disturbance-

551   tolerant species richness (DSR) and forest species richness (FSR) against patch size in ha

552   (b and d) and percentage forest cover (a, c, e and f) for edge (a – d) and matrix (e - f)

553   transects. Plantation matrix fragments are shown in black, pasture in gray. d shows only a

554   single line as matrix type was not found to be influential in this model.
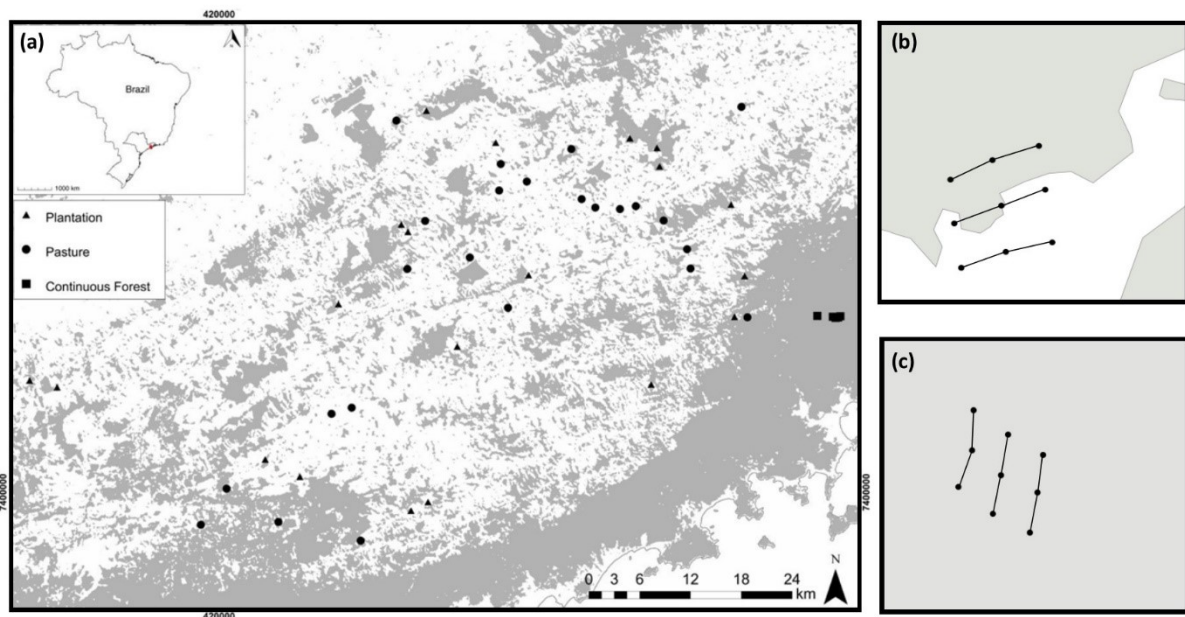
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556 **Figure 5–** Community integrity against forest cover percentage (a) and species richness (b)

557 compared between the two matrix types - *Eucalyptus* plantation (Eu) and pasture (Pa). Gray

558 is used for pasture matrix fragments with black representing plantation.

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563 **Figure 1 – (**A): Map of sample site locations. Forest cover (all forest types) is shown in gray

564 and represents areas with > 50% canopy closure in 2000 (Appendix S1: Hansen et al.

565 (2013)/UMD/Google/USGS/NASA - Licensed under a Creative Commons Attribution 4.0

566 International License - https://creativecommons.org/licenses/by/4.0/). (B) and (C): composite

567 forest cover map and sampling points within transects for a fragmented site (B) and a

568 continuous site (C), forest is shown in gray and non-forest in white. Point counts formed a

569 regular (where terrain, patch size and edge shape allowed) nine-point grid spaced by 75m.

570 Three points were situated in each position – interior, edge and matrix.

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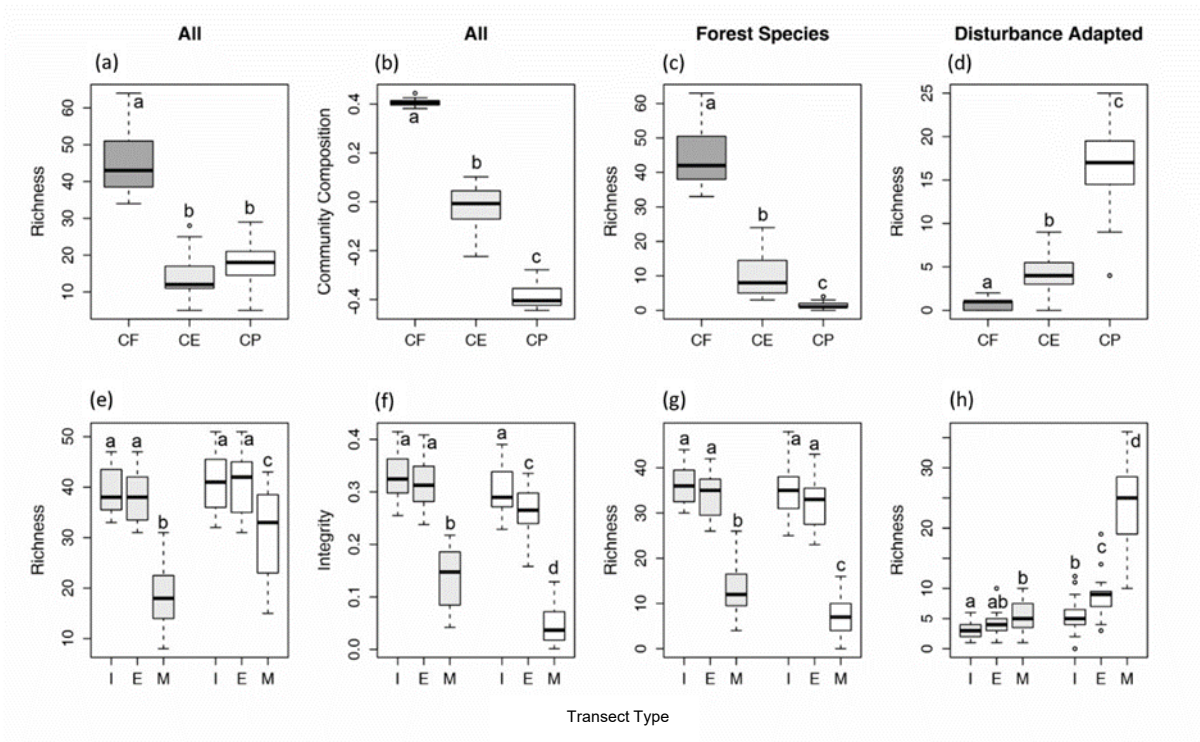
581
582 **<u>Figure 2 –</u>** Richness and composition measures for bird communities found at each site

583 partitioned by transect type for control forest (CF), control plantation (CE), control pasture

584 (CP), fragment interiors (I), fragments edges (E) and the surrounding matrix (M). Results are

585 shown for control landscapes (top) and fragments (below) as well as for all species, forest

586 species and disturbance adapted species. Letter labels show transect type groupings based

587 on post-hoc significance tests. Fragments with pasture matrices are represented in white

588 and plantation matrices in light gray. Control forest is indicated in dark gray.

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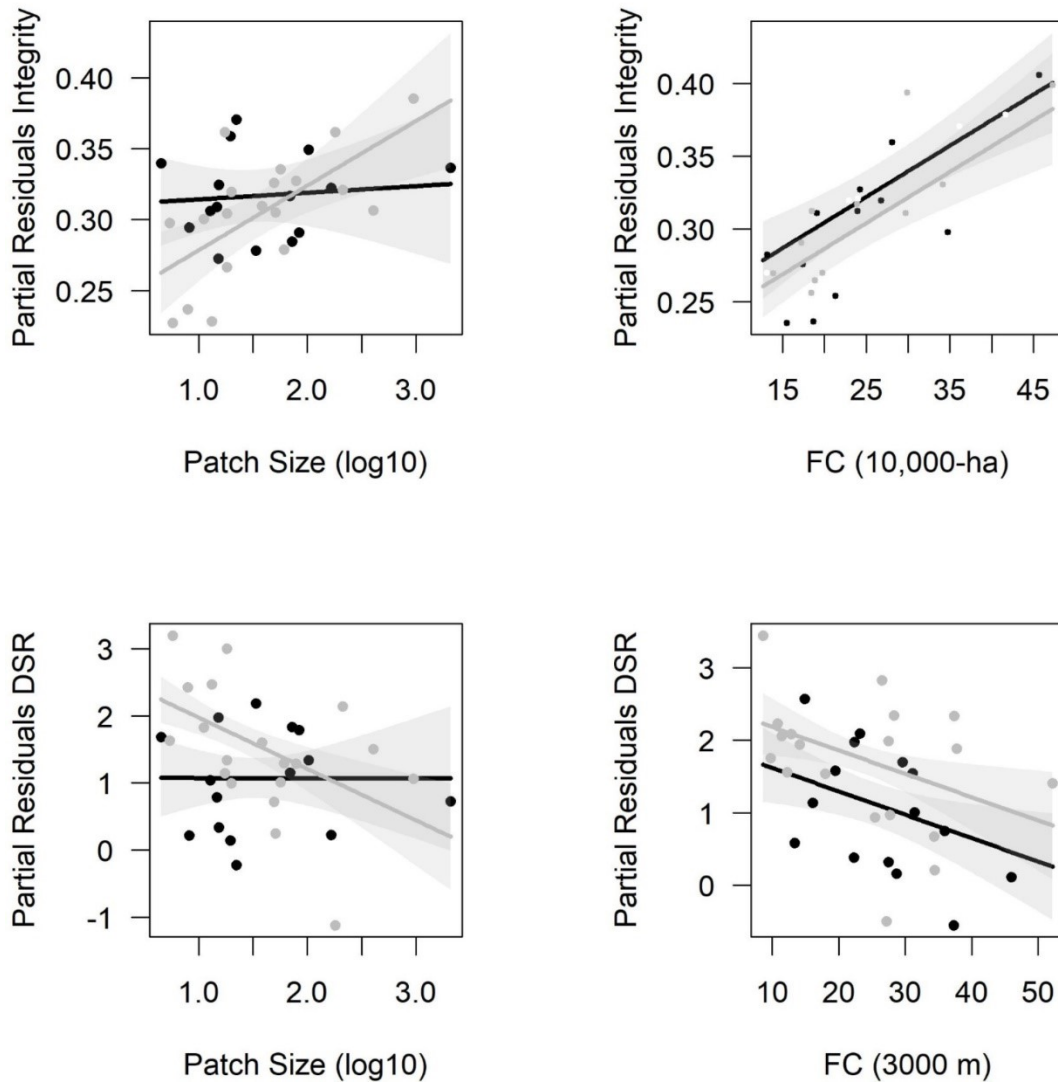
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Figure 3 – Partial residual values for community integrity and disturbance-tolerant species richness (DSR) against patch size in ha (a and c) and percentage forest cover (b and d) for interior transects. Plantation matrix fragments are shown in black,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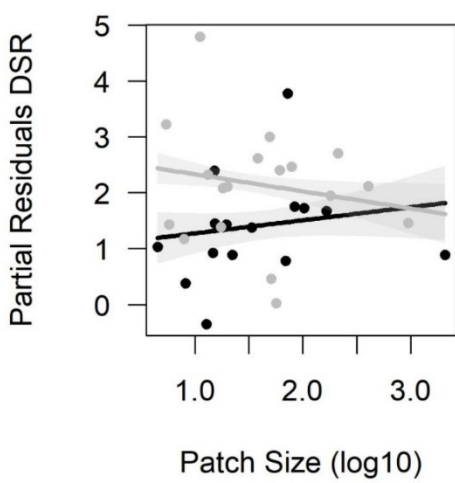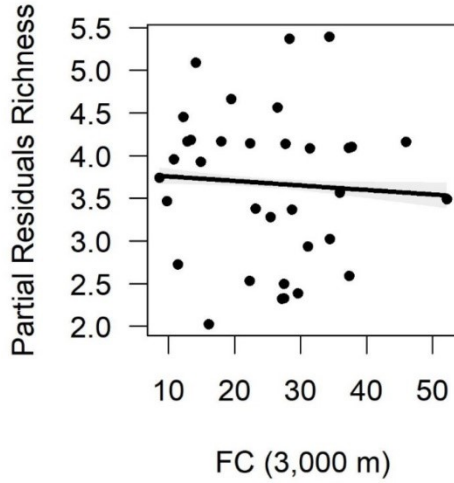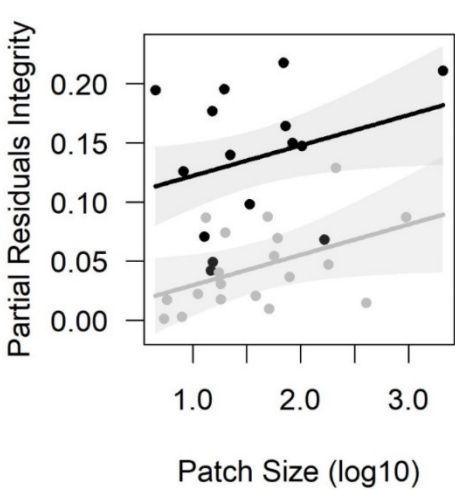
Fragment Edge
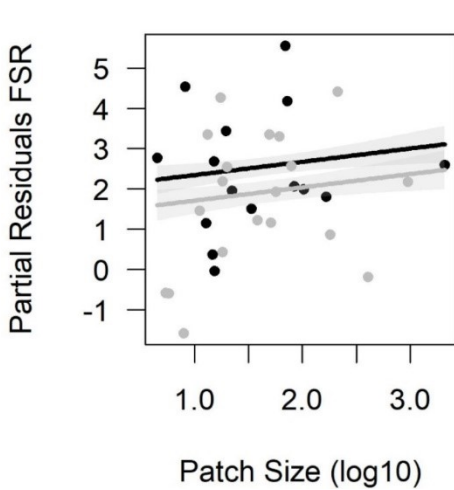
(a)

(b)

(c)

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Matrix

(e)

(f)

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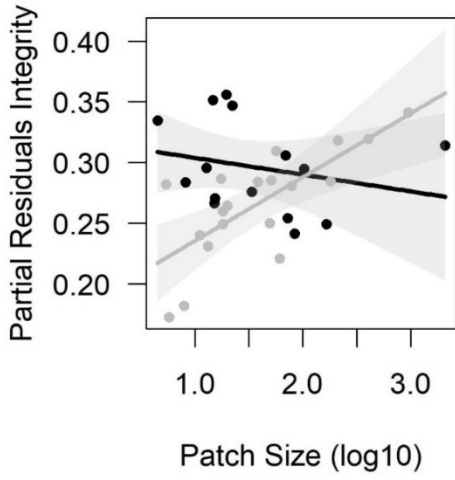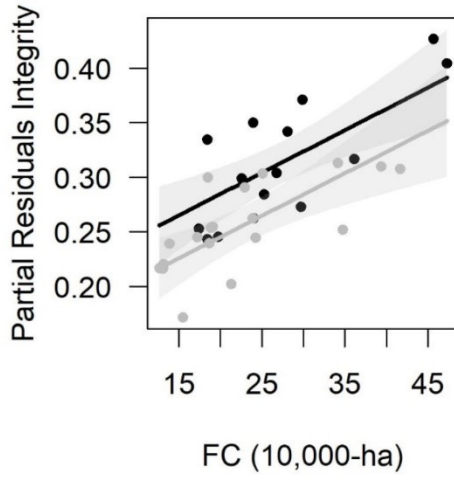
595   **Figure 4 –** Partial residual values for community integrity, species richness, disturbance

596   tolerant species richness (DSR) and forest species richness (FSR) against patch size in ha

597   (b and d) and percentage forest cover (a, c, e and f) for edge (a – d) and matrix (e - f)

598   transects. Plantation matrix fragments are shown in black, pasture in gray. d shows only a

599   single line as matrix type was not found to be influential in this model.

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(a)   (b)
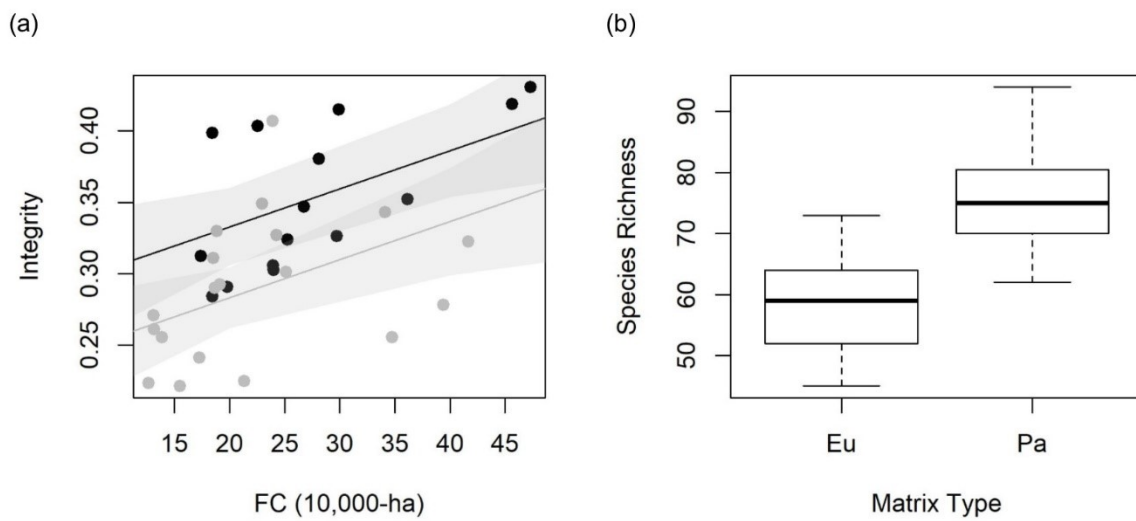
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602   **Figure 5–** Community integrity against forest cover percentage (a) and species richness (b)

603   compared between the two matrix types - *Eucalyptus* plantation (Eu) and pasture (Pa). Gray

604   is used for pasture matrix fragments with black representing plantation.

605