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1 **Edge effects of oil palm plantations on tropical anuran communities in Borneo.**

2

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17

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24 **Abstract**

25 The expansion of industrial agriculture (oil palm) has significantly reduced lowland tropical diversity
26 through direct loss or alteration of habitat, leading to habitat fragmentation and edge effects. Edge
27 effects can have serious impacts on species diversity and community dynamics. To assess the effect of
28 oil palm plantation edges on anuran communities in Sabah, Malaysian Borneo, we surveyed anuran
29 species and measured structural habitat and landscape parameters at 74 sites spread across forest and
30 plantation habitats along the Kinabatangan River. We then evaluated how anuran species richness and
31 assemblage composition varied in relation to these environmental parameters. Relative species
32 richness was higher at forest sites, compared to oil palm plantation sites. Plantation sites were
33 dominated by wide-ranging terrestrial species, and assemblage composition varied mostly in relation
34 to standing surface water. Forest habitats supported both more endemic and arboreal species.
35 Variability on anuran assemblage composition in forest habitats was greatest in relation to distance to
36 forest edge followed by canopy density, which was also partially correlated with forest edge distance.
37 Moreover, anuran species richness in forest habitats declined as proximity to the forest-plantation
38 interface increased, and as canopy density decreased. Our study provides further evidence that oil
39 palm plantations provide little conservation benefit to anurans. Furthermore, oil palm plantations
40 appear to have adverse pervasive impacts on amphibian diversity considerable distances into adjacent
41 forest areas. These findings suggest that in order for small patches or narrow corridors of retained
42 forest in landscapes managed for oil palm to maintain biodiversity values in the long term, their sizes
43 and widths need to adequately account for the considerable influence of edge effects.

44 **Introduction**

45 Conversion of tropical forests to intensive plantation forestry or agriculture has negative impacts on
46 biodiversity, and oil palm plantations are no exception (Fitzherbert 2007, 2008; Danielsen et al., 2008;
47 Foster et al., 2011). Direct negative effects (e.g., a decline in species richness, or changes in
48 community composition) of oil palm plantation establishment on tropical forest biodiversity have
49 been documented for a range of biota, including mammals (Danielsen and Heegaard 1995; Maddox et
50 al., 2007; Bernard et al., 2009), birds (Peh et al., 2006; Azhar et al., 2011), amphibians (Gillespie et
51 al., 2012; Faruk et al., 2013) lizards (Glor et al., 2001; Gallmetzer and Schulze, 2015), various insect
52 groups (Chung et al., 2000; Davis and Philips, 2005; Koh and Wilcove, 2008; Brühl and Eltz, 2010;
53 Fayle et al., 2010) and other invertebrates (Hassall et al., 2006), and plants (Danielsen et al., 2008).

54 In addition to the direct effects of habitat loss and alteration from conversion of rainforests to
55 plantations, there are a range of indirect and pervasive effects on biodiversity that may manifest
56 themselves over time. These include downstream effects of hydrological and nutrient changes in
57 waterways and catchments (Dudgeon et al., 2006), as well as habitat fragmentation and edge effects
58 on adjacent remaining forest areas (Fitzherbert et al., 2007, 2008; Danielsen et al., 2008). Habitat loss
59 and fragmentation are likely to exacerbate the impacts of anthropogenic climate change on tropical
60 species (Nowakowski et al., 2017), and may also result in genetic erosion, leading to a reduction in
61 breeding populations (e.g., see Goossens et al., 2005). Edge effects may also have a number of
62 ecological consequences, including microhabitat alterations resulting from changes in temperature,
63 humidity, wind or light penetration (Laurence et al., 2002; Fischer and Lindenmayer 2007; Broadbent
64 et al., 2008); invasive species, that may cause habitat disturbance (Ickes et al., 2005), competition,
65 predation (Rajaratnam et al., 2007), or introduction of disease (Arroyo-Rodríguez and Dias 2010); and
66 increased human access for resource extraction, such as hunting, timber harvesting and other resource
67 extraction (McMorrow and Talip, 2001; Fitzherbet et al., 2008).

68 Detrimental edge effects in tropical forests from roads, agriculture and silvicultural plantations have
69 been documented for various biota, including mammals (Lidicker 1999; Goosem 2000), birds
70 (Watson et al., 2004; Moradi et al., 2009), invertebrates (Didham et al., 1996) and plants (Hoang et
71 al., 2010). However, evidence of major adverse forest edge effects on amphibians and reptiles is more
72 ambiguous (Gardner et al., 2007a), with a number of studies finding either no effect (Gascon 1993;
73 Biek et al., 2002; Toral et al., 2002), a weak effect (Demaynadier and Hunter 1995), or species-
74 specific effects with no overall change in richness (Schlaepfer and Gavin, 2001; Lehtinen et al.,
75 2003). To date, few studies have examined edge effects on tropical forests from oil palm plantations
76 (Fitzherbert et al., 2008; Yaap et al., 2010; Lucey and Hill 2012). Understanding these pervasive
77 effects is important for the conservation of biodiversity in remnant forest patches that have high
78 conservation value, many of which occur in highly fragmented landscapes.

79 The expansion of oil palm plantations has significantly reduced lowland tropical amphibian diversity
80 through direct loss or alteration of habitat (Gillespie et al., 2012; Faruk et al., 2013; Gallmetzer and
81 Schulze, 2015). Oil palm plantations have lower amphibian species richness, more disturbance-
82 tolerant species and less endemic species (Gillespie et al., 2012; Faruk et al., 2013; Gallmetzer and
83 Schulze 2015; Konopik et al., 2015). These differences in richness and changes to community
84 composition in oil palm plantations compared to forest habitats are underpinned by marked
85 differences in both habitat structure and microclimate characteristics. Oil palm plantations lack
86 microhabitats important for many forest amphibian species and are subject to a greater microclimatic
87 flux (Chung et al., 2000; Peh et al., 2006; Luskin and Potts 2011; Gillespie et al., 2012). Important
88 microhabitats for amphibian reproduction, foraging and shelter may be absent or limited within
89 plantations, excluding many forest-dwelling species. However, quantification of impacts of forest
90 conversion to oil palm plantations on amphibian communities is limited.

91 Forest amphibian communities persisting in forests within close proximity to plantations are also
92 potentially highly vulnerable to pervasive edge effects, such as changes in abiotic conditions (see
93 Urbina-Cardona et al., 2006; Dixo and Martins 2008). The reproductive strategies of many rainforest
94 amphibians are potentially highly sensitive to microclimatic and microhabitat perturbations (Heatwole
95 and Taylor, 1987; Wells, 2007; Bickford et al., 2010). Oil palm plantations are typically colonized by
96 highly dispersive anuran species with more generalized ecological requirements (Gillespie et al.,
97 2012; Faruk et al., 2013), which may in turn penetrate adjacent forests and compete with, or predate
98 on, forest species. Elevated population densities of other species, such as leopard cat (*Prionailurus*
99 *bengalensis*) and bearded pig (*Sus barbatus*), may increase predation on anurans or cause habitat
100 alterations near forest edges (Peters 2000; Ickes et al., 2005). Given that pervasive edge effects may
101 permeate substantial distances into adjacent forest habitats for some taxa (e.g., Broadbent et al.,
102 2008), it is likely that such effects may detrimentally affect forest amphibian communities residing in
103 these fragmented landscapes. Oil-palm induced edge effects and their influence on tropical amphibian
104 communities have received little attention, and so there is currently limited understanding of how
105 species richness and diversity change in relation to plantation edge proximity.

106 We evaluated the influence of forest/oil palm plantation edges on anuran diversity by collecting
107 empirical data on anuran species richness and assemblage composition from 74 sites located within
108 lowland rainforest and adjacent oil palm plantations in Malaysian Borneo. Using a repeated sampling
109 design, we collected data from both edge and interior habitats (~20 m and 100-500 m from the
110 forest/plantation interface, respectively) within secondary forest and established plantations. We then
111 examined differences in anuran species richness and assemblage composition between oil palm
112 plantations and adjacent forest in relation to a number of site-specific structural habitat parameters
113 and local-landscape parameters, including the distances from forest/plantation interfaces. Based on
114 findings from previous studies that have compared amphibian species richness and community

115 composition between oil palm plantations and forest habitats (see Gillespie et al., 2012; Faruk et al.,
116 2013), we hypothesized that: (i) forest sites would support more species than plantation sites, and (ii)
117 plantation sites would support distinct communities of anurans compared to forest habitats, mostly
118 comprising of generalist, widespread (i.e., non-endemic) terrestrial species. Some rainforest species
119 are known to be detrimentally affected by agricultural edges (Urbina-Cardona et al., 2006; Schneider-
120 Maunoury et al., 2016), and anuran communities in particular may be sensitive to changes in habitat
121 structure that result from oil-palm induced edges (Gillespie et al., 2015). Hence, we also hypothesized
122 that: (iii) species richness would increase in forest habitats with increasing distance from the
123 forest/plantation interface; and (iv) both structural habitat and local-landscape parameters (i.e.,
124 proximity to the forest-plantation interface) would strongly influence anuran community composition
125 and species richness within both habitat types.

126 **Methods**

127 *Study Area*

128 Fieldwork was conducted along the Kinabatangan River in Northeast Borneo, within the Malaysian
129 state of Sabah (5°10'-5°50'N; 117°40'-118°30'E) (Fig. 1). The climate is warm, wet and humid with
130 mean monthly temperatures throughout the year ranging from 21-34°C. Mean annual precipitation is
131 usually between 2600-3600 mm and there are seasonal floods between November and March
132 (Sooryanarayana, 1995), which can extend through to May (Gillespie et al., 2012). A large portion of
133 the Kinabatangan floodplain is classified as extreme lowland forest and is flat, low (10-20 m a.s.l.)
134 and poorly drained (Azmi, 1998). Due to logging between the mid 1950's and early 1990s, the
135 lowland forest of the Kinabatangan floodplain is almost exclusively regenerating secondary forest
136 (McMorrow and Talip, 2001).

137 Over the past two decades much of the remaining lowland forest of the Kinabatangan floodplain has
138 been converted to oil palm plantations (Abram et al., 2014). These alterations have left only remnant
139 patches of forest, scattered amongst a matrix of vast oil palm monocultures, along with several small
140 villages, and other agricultural lands (Gillespie et al., 2012; Abram et al., 2014). These forest patches
141 form a partially fragmented corridor, extending from the coastal mangrove swamps for approximately
142 70 km upstream to the dry-land foot hill forests (Gillespie et al., 2012). This corridor includes the
143 27,960 ha Lower Kinabatangan Wildlife Sanctuary (LKWS), gazetted in 2005 (Abram et al., 2014),
144 10,000 ha of private and state forests and 15,000 ha of Virgin Jungle Reserves (VJR) (Ancrenaz et
145 al., 2004).

146 *Site Selection and Local-Landscape Parameters*

147 We established 39 transects, each 120m long, in secondary forest in LKWS and adjacent forest areas,
148 and 35 transects of the same length in oil palm plantations. Transects were spread over a reach of
149 approximately 100 km of the Kinabatangan floodplain and surrounding oil palm plantations (Fig. 1).

150 Transects were placed at varying distances from 100–500 m from the Kinabatangan River. All
151 transects were a minimum distance of 500 m from each other. Within each habitat type (forest or
152 plantation), transects were placed either approximately 20 m from the forest/plantation edge, or
153 between 100 and 500 m from this edge. Where possible, transects ran parallel to the habitat edge
154 irrespective of their distance from the edge. Distances to forest/plantation edges were measured using
155 a GPS. We therefore recorded two local-landscape parameters at each transect for inclusion in our
156 analyses: straight line distance to the Kinabatangan River and the straight line distance to the nearest
157 forest/oil palm plantation edge.

158 *Habitat Parameters*

159 We measured 12 structural habitat parameters considered potentially influential on tropical anuran
160 diversity as evidenced in previous studies (see Gardner et al., 2007b; Wanger et al., 2010; Gillespie et
161 al., 2015). We chose parameters that were indicative of habitat variability in canopy, mid strata,
162 understory and forest floor of both forest and plantation habitats. Canopy cover and tree
163 circumference are indicative of relative disturbance levels in tropical forest habitats and influence
164 ectotherm species composition (Vitt et al., 1998; Whitfield and Pierce 2005); understory vegetation
165 density contributes to habitat structural complexity, which in turn has been shown to influence anuran
166 diversity (Wanger et al., 2009; Gillespie et al., 2015); and fallen logs and leaf litter contribute to
167 heterogeneity of forest floor microhabitats, which can also influence amphibian communities
168 (Gardner et al., 2007b; Wanger et al., 2009).

169 The number of trees and their mean circumference and variance (at 1.5 m high) were recorded. The
170 number and mean diameter of logs and fallen trees (diameter ≥ 0.1 m) were measured at their points
171 of interception with each transect. Canopy density along each transect was measured by taking a
172 digital photo of the canopy from 1.5 m height (using a Nikon Coolpix P100 digital camera, Kaiser
173 RA1, Kaiser, Germany) at every 20 m interval. Saved images (3648 x 2736 pixels) were analyzed
174 using IMAGEJ software (National Institute of Health, USA). In order to reduce unevenness in picture
175 tone before manual thresholding, all images were converted to an 8-bit grey scale. Thresholding then
176 allowed the conversion of pixels with a grey scale lower than the threshold to black (representing the
177 canopy) and those pixels with a grey scale higher than the threshold were converted to white
178 (representing the sky). The canopy density, or number of dark pixels measured by IMAGEJ, was then
179 converted into a percentage against the total number of pixels in each image. Mean canopy density
180 and variance in canopy density per transect was also calculated. Understory vegetation density was
181 estimated at 1.5 m height at 20 m intervals along each transect, using a 2 m graduated pole with 50
182 black bands. In alternate directions, the pole was held horizontally above the ground at a 5 m distance
183 perpendicular to each transect; the number of black bands not obscured by vegetation was recorded by
184 a second observer on the transect. The gradient was also measured in this manner using a clinometer.
185 Forest litter cover (leaves, twigs, small branches < 0.1 m diameter etc.) were measured at the same 20

186 m intervals, across the same alternate 5 m distances using a tape measure. Values for each of these
187 parameters were averaged for each transect.

188 Availability of suitable breeding habitat influences local distribution of anurans (Wells, 2007). Many
189 anuran species in the LKWS region reproduce in waterbodies on, or near the forest floor, with
190 variable levels of ephemerality (Gillespie et al., 2012; Inger et al., 2017). Seasonal availability of
191 ephemeral breeding sites is likely to influence frog activity patterns and detection levels, both
192 spatially and temporally (see Wells, 2007). To account for the potential influence of this variability
193 we measured the relative extent of standing water during each survey at each site. Surface water
194 availability was measured by recording the total length of all ground surface water bodies intercepting
195 each transect (max. = 120 m) immediately after every survey. The mean value was calculated across
196 the three repeated surveys at each site and used as a covariate in analyses. Our transects were linear,
197 so measuring the relative extent of standing water along each transect enabled us to account for local
198 effects of water variability across both space and time during the study. The presence/absence of
199 streams within 10m of each transect was also recorded.

200 *Anuran Sampling*

201 Data were collected between February and July 2011, spanning the wet and dry seasons. To reduce
202 seasonal sampling effects, each transect was sampled three times throughout this period, with repeat
203 censuses a minimum of 28 days apart. Transects were surveyed after 1830 hrs, with two people
204 searching visually and acoustically for anurans. All encounters within 5 m either side of each transect
205 were recorded. Leaf litter, logs, branch piles, tree trunks and understory vegetation were inspected as
206 observers moved along each transect. Amphibians were identified following the nomenclature of Haas
207 et al. (2011) and later revised following that of Inger et al., (2017). Two or three transects were
208 sampled each evening, with all sampling completed by approximately 2200 hrs. The time of evening
209 at which each transect was sampled was rotated across replicates to reduce systematic bias from time-
210 related effects.

211 *Species Composition*

212 All statistical analyses were implemented using R statistical software version 3.0.2. Patterns of
213 variation in anuran community composition across forest and plantation habitats were explored using
214 non-metric multidimensional scaling (NMDS) ordination, with Jaccard's distance measure for binary
215 (presence/absence) data and the subsequent dissimilarity matrix of pairwise dissimilarities between
216 sampling sites (Oksanen, 2013). Twenty random starting configurations were used and the final
217 configuration had the lowest residual stress. In order to reduce residual stress, we used a three
218 dimensional NMDS plot, and residual stress of the final ordination plot was 0.106.

219 We used the function 'envfit' in the R package *vegan* (Oksanen, 2013) to overlay environmental
220 parameters ($P > 0.05$) onto the NMDS plots, without disrupting the original ordinations. Overlaying

221 environmental parameters onto NMDS ordinations using envfit generates correlation coefficients
222 (represented as linear vectors on the ordination plots), R^2 values and significance values based on the
223 probability that 999 random permutations of environmental parameters would give a better fit than the
224 true environmental parameters. We overlaid 12 structural habitat parameters and two local-landscape
225 parameters (distance from edge and distance to river) onto the NMDS ordination. Distance to edge
226 was calculated as the straight line distance into forest from the habitat edge, hence sites inside
227 plantations were assigned negative values in the ordination. The presence/absence of streams within
228 the transect survey area was treated as a categorical variable (i.e., centroids), whilst all other
229 parameters were continuous (i.e., linear vectors).

230 *Species Richness*

231 Generalized additive models (GAMs) (Wood, 2006) were used to examine the effect of environmental
232 parameters on anuran richness. GAMs use non-linear smooth terms to describe the relationship
233 between the dependent variable and each predictor variable, whereby the fitted algorithm selects an
234 optimal level of complexity for each non-linear (smooth) term. Each smooth term is described by the
235 effective degrees of freedom (edf), and if $\text{edf} = 1$, this corresponds to a linear relationship between the
236 dependent variable (i.e., anuran richness) and the predictor variable (Wood, 2006). We fitted GAMs
237 using the R package *mgcv* (Wood, 2011). Pairwise Spearman's correlation analysis of environmental
238 parameters revealed that many were collinear (see Dormann et al., 2013). For those variable pairs
239 with coefficients $> (\pm) 0.6$, one variable was selected that was thought to have the greatest potential
240 influence on anuran species richness, and the others were subsequently excluded from the analyses.
241 The resultant set of seven parameters was included in the GAMs, which comprised the two local-
242 landscape parameters: distance to edge and distance to river; and five structural habitat parameters:
243 canopy density, understory density, litter cover, gradient and surface water.

244 We used backward stepwise selection to determine the most important predictors in our GAMs on
245 anuran richness in all habitats, forest habitats and plantation habitats. We started with a global model
246 where all predictor variables were fitted with a smooth term. Predictor variables with an $\text{edf} = 1$ were
247 simplified to linear terms within the model. The least significant predictor variables within each GAM
248 were successively dropped until the AIC (Akaike's Information Criterion) of the model no longer
249 improved. This resulted in a final model which included the most important structural habitat and
250 local-landscape effects on species richness. The partial effects of each significant predictor variable
251 were plotted to examine the shape of the response curve.

252 **Results**

253 Twenty seven anuran species from five families were detected (Table 1). Of these, 25 species were
254 recorded at forest sites, eight of which were not found at plantation sites. Seventeen species were found
255 at plantation sites, two of which were not found at forest sites. Of the 11 Bornean-endemic species

256 detected, five were restricted to forest sites. One endemic species, *Rhacophorus harrissoni*, was
257 detected on a single occasion in a plantation site near the forest edge (Table 1). Relative species richness
258 (i.e., the number of species found at each site) was higher at forest sites (mean = 10.82 (SE ± 0.36)
259 species per transect), compared to oil palm plantation sites (mean = 7.26 (SE ± 0.35) species per
260 transect). Forest habitats also supported more endemic species, averaging 3.59 (SE ± 0.03) species per
261 transect, compared to only 0.63 (SE ± 0.03) per plantation transect.

262 *Anuran assemblage composition*

263 Forest sites were strongly differentiated from plantation sites by most of the structural habitat
264 parameters that we measured (Fig. 2; Appendix 1). Differences between forest and plantation sites
265 were most strongly explained by tree circumference, litter cover, tree density and log density. Forest
266 sites were characterised by high litter cover, understory vegetation density, tree density, log density
267 and canopy cover, all of which had relatively low values at plantation sites. Plantation sites were also
268 characterised by highly variable canopy cover, high tree circumference, and greater extent of standing
269 surface water (Fig. 2c).

270 Anuran species varied markedly in their level of affinity with either forest or plantation habitats (Fig.
271 2b & c). Species strongly associated with forest sites comprised a range of both arboreal (e.g.,
272 *Metaphrynella sundana* and *Polypedates colletti*) and terrestrial species (e.g., *Microhyla perpava* and
273 *Ingerophrynus divergens*), whereas species strongly associated with plantations were mostly
274 terrestrial, such as *Hylarana erythraea*, *Fejervarya cancrivora*, and *F. limnocharis* (Fig. 2a and b;
275 Table 1). Six species showed no strong associations with either forest or plantation sites: *H.*
276 *glandulosa*, *H. nicobariensis*, *H. meganesa*, *Kaloula baleata*, *Limnonectes paramacrodon* and
277 *Polypedates macrotis*.

278 Forest sites varied with respect to distance from forest edge, variance in canopy cover, tree density,
279 log density and canopy density (Appendices 2 & 3). Log and canopy densities tended to be higher at
280 sites further from forest edges, whereas variability in canopy density was higher at sites near forest
281 edges (Appendix 3). The lack of clustering of anuran species in the centre of the NMDS plot
282 (Appendix 3) suggests that the occurrence of most species was influenced by these parameters.
283 However, the greatest variability on anuran assemblage composition was in relation to canopy density
284 and distance to forest edge (Appendices 2 & 3). Several species, such as *Chaperina fusca*, *L.*
285 *paramacrodon*, *M. sundana*, *Polypedates colletti* and *P. otilophus*, were restricted to forest interior
286 sites. Conversely several species were found only at forest edges, namely *H. erythraea*, *K. baleata*
287 and *Polypedates leucomystax*.

288 Plantation sites varied significantly only with respect to extent of surface water and log density
289 (Appendices 4 & 5). The lack of clustering of anuran species in the centre of the NMDS plot
290 (Appendix 5) suggests that the occurrence of most species was influenced by these parameters.

291 Anuran assemblage composition varied mostly in relation to availability of standing surface water
292 (Appendix 5). Proximity to forest edge was marginally insignificant (Appendix 4).

293 *Species Richness*

294 Across plantation and forest habitats, the best supported GAM for the influence of environmental
295 parameters on anuran richness included canopy density and distance to edge (Table 2). Canopy
296 density had a linear negative relationship with anuran richness (Fig. 3a), whilst the relationship
297 between distance to edge and species richness was non-linear, and complex (Fig. 3b). Overall, species
298 richness was lower at plantation sites compared to forest sites. In plantations, species richness tended
299 to increase somewhat as distance from the forest/plantation edge increased, but there was a much
300 higher increase in species richness with proximity to the forest/plantation edge. Species richness
301 continued to rise at forest sites with increased distance from plantations (Fig. 3b).

302 **Discussion**

303 Biodiversity conservation in intensively managed landscapes is contingent upon the magnitude and
304 nature of both direct and indirect disturbance effects. Expansion of oil palm plantations is a major
305 cause of habitat loss and associated biodiversity in tropical regions (Fitzherbert et al., 2008a; Pirker et
306 al., 2016). In support of our first and second hypotheses, we found further evidence that oil palm
307 plantations support lower species richness, fewer endemic species and mostly disturbance-tolerant
308 species compared to rainforest habitats, and provide little overall benefit to conservation of Bornean
309 anuran diversity.

310 To date, indirect effects of oil palm plantations on biodiversity have had far less evaluation than direct
311 impacts. To our knowledge, our study provides the first evidence of edge effects from oil palm
312 plantations on anuran diversity in adjacent forest landscapes. Moreover, our results suggest that
313 changes in forest anuran diversity associated with plantation edges may extend up to 4 km into
314 adjacent forest. In contrast to the findings of our study, Gardner et al. (2007a) found little support
315 amongst nine studies for impacts of edge effects on either amphibians or reptiles across various
316 tropical regions. However, none of these studies examined effects of oil palm plantations. Oil palm
317 plantations may have different biotic and abiotic edge effects on adjacent forest habitats, such as less
318 protection from wind exposure (e.g., Ferrante et al., 2017). A number of the studies reviewed by
319 (Gardner et al., 2007a) sampled habitat fragments surrounded by heterogeneous matrices of different
320 levels of fragmentation and intensities of agriculture and silviculture, which may have in-part
321 confounded inferences of edge effects *per sé*. The impacts of edges on species diversity in adjacent
322 forest habitats likely depend upon the size, quality and spatial extent of forest fragments within a
323 specific agricultural system, and the structural contrast between the forest habitat and adjacent altered
324 environment (Ferrante et al., 2017; Pfeifer et al., 2017). Nevertheless our findings build on those of
325 Schneider-Maunoury et al. (2016) who found pronounced effects on forest amphibians and reptiles up

326 to 1 km from forest edges in Neotropical landscapes adjacent to agricultural matrices of pasture,
327 secondary regrowth and plantations (including palm groves, cocoa plantations and *Eucalyptus*
328 plantation forests). Similarly, in a recent global study examining the impact of edge effects on
329 amphibians, forest-core habitats supported more amphibian species than forest-edge, matrix-core and
330 matrix-edge habitats (Pfeifer et al., 2017). Collectively these findings suggest that tropical anuran
331 communities are sensitive to edge effects from adjacent agricultural development, but that the nature
332 and magnitude of these effects may vary substantially amongst different types of agricultural edges
333 and how they are managed, as well as the broader level of habitat fragmentation/connectivity and
334 disturbance in surrounding landscapes.

335 Consistent with our third hypothesis, amphibian species richness in forest habitats declined as
336 proximity to the forest-plantation interface increased. Forest sites further from plantation edges tended
337 to have more arboreal species (e.g., *M. sundana*), and more litter-dwelling and direct-developing
338 species compared with sites closer to plantation edges (Table 1). In forest habitats presence of
339 endemic species also declined with increasing proximity to forest-plantation edges (Fig. 2b).

340 Disturbance-tolerant anuran species were present in forest habitats close to plantation edges but were
341 encountered much less frequently in forest areas further from the forest/plantation interface (Fig. 2b).

342 Several mechanisms may underpin the detrimental edge effects of oil palm plantations on forest
343 anurans in lowland Borneo. The creation of abrupt habitat edges alters forest structure and
344 composition, both at the forest edge itself (Didham and Lawton, 1999) and within interior forest
345 habitats (Mesquita et al., 1999). Large trees often die off within 300 m of forest edges (Laurance et
346 al., 2000), leaving numerous canopy gaps that are often filled by disturbance-adapted vines, weeds
347 and pioneer species (Laurance et al., 2002; Laurance et al., 2006). These changes in turn lead to
348 reduced moisture and increased maximum daily temperatures (Didham and Lawton, 1999; Pohlman et
349 al., 2009; Hardwick et al., 2015). Amphibians are especially vulnerable to these altered microclimates
350 (Lehtinen et al., 2003), as they are sensitive to desiccation in drier environments and depend upon a
351 variety of aquatic microhabitats for reproduction. Changes in forest structure and composition,
352 accompanied by disruptions in plant–animal interactions (Rodríguez-Cabal et al., 2007), can also alter
353 the community composition and abundance of many different faunal groups (Goosem, 2000;
354 Laurance et al., 2002; Laurance, 2004; Lehtinen et al., 2003; Watson et al., 2004). Such changes can
355 often lead to invasion of disturbance-adapted animal species, including reptiles (Schlaepfer and
356 Gavin, 2001), birds (Hagan et al., 1996), pigs (Peters, 2000) and other mammals (Kinnaird et al.,
357 2003), which may predate or compete with amphibians. Pesticides and fertilizers are often used
358 intensively in oil palm plantations with potentially serious implications for nearby streams and
359 wetlands (Obidzinski et al., 2012). How these substances affect tropical amphibian assemblages are
360 unknown. However, given the dependence of many anuran species on aquatic habitats and their
361 sensitivities to pesticides (Bidwell and Gory, 1995; Brühl et al., 2013), many species may be

362 adversely affected by residual chemical runoff into forests near oil palm plantations. We did not
363 evaluate chemical residues or runoff in this study; hence this is topic may warrant further research.

364 Consistent with our fourth hypothesis, we found that amphibian diversity was influenced to various
365 degrees by both structural habitat and landscape parameters. Our findings suggest that amphibian
366 species richness increased, and species composition changed with variability in canopy density.
367 Canopy density within forest habitats also tended to increase with distance from forest-plantation
368 edges, possibly suggesting lower levels of selective logging and other direct human disturbances
369 further from plantations and associated road networks. Human disturbance levels in tropical forests
370 are typically strongly related to human access (Laurance et al., 2009; Bhat et al., 2011; Kodandapani
371 et al., 2014). Thus, in this landscape, plantations and associated road networks may facilitate human
372 access to forest edges, increasing encroachment and forest habitat disturbance. Other studies have
373 found that tropical amphibian species richness may vary with respect to relatively low levels of
374 human disturbance (e.g., Gillespie et al., 2015). Therefore interactions may exist between edge effects
375 *per sé* and other anthropogenic disturbance processes operating in forests facilitated by access
376 provided by plantations, which in turn may contribute to the large distance over which changes in
377 anuran diversity were observed.

378 Biodiversity conservation in Southeast Asia is becoming increasingly dependent on landscapes with
379 varying levels and patterns of habitat retention, and habitat patches with varying levels of
380 anthropogenic disturbance (Sodhi et al., 2010; Giam et al., 2011). A greater understanding is needed
381 of the relationships between these disturbance processes and biodiversity change in order to determine
382 management priorities and practices (Sodhi et al., 2010; Gillespie et al., 2015). The effects of forest
383 conversion to oil palm plantations and/or their management are likely having significant and
384 pervasive effects on amphibians, and probably other biota, that extend well beyond plantation
385 boundaries.

386 Current or modified management practices of oil palm plantations in themselves are unlikely to
387 improve their biodiversity conservation value for many taxa (Edwards et al., 2010; Faruk et al., 2013).
388 Therefore biodiversity conservation in oil palm-managed landscapes is likely to be largely dependent
389 upon retention of forest patches and corridors (e.g., High Conservation Value (HCV) areas: see
390 <http://www.rspo.org>). However, for such retained areas to maintain biodiversity values in the long
391 term, their sizes and widths need to adequately account for the considerable influence of edge effects.
392 These considerations are most pertinent in high biodiversity-value regions where forest conversion to
393 oil palm plantations is expanding (Pirker et al., 2016), such as the island of New Guinea (Fitzherbert
394 et al., 2008). Our findings, along with those of Schneider-Maunoury et al. (2016), provide snapshots
395 of patterns of amphibian biodiversity in space at specific times in fragmented tropical forest
396 landscapes. However, on-going monitoring is required to evaluate how these amphibian assemblages

397 continue to change through time and what the ultimate effects of these landscape changes will be on
398 biodiversity in remaining rainforest habitats.

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408

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614 **List of Figures**

615 Figure 1. Lower Kinabatangan River Floodplain and sampling sites; inset shows location on Borneo.
616 Grey shaded areas are forest and adjacent unshaded areas are oil palm plantations; black triangles
617 represent survey sites and red circles represent villages. All forest sites were located within the Lower
618 Kinabatangan Wildlife Sanctuary (LKWS).

619 Figure 2. Non-metric multidimensional scaling (NMDS) ordination diagrams (first two axes) for all
620 forest and plantation sites: (a) sampling sites: o = forest sites: Δ= plantation sites; (b) species, refer to
621 Table 1 for species abbreviations; and (c) direction and magnitude (vector length) of significant ($P >$
622 0.05) fitted environmental parameters overlaid into the ordination space, refer to Table 2 for
623 environmental parameter abbreviations.

624 Figure 3. Partial effects of significant parameters retained in the final GAM for overall species
625 richness in all habitat types. (a) Distance to edge; b) canopy density. The values on the y-axes are
626 centred on zero and based on partial residuals, and thus indicate the relative influence of each
627 explanatory variable on the prediction. Dashed lines are ± 2 standard errors.

628

629 **List of Appendices**

630 Appendix 1. Fitted environmental vectors in the NMDS ordination of anuran assemblage similarity
631 across all sites.

632 Appendix 2. NMDS loadings and P values for habitat parameters at forest sites.

633 Appendix 3. NMDS ordination diagrams (first two axes) for forest sites. (a) Species, refer to Table 1
634 for species abbreviations; (b) direction and magnitude (vector length) of significant ($P > 0.05$) fitted
635 environmental parameters overlaid into the ordination space, refer to Table 2 for environmental
636 parameter abbreviations.

637 Appendix 3. Partial effects of significant parameters retained in the final GAM for overall species
638 richness in all habitat types: (a) distance to edge; b) canopy density. The values on the y-axes are centred
639 on zero and based on partial residuals, and thus indicate the relative influence of each explanatory
640 variable on the prediction. Dashed lines are ± 2 standard errors.

641 Appendix 4. NMDS loadings and P values for habitat parameters at plantation sites.

642 Appendix 5. NMDS ordination diagrams (first two axes) for plantation sites. (a) Species, refer to
643 Table 1 for species abbreviations; and (b) direction and magnitude (vector length) of significant ($P >$
644 0.05) fitted environmental parameters overlaid into the ordination space, refer to Table 2 for
645 environmental parameter abbreviations.