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**Riparian reserves help protect forest bird communities in oil palm dominated landscapes**

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|                               |   |

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Manuscripts

1 **Riparian reserves help protect forest bird communities in oil**  
2 **palm dominated landscapes**

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16

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1

## 23 **Summary**

- 24 1. Conversion of forest to oil palm agriculture is a significant and continuing threat to  
25 tropical biodiversity. Despite this, little is known about the value of riparian reserves  
26 in oil palm and how these conservation set-asides might best be managed to maintain  
27 biodiversity.
- 28 2. We characterised bird communities of 28 sites in an oil palm-forest mosaic in Sabah,  
29 Malaysia using 6104 encounters from 840 point counts. Sites included oil palm  
30 riparian reserves of various vegetation quality and reserve widths, which were  
31 compared to oil palm streams without a riparian reserve as well as riparian and non-  
32 riparian control areas in continuous logged forest.
- 33 3. Riparian reserves, oil palm waterways, and control sites in riparian and non-riparian  
34 forest supported distinct avifaunal communities. Riparian reserve width, forest  
35 quality and amount of forest cover were the strongest predictors of bird species  
36 richness. For forest-dependent species, each of these predictors had stronger effect  
37 size when compared with all species. On average, reserves held 31% of all species  
38 and 30% of forest specialists, whereas riparian forest controls averaged 32% of all  
39 species, but 38% of forest species.
- 40 4. Riparian reserves with >40 m of natural vegetation on each bank supported similar  
41 bird diversity to riparian forest control habitats found in continuous forest. However,  
42 to support equivalent numbers of forest-dependent species and species of  
43 conservation concern, reserves would need to be at least 100 m wide on each bank.  
44 The highest numbers of species were found in riparian reserves with above-ground  
45 carbon densities exceeding  $75 \text{ tC ha}^{-1}$ , highlighting the importance of forest quality,  
46 as well as width, in supporting riparian bird communities.
- 47 5. *Synthesis and applications.* If designed and protected appropriately, riparian reserves  
48 in oil palm estates support diverse bird communities, including many species of  
49 conservation concern. This can be achieved by designating large reserves (80-200 m

50 total width), but to maximize species numbers forest disturbance should also be  
51 minimised prior to conversion as well as during plantation operations.

52

53 **Key-words:** agriculture, riparian buffer, riparian zone, biodiversity, land-use change,  
54 fragmentation, landscape configuration, forest management.

55

## 56 **Introduction**

57 Human activities are causing unprecedented biodiversity decline (Pimm *et al.* 2014), with  
58 agricultural expansion being a primary cause of tropical species loss (Gibson *et al.* 2011). At  
59 least 522 Mha of tropical forest was converted between 1980 and 2000 (Gibbs *et al.* 2010)  
60 and a further 150 Mha was lost between 2000 and 2012 (Hansen *et al.* 2010). A major  
61 contributor to this problem has been oil palm cultivation (*Elaeis guineensis*), which is now  
62 one of the most profitable land-uses in the tropics, with continued demand (Vijay *et al.* 2016).  
63 Meeting this demand will require improved productivity on existing estates, as well as  
64 expansion of the crop into new areas.

65 Tropical production landscapes harbour significantly less biodiversity than native  
66 forest (Gibson *et al.* 2011); a pattern documented in many agricultural land-uses, including  
67 fruit orchards (Round *et al.* 2006), rubber plantations (Warren-Thomas *et al.* 2015), and oil  
68 palm under both smallholder cultivation (Azhar *et al.* 2011) and industrial production  
69 (Edwards *et al.* 2010). Retaining forest remnants within human-modified tropical landscapes  
70 can therefore enhance biodiversity levels (Laurance *et al.* 2018), although crop yields are  
71 likely to be reduced as a consequence (Edwards *et al.* 2010). Forest patches are maintained  
72 typically on slopes, floodplains, or along waterways.

73 Waterways and riparian areas are often afforded legal protection in tropical countries  
74 to mitigate flooding and sedimentation (Mayer *et al.* 2007). In Malaysia, for example,

75 agricultural companies are required to maintain riparian reserves of between 5 and 50 m from  
76 each riverbank, with most being 20-30 m (Government of Malaysia, 2012). In Brazil reserves  
77 can be 30-500m wide depending on channel width, but recent policy changes drastically  
78 reduce the prescribed widths (da Silva *et al.*, 2017). In addition, oil palm companies that  
79 adhere to guidelines under the Roundtable for Sustainable Palm Oil (RSPO), the primary  
80 environmental certification scheme for this crop, agree to retain riparian reserves, and there  
81 are ambitions to increase the width requirements (Luke *et al.* Submitted).

82         While the main rationale for protecting riparian reserves is hydrological, these  
83 habitats may also be important for maintaining wildlife populations. In Sumatra, riparian  
84 reserves in paper-pulp plantations support large-mammal communities comparable to those in  
85 continuous forest (Yaap *et al.* 2016), and in Amazonia large and undisturbed riparian reserves  
86 retain near-complete mammal and bird assemblages when compared to large forest patches  
87 (Lees & Peres, 2008; Zimbres *et al.* 2017). In Borneo, fish (Giam *et al.* 2015), dung beetle  
88 and leaf-litter ant (Gray *et al.* 2014, 2016) assemblages in oil palm riparian reserves are more  
89 similar to those in contiguous logged forests than the surrounding oil palm matrix in terms of  
90 composition, species diversity and functional group diversity.

91         The species composition of riparian remnants is likely to be influenced by many of  
92 the processes associated with habitat fragmentation, such as area, isolation and edge effects  
93 (Laurance *et al.* 2018). Area, or width of the riparian remnant, is expected to be a primary  
94 determinant of diversity, yet few researchers have documented this in tropical regions, and  
95 even fewer provide explicit width recommendations to inform riparian reserve design (Luke  
96 *et al.* Submitted). In the neotropics, riparian zones are reported to extend to 60-250 m for  
97 plants (Schiatti *et al.* 2014), 100 m for snakes (de Fraga *et al.* 2011) and 140 m for understory  
98 birds (Bueno *et al.* 2012), but since these studies were undertaken in forested areas it is  
99 unclear whether the same width thresholds would apply in fragmented habitats or agricultural  
100 systems, or indeed to other tropical regions (van der Hoek *et al.*, 2015).

101           Here, we explore the relationships between riparian reserve width, forest quality, and  
102 the birds present in a modified tropical landscape of Southeast Asia. Specifically, we  
103 characterised bird communities in riparian reserves set in forest or oil palm to evaluate the  
104 relative value for riparian and non-riparian biodiversity. Reserve width, the main criterion  
105 stipulated in environmental policy, is expected to correlate positively with species richness,  
106 with more species supported in wider reserves (e.g. Lees and Peres, 2008; Gray *et al.* 2014;  
107 Zimbres *et al.* 2017). However, the expected levels of species richness might not be supported  
108 if the habitat quality is low (Luke *et al.* Submitted). Given the roles of other confounding  
109 variables in the fragmentation literature (Laurance *et al.* 2018), it is important to understand  
110 how measures of patch size (i.e. width) and quality affect riparian remnant biodiversity in the  
111 context of the wider landscape covariates (e.g. elevation, isolation). There is also fundamental  
112 policy interest in establishing whether the largest riparian reserves can support similar levels  
113 of biodiversity to continuous forest sites, since protecting larger/wider reserves involves a  
114 trade-off between conservation interests and making land available for agriculture. We sought  
115 to address these questions, while also examining whether riparian reserves are valuable for  
116 forest-dependent species and species of conservation concern, since these taxa are the focus  
117 of environmental policy in the certification sector.

118

## 119 **Methods**

### 120 ***Study system***

121 The study was set in and around the Stability of Altered Forest Ecosystems (SAFE) project  
122 (117.5°N, 4.6°E) in Sabah, Malaysian Borneo (Fig. 1, Ewers *et al.* 2011). The 80,000 ha area  
123 comprises both forest and plantations of oil palm and *Acacia*, with all matrix study sites  
124 surrounded by oil palm. Most of the remnant forest has been logged two to four times over 30  
125 years and contains few mature trees (Struebig *et al.* 2013), although some parts are less



126 disturbed and are formally protected. The surrounding agricultural matrix comprises multiple  
127 oil palm estates with trees planted 8-12 years before the study. Within this matrix, remnants  
128 of logged forest are protected alongside watercourses as riparian reserves. Reserves typically  
129 extend ca. 50 m on each bank from the river channel, but vary between 10 and 470 m  
130 (median=54 m, SD=135 m) across the landscape. Reserves also vary in altitude, topographic  
131 ruggedness and substrate (rocky to sandy).

132 We sampled bird communities alongside 20 rivers. Ten of the rivers were within oil  
133 palm plantation and had riparian reserves (RR), two were in the oil palm with no riparian  
134 reserve and were used as controls (OPR), and a further eight rivers were used as controls  
135 within the logged forest (hereafter riparian forest control; RFC). The rivers sampled in oil  
136 palm were selected to represent the range and distribution of reserve widths present across the  
137 study area and plantations elsewhere in Southeast Asia. Larger riparian reserves were scarce  
138 and only one site of >100m was available in our study area (RR17, width = 470 m). Forest  
139 quality, indicated by above-ground carbon density measured via LiDAR (Jucker *et al.* 2018),  
140 also varied substantially across the landscape. Finally, to document any differences between  
141 riparian and non-riparian bird communities, we also surveyed eight non-riparian control sites  
142 in continuous forest (hereafter forest control; CF), all of which had also been previously  
143 logged, reflecting the dominant remnant forest type in lowland Southeast Asia.

144

#### 145 ***Bird sampling***

146 At each riparian site, birds were sampled via ten point counts set at 180-220 m intervals  
147 (Euclidian distance) along a 2 km transect following the course of the river. The stations were  
148 situated up to 10 m up the riverbank to minimise interference from the sound of running  
149 water. During each count, a single experienced observer (SLM) recorded all bird species  
150 heard or seen within a 50 m radius of the point for 15 minutes including fly-overs. Average

151 river width ranged between 5 and 13 m, meaning that the detection radius encompassed both  
152 terrestrial vegetation and the river. However, the river itself never accounted for more than  
153 5% of the total point count area. Counts were conducted between 05:50 and 11:00 in clear  
154 weather, and were repeated on three separate occasions at each site between 2014 and 2016.  
155 For non-riparian sites, the ten point counts were spatially configured at comparable distances  
156 along access trails. Sites were sampled at mean intervals of 72 days between visits (Table S1).  
157 Three species of swift (*Aerodramus maximus*, *A. salangana* and *A. fuciphagus*) could not be  
158 reliably separated and are considered as *Aerodramus spp.* The bird sampling data from the  
159 three surveys were pooled across the ten stations at each site. Taxonomic nomenclature  
160 follows Eaton *et al.* (2017).

161

#### 162 ***Environmental predictors of bird community structure***

163 For each site above-ground carbon density (mean values across the ten point counts sites)  
164 were derived from remotely sensed data, and used as a proxy for overall forest quality, since  
165 lower carbon densities were evident in areas that experienced the most degradation via  
166 logging (Jucker *et al.*, 2018). Similarly, we also calculated altitude and topographic  
167 ruggedness for each site as an average of values extracted within a 50 m radius of each of our  
168 ten point stations. Above-ground carbon density was extracted from LiDAR-derived datasets  
169 (30 x 30 m), which were gathered in November 2014 using a Leica ALS50-II sensor (Jucker  
170 *et al.* 2018). Altitude (30 x 30 m) was estimated from the Shuttle Radar Topography Mission  
171 (SRTM; <http://www2.jpl.nasa.gov>). Likewise, topographic ruggedness was derived using the  
172 SRTM, according to Wilson *et al.* (2007). Average values for each raster layer were  
173 calculated within the buffer radius of each station using the R 3.2.3 (R Core Development  
174 Team, 2015) packages 'raster', 'sp', 'rgdal', 'gtools' 'doMC' and 'maptools' (Hijmans & van  
175 Etten, 2002; Pebesma & Bivand, 2005; Bivand *et al.*, 2016; Analytics Revolution, 2014;  
176 Bivand & Levin-Koh, 2013)

177 For each riparian reserve sampled, we estimated reserve width at each station from  
178 the LiDAR canopy height layer (5 m resolution). The width of the river channel was included  
179 in this remote measurement as vegetation often obscured the riverbanks. River channel width  
180 was recorded in the field, between the high water marks of the two banks, using a laser  
181 rangefinder (Leica Rangemaster CRF 1000). Subsequently, this value was subtracted from the  
182 reserve width estimate to determine the actual land surface within each reserve. Mean bank  
183 reserve width is typically referenced within environmental policy documents, so we use this  
184 metric throughout the paper.

185 As a measure of landscape-scale forest availability, we also calculated percentage  
186 forest cover within a 1000 m radius of each point count station, capturing the availability of  
187 forest in the landscape without overlapping forest associated with other sample sites. All  
188 environmental predictors were average values across the ten point count stations per site.

189

### 190 *Statistical analyses*

191 Species accumulation curves were constructed for each site and habitat type, and inspected  
192 for being close to asymptote to confirm that sampling was adequate (Fig. S1). Rarefied  
193 curves, based on 100 iterations, were produced using the ‘vegan’ package in R (Dixon, 2003).  
194 We used the number of bird encounters, rather than absolute numbers, to generate curves, as  
195 early morning roost flights of Sunda yellow-vented bulbul (*Pycnonotus analis*) occasionally  
196 resulted in >100 individuals recorded from a single point. In this case, large numbers of a  
197 single species recorded within one visit were treated as a single encounter.

198 We used a generalised linear modelling (GLM) framework in ‘lme4’ to explore the  
199 partitioning of species abundance and richness by habitat type. Spatial autocorrelation was  
200 assessed using a Moran’s I test on the residuals of the GLM for richness across all riparian  
201 sites to test for unforeseen associations between nearby sites. The package ‘multcomp’ was

202 used to perform Tukey tests between pairwise habitat combinations (RFC vs. CF, RFC vs.  
203 OPR, etc.), and the procedure repeated for two subsets of our community: forest-dependent  
204 species (defined by consensus of five expert ornithologists in Southeast Asia, Nick Brickle,  
205 Frank Rhiendt, Dave Bakewell, Craig Robson and Simon Mitchell), and species of  
206 conservation concern (status of near-threatened through to critically endangered, IUCN,  
207 2017).

208 To visually demonstrate the associations between both carbon density and reserve  
209 width, and community structure we plotted the relationships graphically. Community integrity  
210 was measured using the Bray Curtis dissimilarity index on an abundance matrix (sensu  
211 Banks-Leite *et al.* 2014). We used mean differences in species composition between riparian  
212 reserves (RR) and each of the riparian forest controls (RFC) to reflect reductions in  
213 community integrity.

214 Ordinations were used to explore bird species composition in relation to habitat type  
215 and our environmental predictors. Pairwise Bray Curtis dissimilarity coefficients were  
216 calculated between species abundances pooled from across the three visits at each site and  
217 non-metric multidimensional scaling (NMDS) ordinations generated using PC-ORD 6.07  
218 (McCune & Mefford 2011), to organise sites by similarity in species composition. The  
219 reliability of the ordinations was determined by comparing NMDS solutions produced from  
220 250 runs of real data, with those produced from randomised species-site matrices using a  
221 Monte Carlo test. The ordinations were then repeated to ensure that they reflected  
222 representative signals in community data and were not being disproportionately impacted by  
223 either rare (by removing species recorded only once within the dataset) or highly abundant  
224 species (by square-root transformation of all abundances) following Struebig *et al.* (2013).  
225 Non-parametric permutations tests (ADONIS, in 'vegan') were used to examine  
226 compositional differences between habitat types. We also investigated which species were  
227 most associated with particular habitat types using the indicator species analysis INDVAL in  
228 PC-ORD (Dufrene & Legendre, 1997).

229 GLMs were used to determine whether species richness was driven by our potential  
230 environmental predictors (river channel width, riparian reserve width, landscape-scale forest  
231 cover and above-ground carbon density) at our 20 riparian sites. We selected Gaussian family  
232 models, as this best reflected the probability distribution of species richness. All predictor  
233 variables were tested for collinearity. As ruggedness and altitude were correlated ( $r > 0.18$ ),  
234 ruggedness was retained in the riparian reserve models, because the range of values was  
235 greater than for altitude, and altitude was retained in the other models for the same reason.

236 To examine the influence of the environmental predictors on species composition, we  
237 constructed generalised linear mixed effects models (GLMMs) for our two NMDS axes for  
238 all habitat types. Habitat type was included as a random variable. Oil palm river communities  
239 were excluded from these analyses as species composition was very different from that in  
240 other habitat types and this signal obscured any other potential patterns of interest. Parameters  
241 were model-averaged across all models within  $\Delta AIC < 4$  of the best model. The modelling  
242 process was repeated for forest-dependent species and species of conservation concern  
243 separately.

244

## 245 **Results**

### 246 *Species abundance and richness*

247 Across the 28 sites, we detected 8784 individual birds (6104 encounters), of 202 species,  
248 including 133 forest-dependent species (3838 encounters, 4939 individuals) and 62 (821  
249 encounters, 1094 individuals) species of conservation concern. Our species accumulation  
250 curves approached an asymptote for both site and habitat type, confirming that we had  
251 sampled the avifauna well enough to assess differences in richness and community structure  
252 between them (Fig. S1).

253 Birds were more abundant in riparian reserves than riparian forest controls and oil

254 palm rivers, but similar to those in non-riparian forest controls (Fig. 2a). Riparian reserves  
255 supported similar levels of bird species richness to riparian forest controls, and double that  
256 recorded in oil palm rivers (Fig. 2b).

257 Forest-dependent species accounted for 65% of all individuals across the whole  
258 community, and were significantly more prevalent in both non-riparian and riparian forest  
259 controls than in riparian reserves or oil palm rivers (70% in CF; 74% in RFC; 54% in RR;  
260 20% in OPR; Fig. 2c). Forest-dependent species richness was highest in both forest control  
261 types and significantly lower in oil palm rivers (Fig. 2d).

262 Species of conservation concern comprised 13% of all individuals across the  
263 landscape, and formed a larger component of the bird community in riparian (18%) and non-  
264 riparian forest controls (16%), compared to those in riparian reserves (11%) and oil palm  
265 rivers (2%). There was no significant difference in the number of species of conservation  
266 concern found in riparian reserves and riparian forest control sites in terms of either  
267 abundance or richness (Fig 2f, g). Species richness was not influenced by spatial  
268 autocorrelation (Moran's I test; observed = -0.04,  $P=0.80$  of GLM residuals for model  
269 including habitat type, above-ground carbon density and reserve width).

#### 270 ***Bird community composition***

271 Our NMDS ordination of community composition performed better than those based on  
272 randomised data (Monte Carlo test: observed stress=12.4; simulated stress=28.7;  $P=0.004$ ;  
273 Fig. 3a), and showed four clear habitat groupings. The most divergent were the oil palm  
274 rivers, which supported an almost entirely different bird community to other sites.  
275 Communities in riparian reserves were more similar to those in riparian and non-riparian  
276 controls, but still distinct from both habitat types in terms of species composition. Since the  
277 oil palm rivers had such a strong influence on the landscape-wide ordination, we removed  
278 them in our subsequent analyses to better discriminate between the remaining habitat types.

279 Our subsequent NMDS represented 89% of the variation in bird community structure  
280 (stress=14.8). None of the models were improved significantly after removal of singletons  
281 and square-root transformation of species abundance; as indicated by an increase in stress  
282 (16.35).

283 Species composition was significantly different across all four habitat types  
284 (ADONIS:  $R^2=0.11$ ,  $P=0.01$ ). The same pattern was evident when restricted to just forest-  
285 dependent species and species of conservation concern (Fig. 3; forest-dependent species:  
286  $R^2=0.13$   $P=0.01$ ; species of conservation concern:  $R^2=0.14$ ,  $P=0.01$ ).

287 Community integrity in riparian sites showed similar patterns to our ordinations, in  
288 that riparian reserves were intermediate to riparian forest controls and oil palm rivers (Fig 2c,  
289 e, h).

290 Indicator species analysis revealed 13 significant associations between particular bird  
291 species and habitat types, including four species associated with non-riparian forest controls,  
292 seven of oil palm rivers, and one each for riparian reserves and the riparian forest controls  
293 (Table S2).

#### 294 *Environmental predictors of riparian reserve communities*

295 Our GLMMs demonstrated that riparian reserve width was an important predictor of bird  
296 species richness and avian community composition (Table 1; Fig. 4). Reserve width and  
297 above-ground carbon density affected bird richness in a consistent manner. None of the other  
298 environmental metrics we tested had a demonstrable effect in our final models.

299 Riparian reserve width, above-ground carbon density and forest cover were all  
300 significant positive predictors of observed species richness for the full community (Table 1).  
301 This pattern was the same for forest-dependent species, though did not apply to species of  
302 conservation concern. Across all riparian habitats, above-ground carbon was a significant  
303 positive predictor of species richness for both forest-dependent taxa and species of

304 conservation concern. However, our final model for riparian habitats did not reveal any  
305 significant predictors across all species. Forest cover was an important predictor of  
306 community structure as reflected by the NMDS axis 1 for species of conservation concern.  
307 The second axes of our NMDS analyses exhibited no significant relationship with the  
308 environmental predictors.

309 Community subsets for all species, forest-dependent species and species of  
310 conservation concern differed in the reserve width at which richness was equal to that found  
311 in riparian forest controls (Fig. 4). Trend lines intersected mean richness levels for riparian  
312 controls at ca. 40 m when all species were examined. However, for forest-dependent taxa and  
313 species of conservation concern, riparian reserves did not reach equivalent richness levels to  
314 that found at control sites. The extent of this pattern with above-ground carbon density also  
315 varied between community subsets (Fig. 4d, e, f). Notably, reserve richness reached  
316 equivalent levels to control sites at around 65 tC ha<sup>-1</sup> for all species, but at around 100 tC ha<sup>-1</sup>  
317 for forest-dependent and species of conservation concern subsets.

318

## 319 **Discussion**

320 We found that riparian reserves in oil palm, supported comparable levels of bird diversity to  
321 sites in continuous forest (both CF and RFC), especially when reserves are wide and comprise  
322 high carbon forest. However, these reserves contained fewer forest-dependent taxa and  
323 species of conservation concern, which likely require larger tracts of continuous forest for  
324 long-term population viability. These results suggest that the mandated reserve width in many  
325 tropical countries should be increased. In tandem, forest quality in riparian reserves should be  
326 improved: in new plantations by delineating reserves prior to clearance and preventing  
327 additional logging within them; in existing heavily degraded reserves via vine cutting and  
328 planting with native trees, plus by replanting in areas where crops were planted to river banks  
329 and no riparian reserves retained. Our appraisals of forest-dependent taxa and species of



330 conservation concern also demonstrate that not all species are well represented in riparian  
331 reserves and it is likely that these taxa require larger tracts of continuous forest for long-term  
332 population viability.

333         Despite a growing number of ecological studies on tropical riparian reserves, there is  
334 still little information regarding which features have the greatest benefit for biodiversity  
335 (Luke *et al.*, 2018.). For birds in oil palm, we find that riparian reserve width is an important  
336 predictor of overall number of species, with reserves at least 40 m wide (i.e., 80 m total  
337 width) supporting comparable numbers of species to riparian forest controls. Nonetheless, to  
338 support equivalent numbers of forest-dependent taxa and species of conservation concern,  
339 riparian reserves would need to be much larger - at least 100 m wide (200 m total width),  
340 based on extrapolation of observed trend lines (Fig. 4b, c). We can only extrapolate, as large  
341 riparian reserves are scarce in our study system and oil palm landscapes in general. It  
342 therefore remains to be seen whether all forest-dependent taxa and species of conservation  
343 concern present in logged forest would actually use riparian reserves even if they were of  
344 substantial width and close to continuous forest.

345         Uniquely for oil palm landscapes, our results demonstrate the influence of forest  
346 quality (as measured by above-ground carbon density), as well as reserve width, on the  
347 riparian reserve avifauna. These finding suggests that protecting reserves of poor forest  
348 quality will offer few conservation gains without habitat restoration. Similar findings have  
349 been reported from cattle ranching areas in Amazonia, where riparian reserve width and  
350 percentage canopy cover were both positively related to bird and mammal richness (Lees &  
351 Peres, 2008; Zimbres *et al.* 2017). This result implies that approaches to restore biodiversity  
352 in agricultural areas may be less successful than sparing areas for conversion in the first place,  
353 especially because small forest patches, such as riparian reserves, are susceptible to further  
354 degradation via edge effects (Laurance *et al.* 2018). Disentangling this relationship is  
355 difficult, however, as both larger fragments and reserves tend to be of higher forest quality  
356 than smaller ones (e.g. Lees and Peres 2008).

357 Many previous studies have only compared riparian reserves with the communities of  
358 continuous non-riparian forest controls (e.g. Gray *et al.*, 2014). We show that, while overall  
359 richness remains comparable to non-riparian control sites in continuous forest, bird  
360 community composition in riparian reserves is intermediate between that of riparian controls  
361 (RFC) and oil palm rivers (OPR) (Fig 2, 3). While there were many species shared between  
362 riparian reserves and riparian forest habitat, reserves also had some generalist species (e.g  
363 *Spilopelia chinensis* [spotted dove], *Geopelia striata*, [zebra dove] *Copsychus saularis*,  
364 [oriental magpie robin] and *Pycnonotus analis* sunda [yellow-vented bulbul]) that were rare  
365 or absent in both riparian and non-riparian forests controls (i.e. CF and RFC). These matrix-  
366 dwelling species are known to be abundant in both industrial oil palm plantations (Edwards *et*  
367 *al.* 2010) and mixed smallholder cultivation (Azhar *et al.* 2011). Riparian reserves also lacked  
368 several forest-dependent taxa and species of conservation concern, in accordance with  
369 previous studies, which found small forest fragments to support few specialist species  
370 (Laurance *et al.* 2018). Across all riparian reserves, we recorded over 70% of the community  
371 found in non-riparian forest and over 80% (Fig. S1) of the community found in riparian forest  
372 control areas. However, the highly different community composition (Fig. 3) and lower site-  
373 level species richness (Fig. 2) suggests that such forest species are found in greatly reduced  
374 numbers in riparian reserves.

375 We found that bird communities around oil palm rivers without a reserve were highly  
376 depauperate, consistent with species richness observed in previous oil palm studies (Edwards  
377 *et al.* 2010; Azhar *et al.* 2011). Thus, the presence of rivers *per se* appears to have little effect  
378 on bird diversity in the absence of significant amounts of natural vegetation. This stark  
379 difference was clear even for sites with degraded reserves, highlighting that narrow, low  
380 quality riparian reserves can still have a significant positive effect on bird community  
381 structure albeit a small one. Crucially, narrow and degraded reserves still held more forest-  
382 dependent taxa and species of conservation concern than oil palm on its own, although at  
383 much lower numbers than in large riparian forest areas.

384           It is possible that species recorded in riparian habitats are not part of a viable  
385 population and that the reserves are sinks (Gilroy & Edwards, 2017). For example, Weldon &  
386 Haddad (2005) demonstrated that indigo buntings (*Passerina cyanea*) in small fragments  
387 continued to nest in patches with greater forest edge despite increased mortality. Likewise,  
388 small fragmented areas of habitat are far more susceptible to further perturbations and edge  
389 effects than large continuous forests (Ewers *et al.* 2007), which can result in extinction  
390 cascades long after fragmentation has taken place (Kitzes and Hartle, 2015). Alternatively,  
391 riparian reserves could act as movement corridors between larger, higher quality, areas of  
392 forest. In the context of land-use change, facilitating species dispersal in this way could be  
393 vital in maintaining viable populations in otherwise isolated remnant habitat fragments  
394 (Capon *et al.* 2013), particularly for interior forest bird species (Gillies & St. Clair, 2008).

395           Riparian forest in both riparian controls and riparian reserves held distinct bird  
396 communities to other sites. For instance, *Butorides striatus* and *Alcedo meninting* were only  
397 recorded in riparian habitats, while *Enicurus ruficapillus*, a species of conservation concern  
398 (near-threatened), was identified as an indicator of riparian forest controls (Table S2).  
399 Microclimate, vegetation structure and prey abundance have been found to differ between  
400 riparian and non-riparian habitats in Hong Kong, and these changes correlated with  
401 differences in bird species richness and abundance (Chan *et al.* 2008). This emphasises the  
402 value of including a riparian forest as a comparator, rather than just non-riparian continuous  
403 forest. It also demonstrates that spatial turnover in species composition between riparian and  
404 non-riparian sites is greater than that within just one habitat type, indicating that riparian areas  
405 have an additional effect on regional species richness (Sabo *et al.* 2005).

406

#### 407 ***Management recommendations***

408 Our results warrant several recommendations for the improved management of riparian  
409 reserves in the tropics. These are not mutually exclusive, but each would have different

410 outcomes for bird communities if adopted. First, increasing minimum reserve widths to at  
411 least 40 m on each bank would improve bird diversity to levels typical of riparian areas in  
412 large forest blocks. In tandem with the vine cutting and replanting of native tree species, this  
413 could also benefit forest-dependent species, since reserve width showed a stronger  
414 relationship with forest species richness than it did for overall community richness.

415         Second, the greatest gains in species richness for the smallest loss of cultivated area  
416 could be achieved by replanting vegetation in reserves narrower than 30 m to meet existing  
417 legislative guidelines. This is because the relationship between reserve width and species  
418 richness is non-linear, with the greatest gains in richness occurring at small widths. However,  
419 this would only maximise species richness at the level of individual rivers, whereas effects on  
420 landscape-scale richness and the benefit to forest-dependent species would be less significant.

421         Finally, the biodiversity protection of any future riparian reserves could be greatly  
422 improved by increasing the quality of reserve habitat. This is not just achieved by restoring  
423 degraded habitat in existing plantations, but also by ensuring that contractors follow  
424 environmental regulations while forests are being converted. In countries such as Malaysia,  
425 these restrictions already exist for conventional logging operations (Forest Enactment for  
426 Sabah, 1968). However, narrow riparian reserves are difficult to define and map prior to  
427 clearance and may endure opportunistic removal of valuable timber as a result. Once land has  
428 been re-designated after logging for plantation, this can result in riparian reserves of  
429 substandard forest quality. By improving the enforcement of riparian reserve policy prior to  
430 and during conversion operations, riparian areas of higher forest quality could be maintained.  
431 This is likely to not only benefit threatened biodiversity, but could also have knock on  
432 benefits to other wildlife, hydrological regimes, and water quality downstream.

433

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444

445 **Author contributions:**

446 SLM, MJS, DPE, HB and ZGD conceived and designed the methodology; SLM collected,  
447 processed and analyses bird encounter data; DC and TJ processed LiDAR data; SLM, MJS,  
448 ZGD and DPE led the writing of the manuscript. All authors contributed critically to the  
449 drafts and gave final approval for publication.

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582

583 **Figures**

584 **Fig. 1.** Twenty-eight bird sample sites in riparian (n=20) and non-riparian (n=8) habitat types  
585 in the Stability of Altered Forest Ecosystems (SAFE) landscape and surrounding agricultural  
586 matrix in Sabah, Malaysian Borneo. A site comprised ten point count stations (indicated by  
587 points on the map), each of which were sampled for birds on three separate occasions. Forest  
588 is shown in grey; tree plantations (predominantly oil palm), and cleared areas in white. Forest  
589 cover was derived from Hansen *et al.* (2013) and updated to represent the landscape in 2014  
590 accurately. Black lines denote the river courses.

591

592 **Fig. 2.** Boxplots of site-level bird abundance and species richness across the different habitat  
593 types for: all species; forest-dependent species; and species of conservation concern. General  
594 linear model derived linear hypothesis Tukey tests revealed significant differences in richness  
595 ( $P < 0.05$ ) between all habitat types except for those cases marked non-significant (n.s).

596

597 **Fig. 3.** Nonmetric multidimensional scaling ordinations of bird community structure across  
598 riparian and non-riparian habitat types. Plots show dissimilarity across (a) all species; (b)  
599 forest-dependent species; and (c) species of conservation concern. Oil palm river sites were  
600 excluded from (b) and (c) because they included only seven forest-dependent species and  
601 three species of conservation concern, and therefore could not be plotted within the same  
602 ordination space. Axis scores denote  $R^2$  values.

603

604 **Fig. 4.** Observed species richness for riparian reserve (circles) and oil palm river (squares)  
605 sites in relation to reserve width (on each bank) for all species; forest-dependent species; and  
606 species of conservation concern (a, b, c). Richness values are expressed as percentages of the  
607 median richness from the eight riparian forest control (RFC) sites. Observed species richness  
608 was also significantly positively associated with above-ground carbon density (d, e, f).  
609 Horizontal red shading demonstrates the first and third quartile in the distribution of species  
610 richness across all RFC control sites, with median shown as the black dotted line. Grey  
611 shading around trend lines denotes 95% confidence intervals. One riparian reserve (RR17)  
612 was excluded from the models because of missing environmental data for the site.

613 **Table 1.** Outputs of generalised linear models (GLM) and generalised linear mixed effects  
 614 models (GLMM) showing model averaged parameter estimates, standard error and  
 615 confidence intervals for important predictors of observed species richness and community  
 616 structure. The  $\Delta AIC < 4$  model set was used to estimate averaged outputs. n represents the  
 617 number of sites included in each model. One riparian reserve (RR17) was excluded several  
 618 environmental predictors were missing for this site.

| <b>Predictor</b>  | <b>Parameter estimate</b> | <b>SE</b> | <b>Lower<br/>95% CI</b> | <b>Upper<br/>95 % CI</b> |
|---|---------------------------|-----------|-------------------------|--------------------------|
| <b>GLM: Richness in riparian reserves and oil palm rivers (RR, OPR, n=11)</b> |                           |           |                         |                          |
| <b>All species</b>  |                           |           |                         |                          |
| Intercept   | 63.8                      | 1.1       | 61.2                    | 66.4                     |
| Above-ground carbon density   | 6.1                       | 2.2       | 0.9                     | 11.3                     |
| Forest cover  | 8.3                       | 2.3       | 2.9                     | 13.8                     |
| Riparian reserve width  | 8.6                       | 2.5       | 2.9                     | 14.3                     |
| <b>Forest-dependent species</b>   |                           |           |                         |                          |
| Intercept   | 36.7                      | 1.3       | 33.6                    | 39.8                     |
| Above-ground carbon density   | 6.6                       | 2.6       | 0.5                     | 12.7                     |
| Riparian reserve width  | 10.3                      | 3.0       | 3.4                     | 17.2                     |
| Forest cover  | 8.9                       | 3.0       | 1.9                     | 15.9                     |
| <b>Species of conservation concern</b>  |                           |           |                         |                          |
| Intercept   | 13.4                      | 0.9       | 11.4                    | 15.4                     |
| <b>GLM: Richness in riparian habitats (RR, OPR, RFC, n = 19)</b>              |                           |           |                         |                          |
| <b>All species</b>  |                           |           |                         |                          |
| Intercept   | 59.6                      | 2.5       | 54.3                    | 64.9                     |
| <b>Forest-dependent species</b>   |                           |           |                         |                          |

|                             |       |     |      |      |
|-----------------------------|-------|-----|------|------|
| Intercept                   | 36.1  | 2.0 | 31.9 | 40.3 |
| Above-ground carbon density | 156.0 | 5.3 | 5.0  | 27.0 |

**Species of conservation concern**

|                             |      |     |      |      |
|-----------------------------|------|-----|------|------|
| Intercept                   | 13.3 | 0.8 | 11.6 | 15.0 |
| Above-ground carbon density | 5.2  | 2.6 | 1.8  | 10.0 |

**GLMM: Community structure (NMDS axis 1) in all forest or riparian reserve (RR, RFC, CF, n = 26)**

**All species**

|                             |      |     |      |      |
|-----------------------------|------|-----|------|------|
| Intercept                   | 0.0  | 0.0 | -0.1 | 0.0  |
| Above-ground carbon density | -0.2 | 0.1 | -0.3 | -0.1 |
| Forest cover                | -0.4 | 0.1 | -0.5 | -0.3 |

**Forest-dependent species**

|           |     |     |      |     |
|-----------|-----|-----|------|-----|
| Intercept | 0.1 | 0.4 | -0.7 | 0.9 |
|-----------|-----|-----|------|-----|

**Species of Conservation Concern**

|              |      |     |      |      |
|--------------|------|-----|------|------|
| Intercept    | -0.0 | 0.1 | -0.2 | 0.1  |
| Forest cover | -1.1 | 0.2 | -1.6 | -0.7 |

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619

620

## Supplementary Materials

### Riparian reserves in oil palm can protect forest bird communities

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**Figure S1.** Rarefied bird species accumulation curves for each riparian and control habitat type based on 100 iterations. Grey buffers denote one 95% confidence intervals either side of mean richness values.

**Table S1:** Sampling dates and mean intervals for each site.

| Habitat | Site     | Visit 1    | Visit 2    | Visit 3    |
|---------|----------|------------|------------|------------|
| CF      | A        | 09/05/2014 | 07/07/2014 | 04/08/2015 |
| CF      | B        | 15/05/2014 | 05/06/2014 | 03/03/2015 |
| CF      | C        | 29/04/2014 | 30/06/2014 | 16/05/2015 |
| CF      | D        | 07/05/2014 | 10/06/2014 | 10/03/2015 |
| CF      | E        | 17/05/2014 | 12/06/2014 | 25/06/2015 |
| CF      | F        | 23/05/2014 | 06/07/2014 | 23/06/2015 |
| CF      | LF1      | 05/03/2015 | 24/07/2015 | 25/07/2015 |
| CF      | LFE      | 15/07/2015 | 16/08/2015 | 25/08/2015 |
| RCF     | R0       | 26/05/2014 | 10/02/2015 | 19/02/2015 |
| RCF     | R120     | 28/05/2014 | 17/02/2015 | 26/02/2015 |
| RCF     | R15      | 21/05/2014 | 13/02/2015 | 24/02/2015 |
| RCF     | R30(OLD) | 06/06/2014 | 18/02/2015 | 27/02/2015 |

|     |       |            |            |            |
|-----|-------|------------|------------|------------|
| RCF | R5/30 | 27/05/2014 | 11/02/2015 | 20/02/2015 |
| RCF | R60   | 19/05/2014 | 14/02/2015 | 23/02/2015 |
| RCF | RLF   | 01/05/2014 | 12/02/2015 | 22/02/2015 |
| RCF | VJR   | 30/07/2015 | 11/07/2015 | 06/08/2015 |
| RR  | RR10  | 29/10/2016 | 14/11/2016 | 15/11/2016 |
| RR  | RR12  | 14/07/2015 | 28/07/2015 | 03/08/2015 |
| RR  | RR14  | 27/06/2015 | 30/06/2015 | 27/07/2015 |
| RR  | RR16  | 28/06/2015 | 10/07/2015 | 07/08/2015 |
| RR  | RR17  | 21/11/2016 | 23/11/2016 | 24/11/2016 |
| RR  | RR19  | 20/11/2016 | 05/12/2016 | 05/12/2016 |
| RR  | RR2   | 22/07/2016 | 23/07/2016 | 19/11/2016 |
| RR  | RR20  | 28/11/2016 | 30/11/2016 | 02/12/2016 |
| RR  | RR3   | 19/07/2016 | 20/07/2016 | 21/07/2016 |
| RR  | RR7   | 06/06/2014 | 24/05/2015 | 24/06/2015 |
| OPR | ROP10 | 27/11/2016 | 29/11/2016 | 30/11/2016 |
| OPR | ROP2  | 16/11/2016 | 17/11/2016 | 18/11/2016 |

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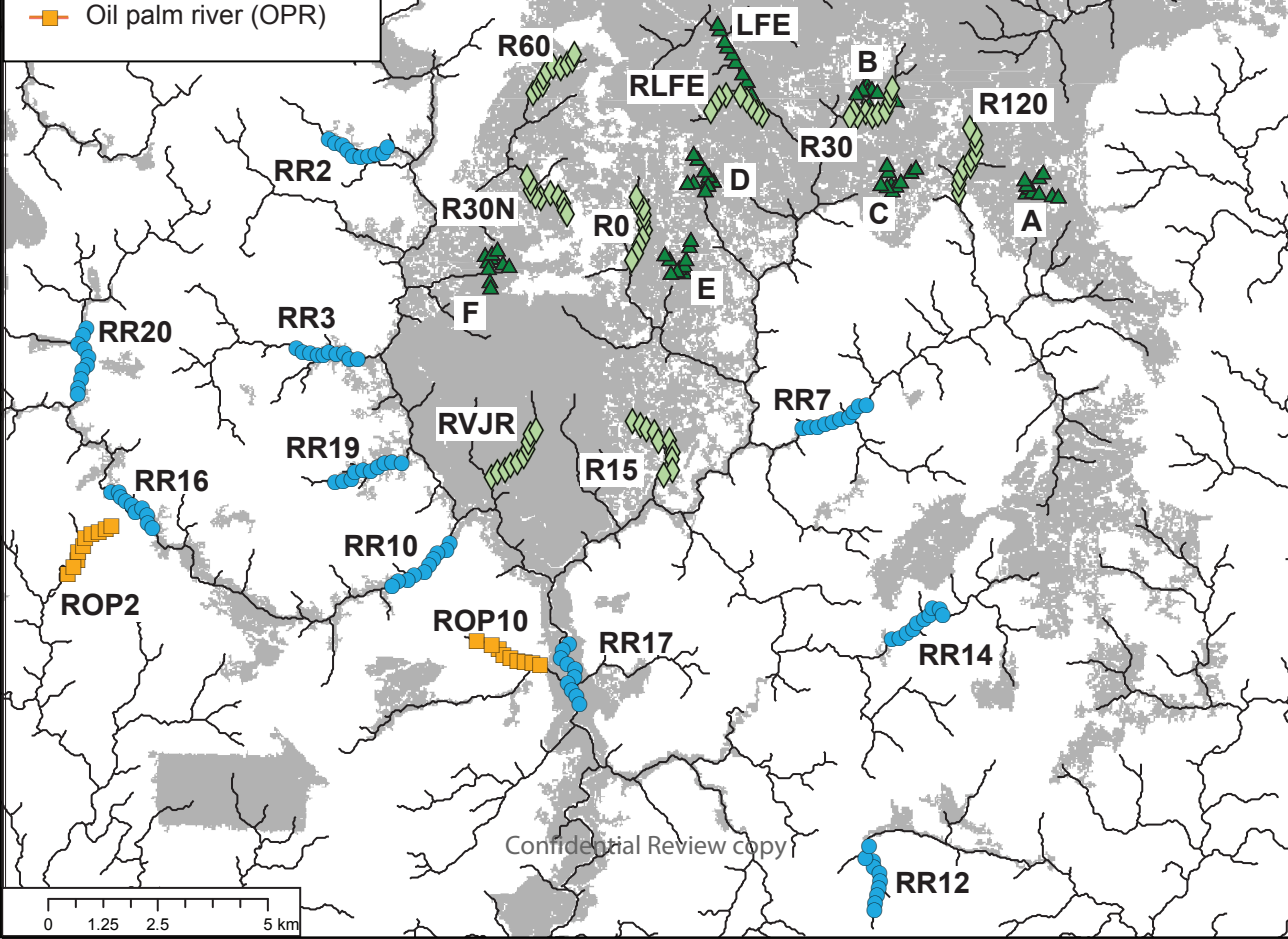
**Table S1.** Thirteen indicator bird species showing significant associations ( $p < 0.05$ ) with different habitat types (continuous forest, CF; logged forest riparian, LFR; riparian reserves, RR; oil palm riparian controls, OPR), according to the INDVAL algorithm (Dufrene & Legendre, 1997). Relationships with non-metric multidimensional scaling axes (Axis 1=A1, Axis 2=A2) for each species are shown as  $R^2$  and Tau correlation coefficients.

| Species                             | Habitat | IV   | Mean | SD    | A1 $R^2$ | A1<br>Tau | A2<br>$R^2$ | A2<br>Tau |
|-------------------------------------|---------|------|------|-------|----------|-----------|-------------|-----------|
| <i>Malacopteron<br/>magnirostre</i> | CF      | 61.4 | 29.1 | 10.43 | 0.242    | -0.48     | 0.32        | -0.46     |
| <i>Pycnonotus<br/>simplex</i>       | CF      | 54.7 | 29.4 | 9.65  | 0.015    | -0.03     | 0.31        | -0.43     |
| <i>Copsychus<br/>pyrropygus</i>     | CF      | 50.0 | 20.6 | 12.46 | 0.774    | 0.69      | 0.003       | -0.04     |
| <i>Phaenicophaeus<br/>diardi</i>    | CF      | 43.1 | 21.5 | 11.66 | 0.028    | -0.15     | 0.30        | -0.44     |
| <i>Enicurus<br/>ruficapillus</i>    | LFR     | 61.6 | 25.1 | 12.08 | 0.212    | -0.46     | 0.00        | 0.06      |
| <i>Pelargopsis<br/>capensis</i>     | RR      | 40.0 | 20.7 | 12.12 | 0.017    | 0.22      | 0.10        | 0.22      |
| <i>Geopelia<br/>striata</i>         | OPR     | 100  | 16.3 | 12.43 | 0.503    | 0.36      | 0.00        | 0.08      |
| <i>Cinnyris</i>                     | OPR     | 88.9 | 18.9 | 13.02 | 0.279    | 0.21      | 0.00        | 0.14      |

|                       |     |      |      |       |       |      |      |       |
|-----------------------|-----|------|------|-------|-------|------|------|-------|
| <i>ornatus</i>        |     |      |      |       |       |      |      |       |
| <i>Lonchura</i>       |     |      |      |       |       |      |      |       |
|                       | OPR | 70.6 | 27.8 | 12.99 | 0.358 | 0.47 | 0.00 | -0.14 |
| <i>fuscans</i>        |     |      |      |       |       |      |      |       |
| <i>Egretta</i>        |     |      |      |       |       |      |      |       |
|                       | OPR | 41.7 | 18.8 | 12.23 | 0.303 | 0.37 | 0.02 | 0.14  |
| <i>garzetta</i>       |     |      |      |       |       |      |      |       |
| <i>Actitis</i>        |     |      |      |       |       |      |      |       |
|                       | OPR | 45.5 | 16.2 | 12.28 | 0.252 | 0.28 | 0.02 | 0.16  |
| <i>hypoleucos</i>     |     |      |      |       |       |      |      |       |
| <i>Chrysocolaptes</i> |     |      |      |       |       |      |      |       |
|                       | OPR | 46.9 | 16.7 | 11.82 | 0.28  | 0.30 | 0.01 | 0.15  |
| <i>validus</i>        |     |      |      |       |       |      |      |       |
| <i>Centropus</i>      |     |      |      |       |       |      |      |       |
|                       | OPR | 40.8 | 18.9 | 12.12 | 0.21  | 0.26 | 0.01 | 0.076 |
| <i>bengalensis</i>    |     |      |      |       |       |      |      |       |

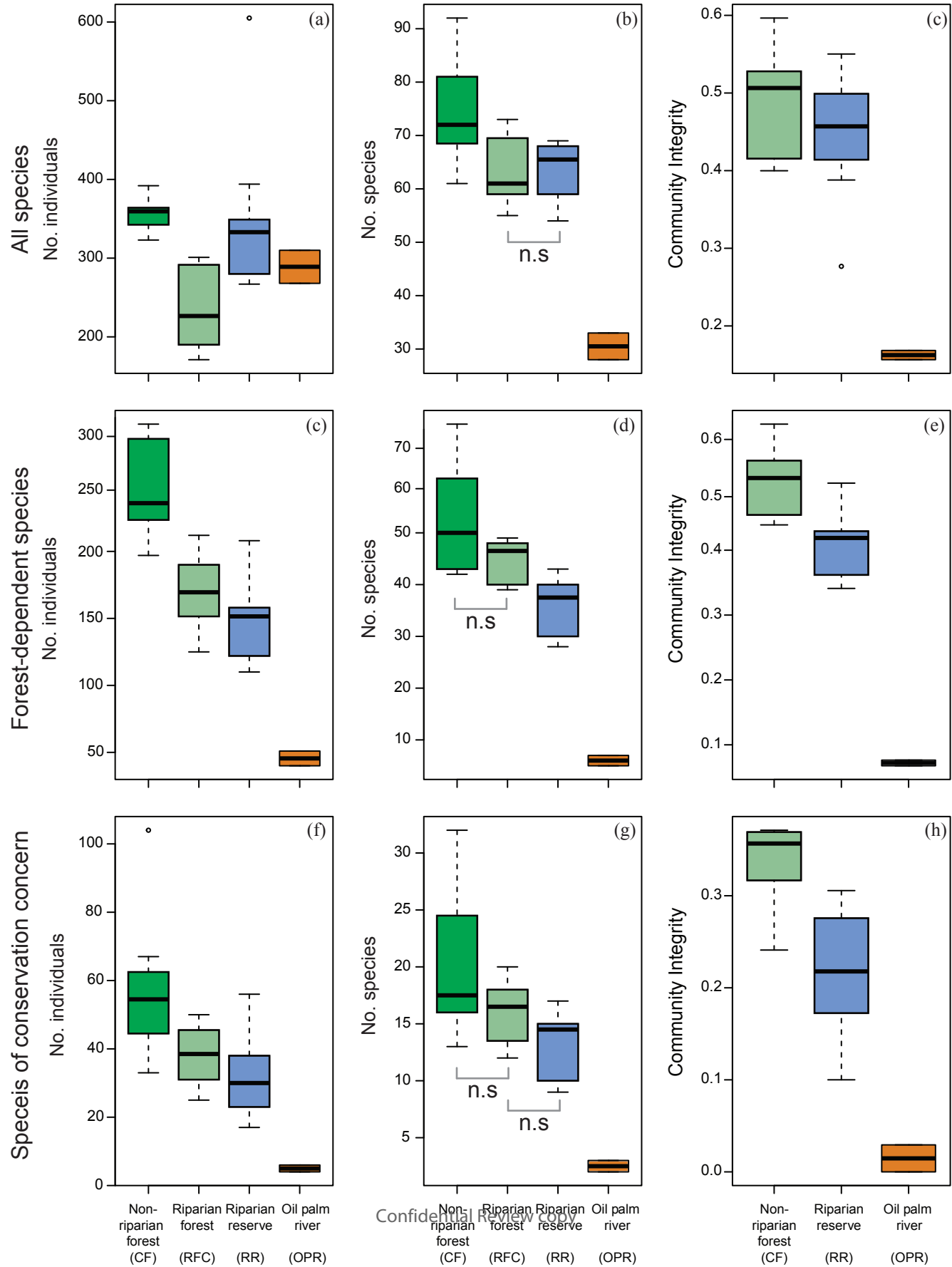
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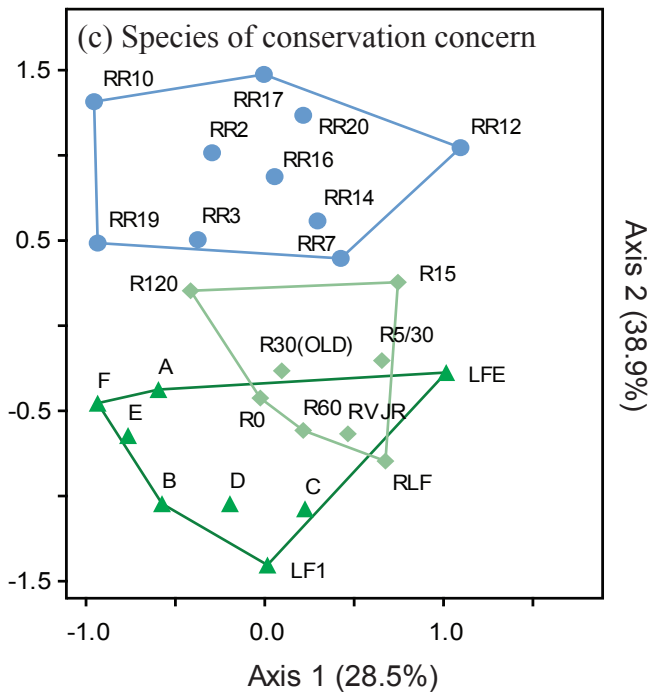
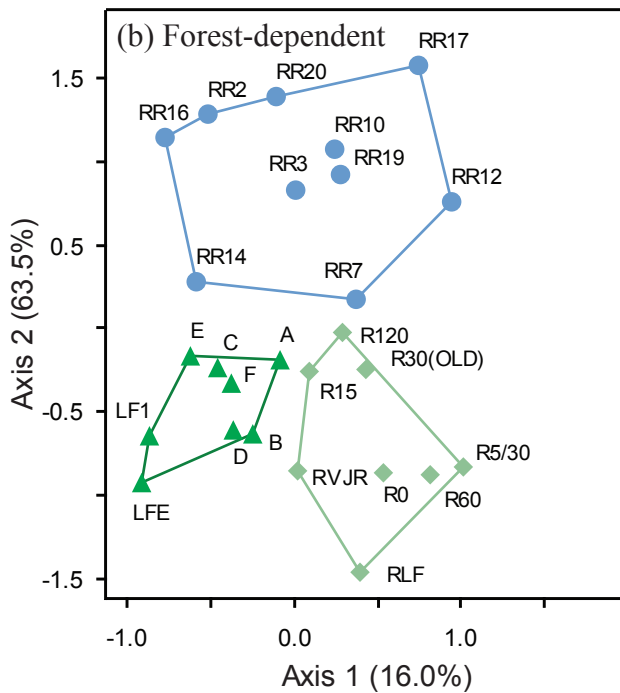
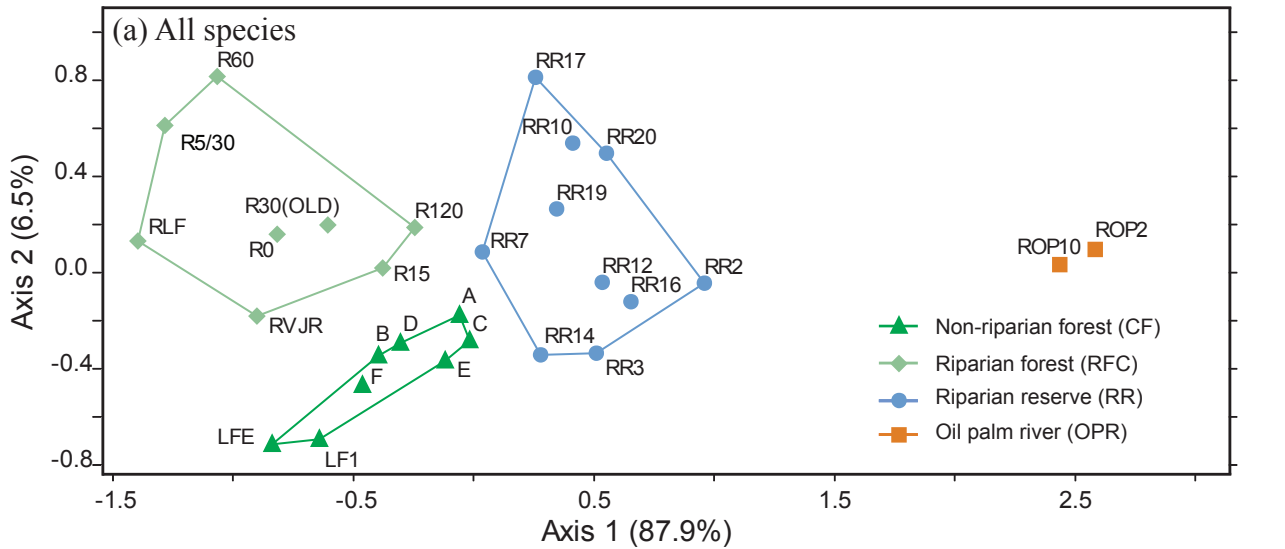
- ▲ Non-riparian forest (CF)
- ◆ Riparian forest (RFC)
- Riparian reserve (RR)
- Oil palm river (OPR)



Abundance

Community integrity



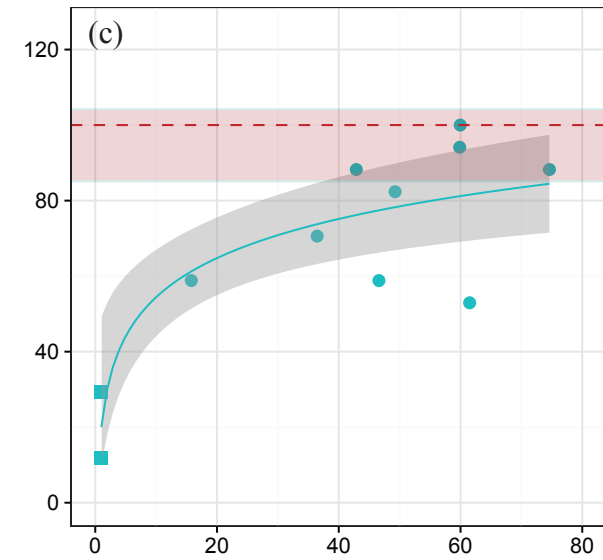
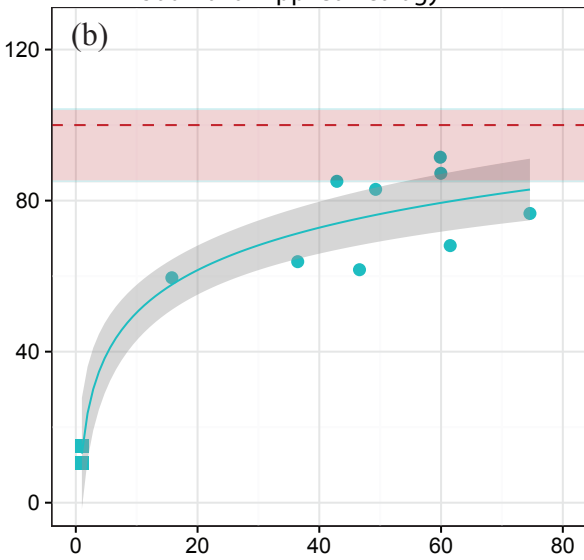
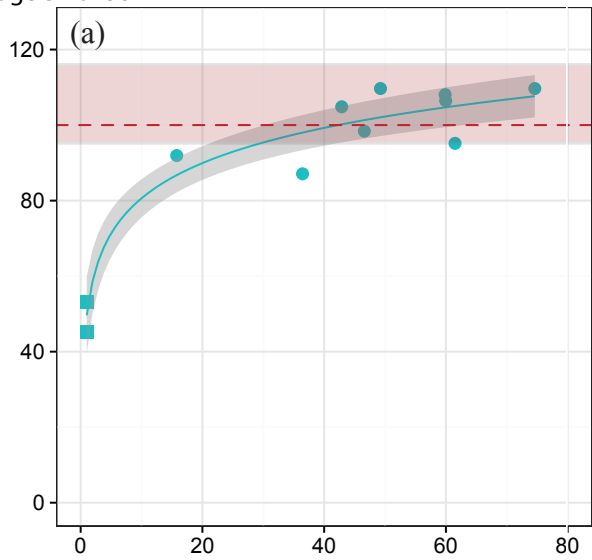


All species

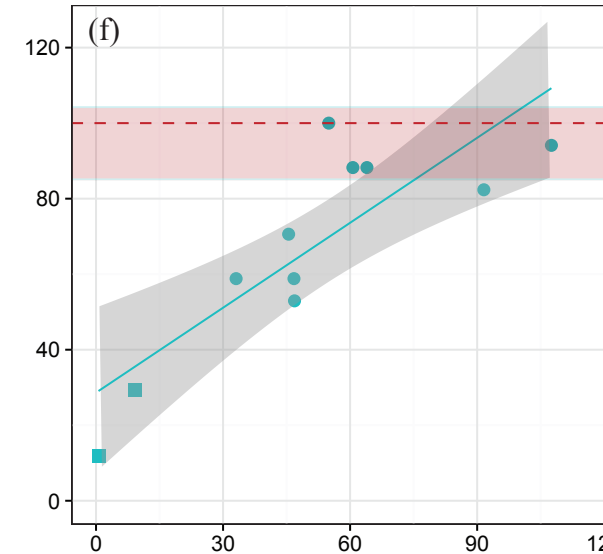
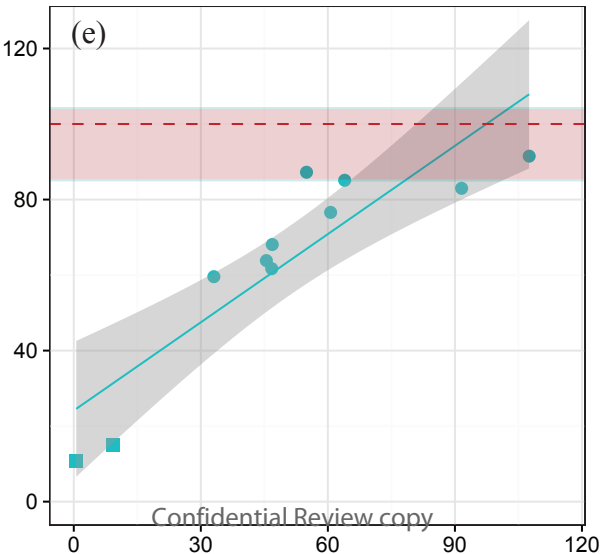
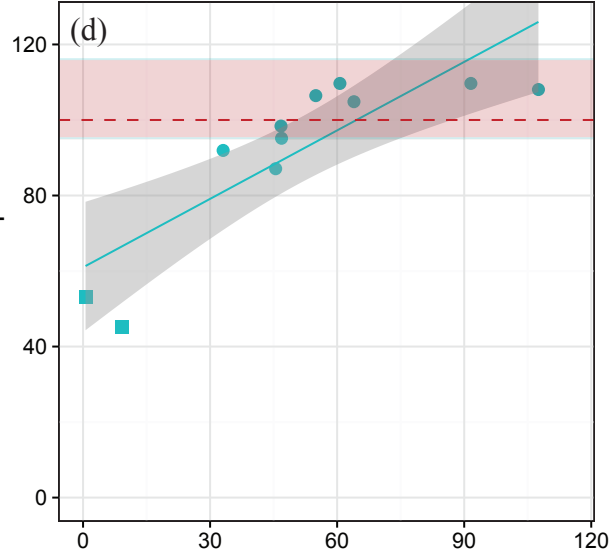
Forest-dependent species

Species of conservation concern

% species found in riparian forest control sites



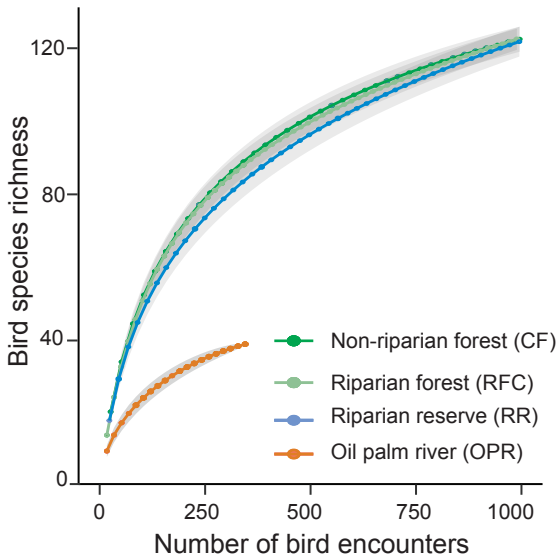
Reserve width (m)



Carbon density (t ha<sup>-1</sup>)

Confidential Review copy





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