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

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Manuscripts

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

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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 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 (Schietti *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⁻¹ for all species, but at around 100 tC ha⁻¹
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.

Predictor	Parameter estimate	SE	Lower 95% CI	Upper 95 % CI
GLM: Richness in riparian reserves and oil palm rivers (RR, OPR, n=11)				
All species				
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
Forest-dependent species				
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
Species of conservation concern				
Intercept	13.4	0.9	11.4	15.4
GLM: Richness in riparian habitats (RR, OPR, RFC, n = 19)				
All species				
Intercept	59.6	2.5	54.3	64.9
Forest-dependent species				

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
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Species of Conservation Concern

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

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

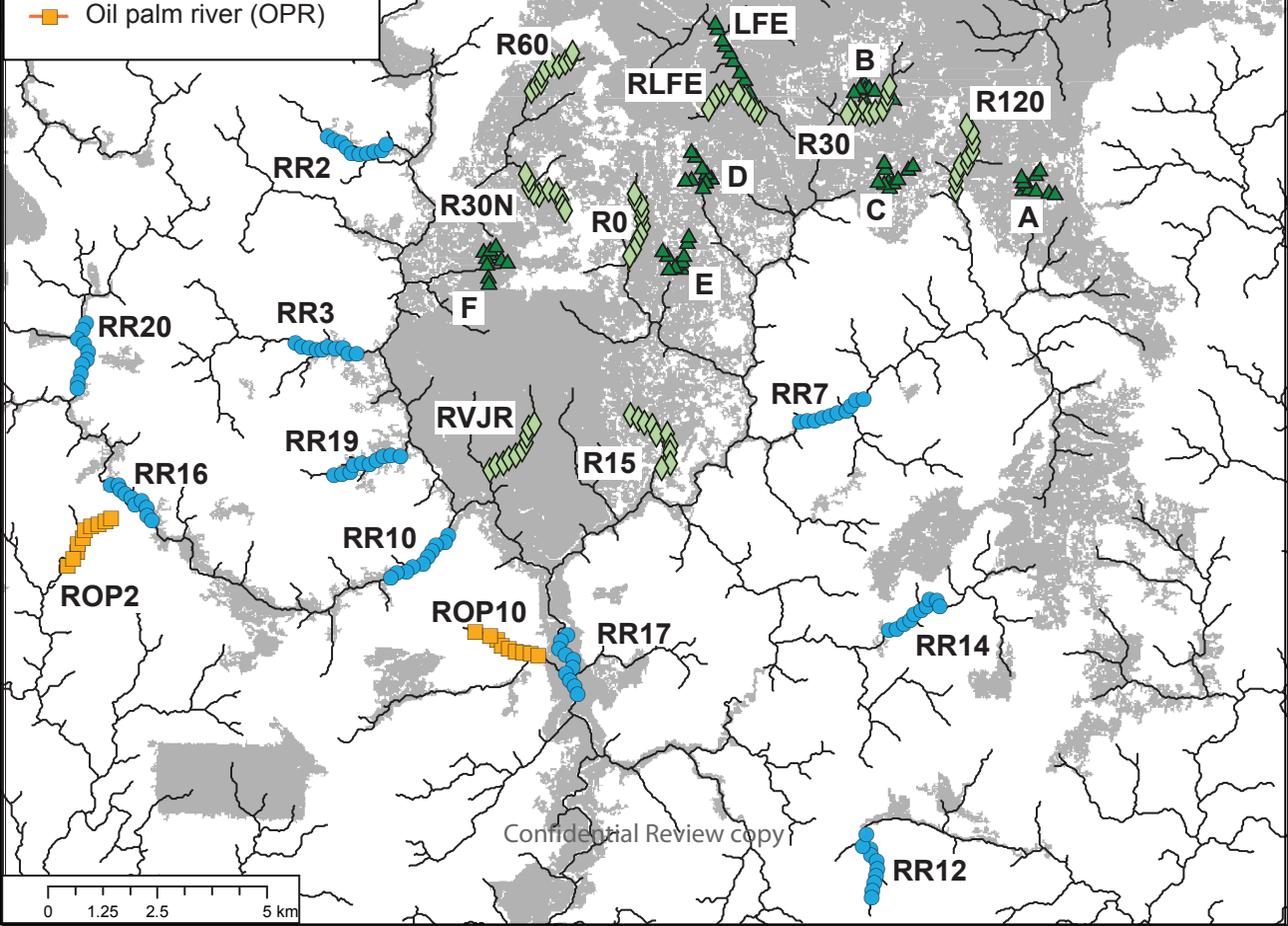
RCF	R5/30	27/05/2014	11/02/2015	20/02/2015
RCF	R60	19/05/2014	14/02/2015	23/02/2015
RCF	RLF	01/05/2014	12/02/2015	22/02/2015
RCF	VJR	30/07/2015	11/07/2015	06/08/2015
RR	RR10	29/10/2016	14/11/2016	15/11/2016
RR	RR12	14/07/2015	28/07/2015	03/08/2015
RR	RR14	27/06/2015	30/06/2015	27/07/2015
RR	RR16	28/06/2015	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

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 Tau	A2 R^2	A2 Tau
<i>Malacopteron magnirostre</i>	CF	61.4	29.1	10.43	0.242	-0.48	0.32	-0.46
<i>Pycnonotus simplex</i>	CF	54.7	29.4	9.65	0.015	-0.03	0.31	-0.43
<i>Copsychus pyrropygus</i>	CF	50.0	20.6	12.46	0.774	0.69	0.003	-0.04
<i>Phaenicophaeus diardi</i>	CF	43.1	21.5	11.66	0.028	-0.15	0.30	-0.44
<i>Enicurus ruficapillus</i>	LFR	61.6	25.1	12.08	0.212	-0.46	0.00	0.06
<i>Pelargopsis capensis</i>	RR	40.0	20.7	12.12	0.017	0.22	0.10	0.22
<i>Geopelia 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

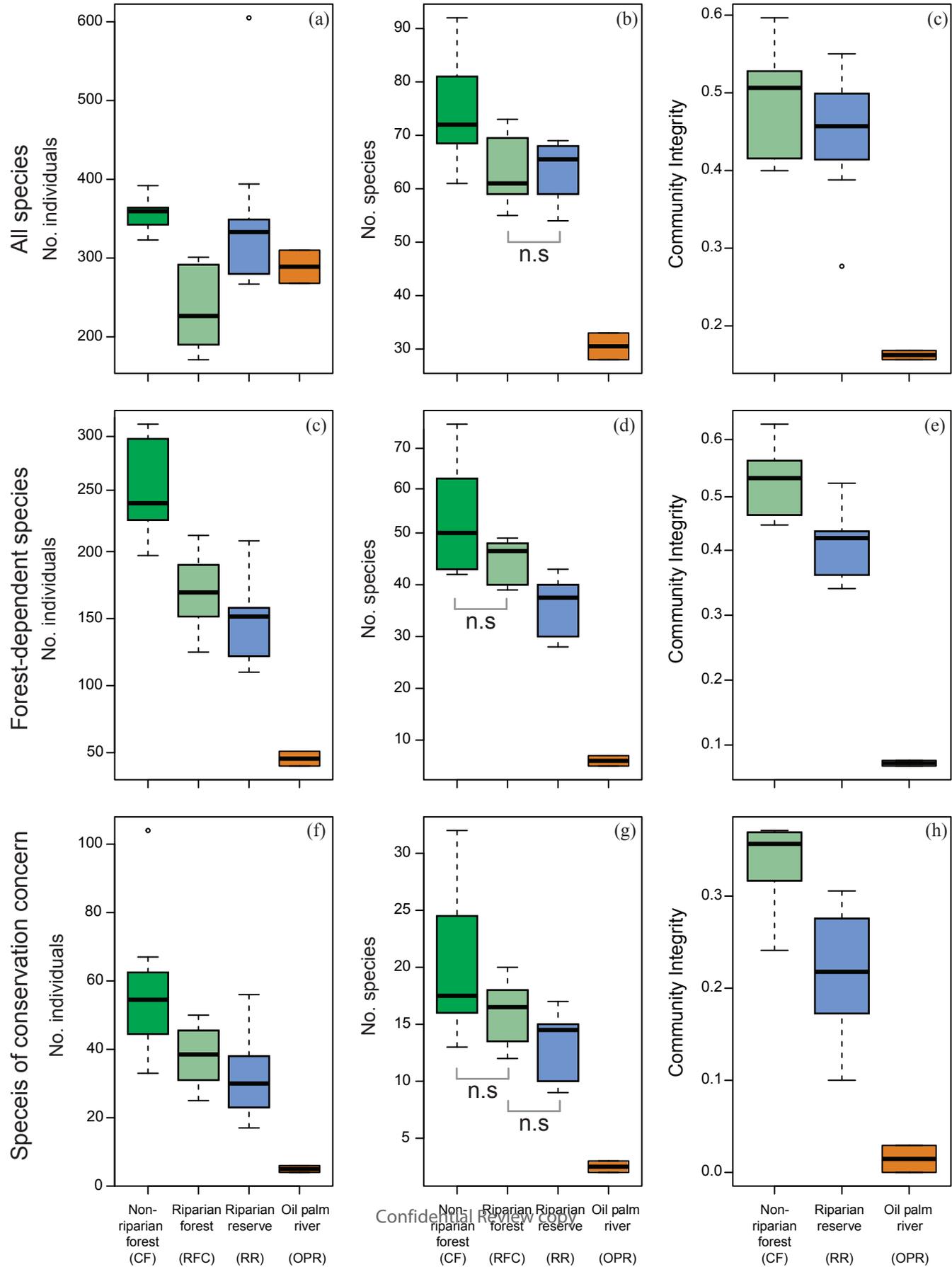
<i>ornatus</i>								
<i>Lonchura</i>								
	OPR	70.6	27.8	12.99	0.358	0.47	0.00	-0.14
<i>fuscans</i>								
<i>Egretta</i>								
	OPR	41.7	18.8	12.23	0.303	0.37	0.02	0.14
<i>garzetta</i>								
<i>Actitis</i>								
	OPR	45.5	16.2	12.28	0.252	0.28	0.02	0.16
<i>hypoleucos</i>								
<i>Chrysocolaptes</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>								

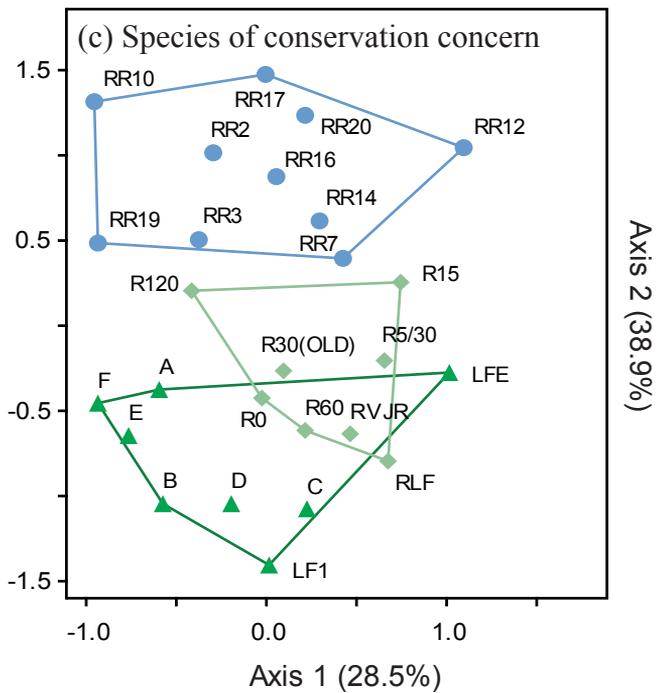
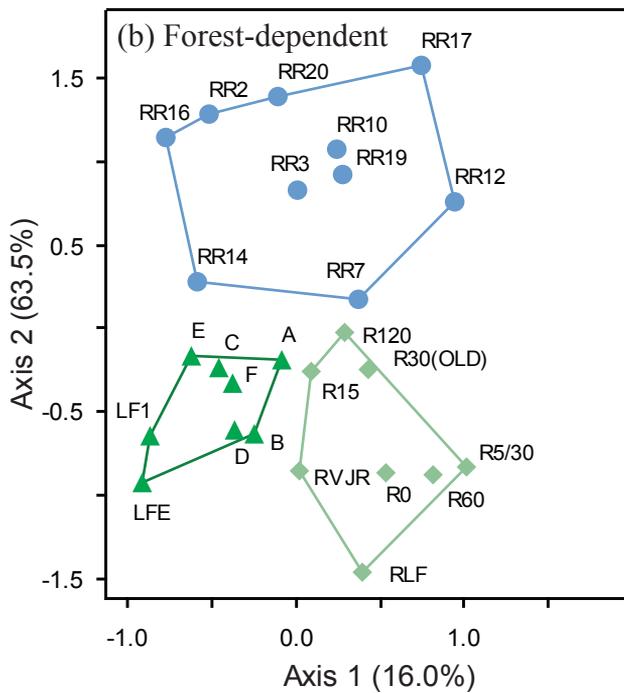
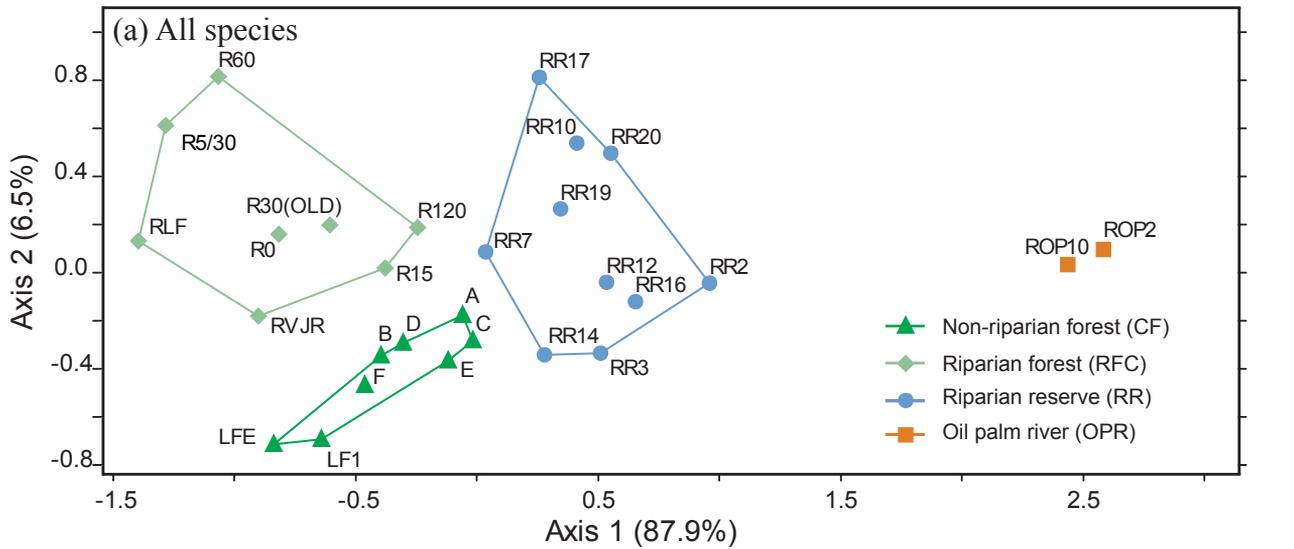
- ▲ Non-riparian forest (CF)
- ◆ Riparian forest (RFC)
- Riparian reserve (RR)
- Oil palm river (OPR)



Abundance

Community integrity

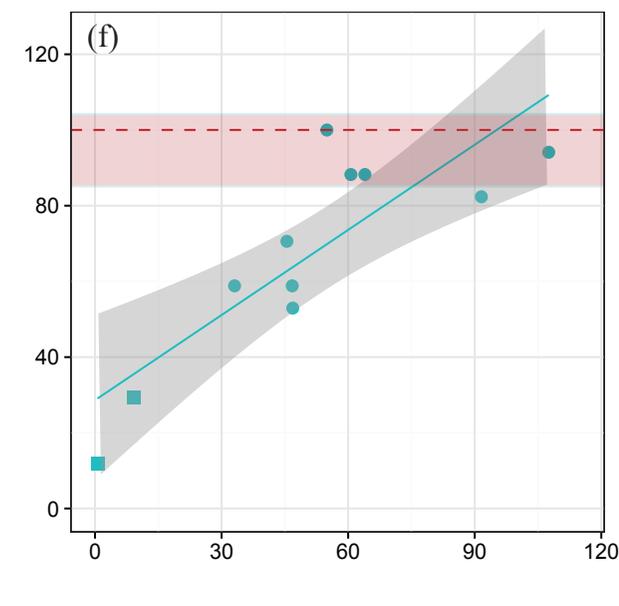
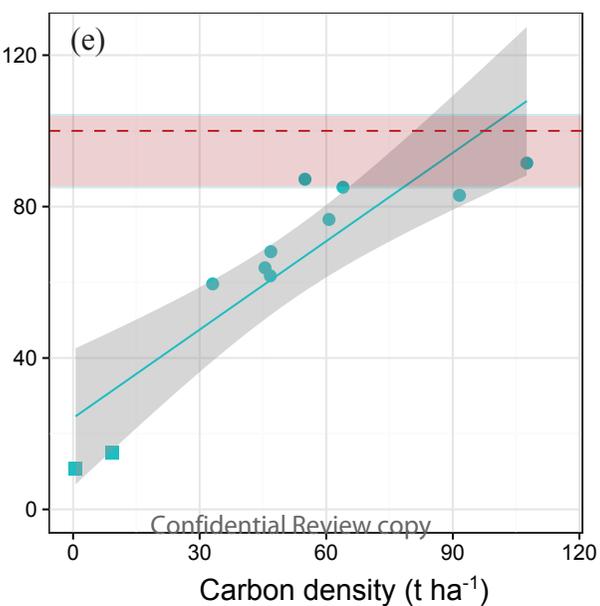
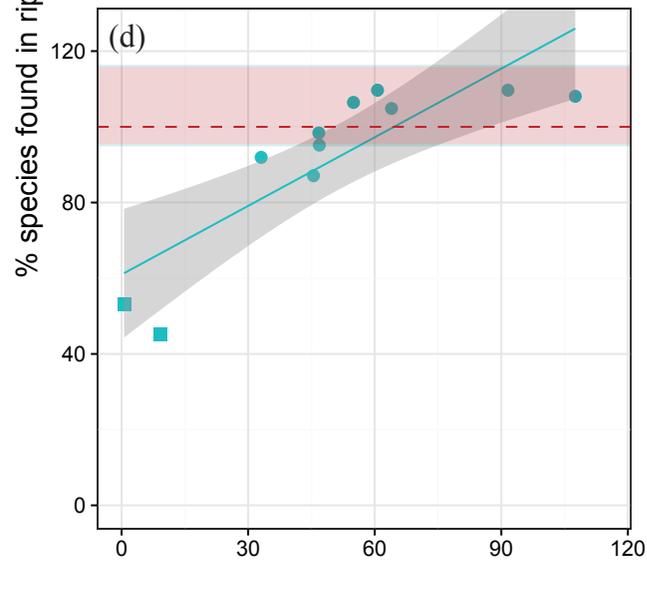
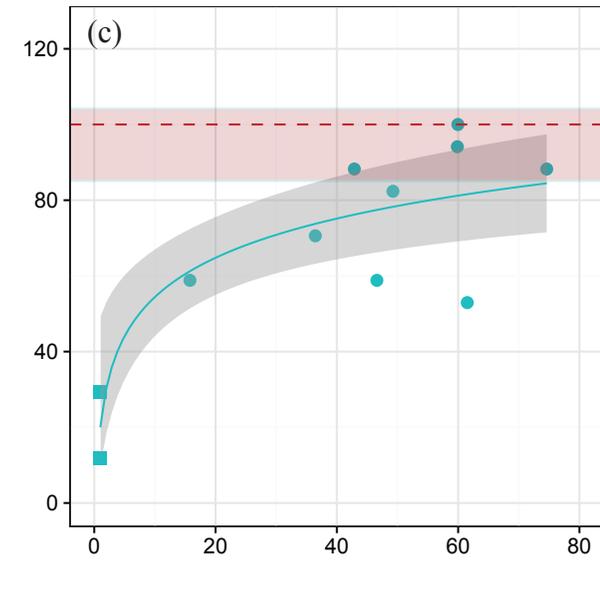
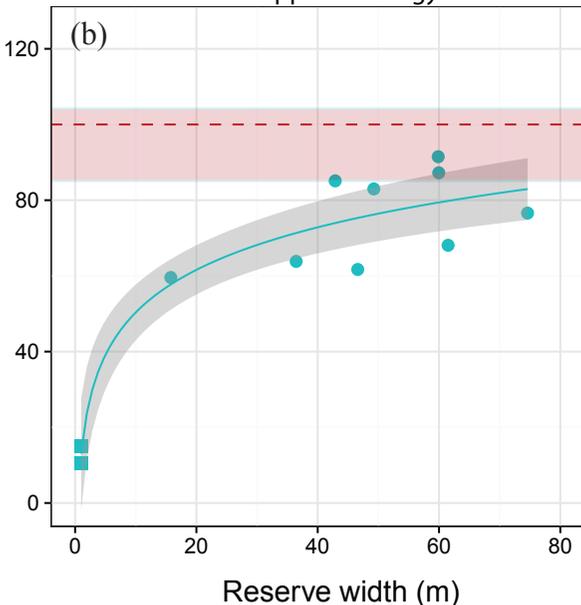
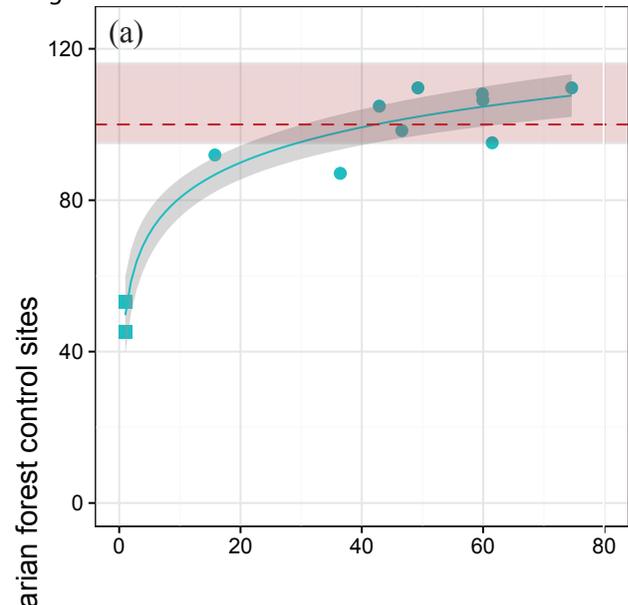


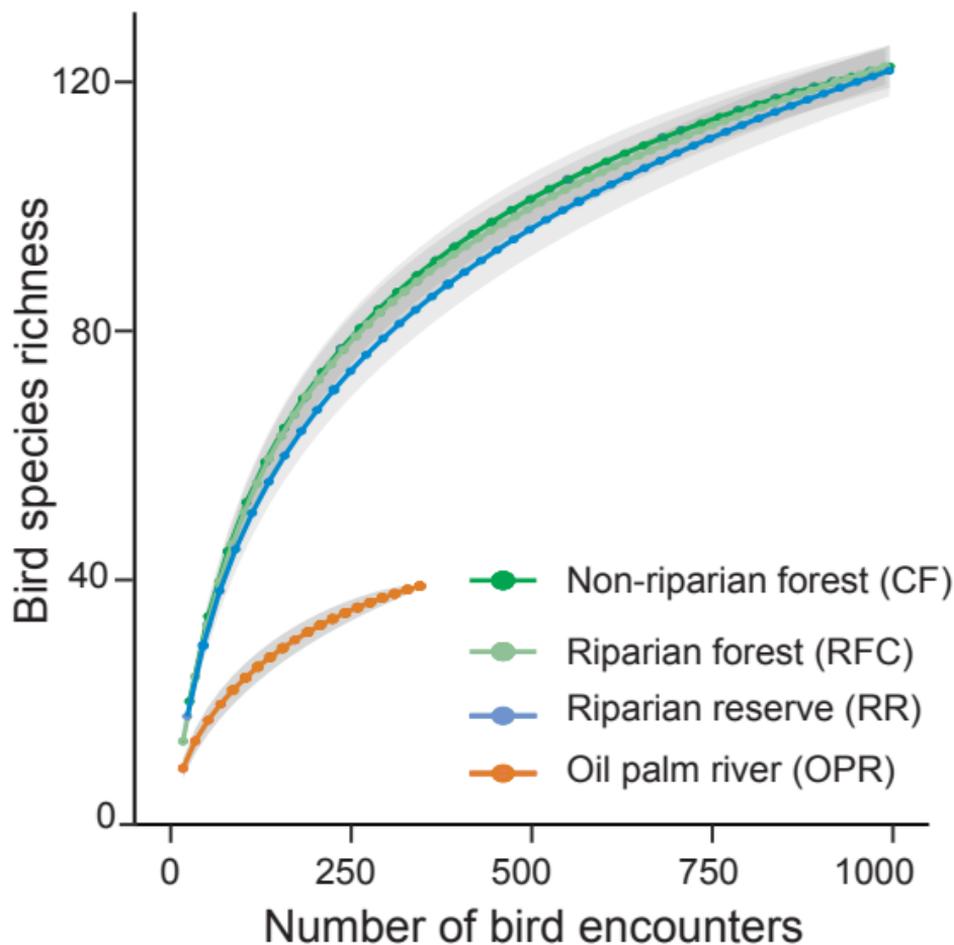


All species

Forest-dependent species
Journal of Applied Ecology

Species of conservation concern





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