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1 **Foraging guild modulates insectivorous bat responses to habitat loss and**
2 **insular fragmentation in peninsular Malaysia¹**

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5

6 **Keywords:** Passive acoustic monitoring; Habitat fragmentation; Hydroelectric dams;
7 Island Biogeography Theory; Land-bridge islands; Tropical forests

8 **Highlights:**

- 9 ● We assessed the diversity of insectivorous bats in dam-induced islands in
10 Malaysia
11 ● Species persistence was modulated by island size and habitat quality
12 ● Forest foragers activity decreased with island isolation and degradation
13 ● Edge foragers benefited from fragmentation, increasing in activity on smaller
14 islands
15 ● By creating multiple small, isolated, degraded islands, damming erodes bat
16 diversity

17 **Abstract**

18 Despite mounting evidence on the ecological impacts of damming for biodiversity,
19 little is known regarding its consequences in the hyper-diverse Southeast Asian
20 tropical forests. Here we assess the effects of habitat loss and fragmentation on the
21 diversity and activity of insectivorous bats within the hydroelectric Kenyir Lake in
22 peninsular Malaysia. We surveyed bat assemblages on 26 islands and two mainland
23 continuous forest sites using passive acoustic monitoring. Echolocation calls were
24 classified into sonotypes, each corresponding to either one or multiple species, and
25 grouped into foraging guilds. We then examined bat overall assemblage (sonotype
26 richness, activity, and composition), guild- and sonotype-specific activity. From 9360
27 hours of recordings, we identified 16 bat sonotypes, including 10 forest (2854 bat
28 passes), three edge (13 703) and three open-space foragers (3651). Sonotype
29 richness increased towards denser canopy structures, as indicated by higher

Abbreviations:

AICc: Akaike Information Criterion corrected for sample size

CF: Constant Frequency

CI: Confidence Interval

FM: Frequency Modulated

FMqCF: Frequency Modulated quasi-Constant Frequency

LF: Low Frequency

LM: Linear Model

NDVI: Normalised Difference Vegetation Index

NMDS: Non-Metric Multi-Dimensional Scaling

QCF: Quasi-constant Frequency

30 Normalized Difference Vegetation Index values (NDVI). Sonotype composition varied
31 across the gradient of forest area. Forest foragers were positively affected by NDVI
32 and negatively affected by distance to the closest neighbour, whereas edge foragers'
33 activity increased in smaller islands. Of the six sonotypes analysed, the activity of
34 one forest sonotype increased with forest area, while that of one edge sonotype
35 decreased. Ensuring habitat quality within insular forest remnants, in addition to their
36 functional connectivity, maximises bat diversity, including the persistence of forest
37 foraging species. Future hydropower development should therefore avoid the
38 creation of a myriad of small, isolated, and habitat-degraded islands further
39 characterised by altered levels of bat diversity and guild-level activity.

40 **1. Introduction**

41 Humanity currently faces a need to reconcile human population growth, increasing
42 energy demands, and the decarbonization of that energy. In this context, hydropower
43 is an increasingly appealing option, representing 73% of the renewable energy
44 produced in the world (The World Bank, 2016). Yet, river damming is also a major
45 driver of habitat loss and insular fragmentation across lowland forests (Gibson et al.,
46 2017). By flooding the lowland areas, dam construction often creates insular forest
47 fragments matching the previous hilltops that become isolated within an inhospitable
48 aquatic matrix (Jones et al., 2016). Although recent efforts have been made to
49 understand the ecological consequences of hydropower (Palmeirim et al., 2022;
50 Terborgh et al., 2009), few studies have targeted the Southeast Asian forests (Jones
51 et al., 2016). Such understanding is therefore considered a priority for biodiversity
52 conservation in the region (Coleman et al., 2019).

53 Species diversity persisting in insular forest fragments is typically affected by
54 fragment size and isolation, which limit species population size and colonisation
55 rates respectively (McArthur & Wilson, 1967). Edge effects arising from
56 insularisation, namely increased exposure to windthrows and floristic transition
57 towards light-wooded fast-growing pioneer assemblages, affect habitat quality *within*
58 insular fragments, thereby influencing remaining species diversity (Benchimol &
59 Peres, 2015a). Likewise, further human disturbances, including logging and fires,
60 affect forest structure and thus habitat quality. Altogether, habitat quality can be
61 assessed using the Normalized Difference Vegetation Index (NDVI), distinguishing
62 between forest with denser canopy (higher NDVI values) and sparser canopy (lower
63 NDVI values) (Tovar, 2011).

64 Species responses to habitat loss and insular fragmentation may further vary
65 between (Palmeirim et al., 2022) and within biological groups (Brändel et al., 2020;
66 Meyer & Kalko, 2008), as influenced by particular species traits (Meyer et al., 2008;
67 Palmeirim et al., 2021). For instance, the persistence of mid-sized mammal species
68 on islands can be related to their swimming capacity (Benchimol & Peres, 2015b),
69 while that of lizard species is dictated by their thermoregulation mode (Palmeirim et
70 al., 2017). Yet, even persisting taxa show general decreases in abundance in insular
71 forest fragments compared to surrounding mainland (e.g., bats: Gorresen & Willig
72 (2004), birds: Yong et al. (2011),) and terrestrial and arboreal mammals: Benchimol &
73 Peres (2021)). As such, while certain species able to use non-forest habitats might
74 become overabundant (Moore et al., 2022), forest-dependent species become rarer
75 or locally extinct (Palmeirim et al., 2018). Understanding the drivers of species
76 response to forest insularisation – considering both environmental and intrinsic
77 species characteristics – allows more efficient management actions to be proposed,

78 which is not trivial given the expansion of the hydropower sector across lowland
79 tropical forests (Couto & Olden, 2018).

80 Although habitat loss and insular fragmentation have been reported as
81 important drivers of bat species' local extinction in the Neotropics (Colombo et al.,
82 2022; Meyer & Kalko, 2008), little is known for Asia. In fact, the only study targeting
83 such effects on insectivorous bats in this region highlighted the importance of island
84 area especially for forest-dependent species in East China (López-Bosch et al.,
85 2021). In addition, in a non-insular matrix setting in peninsular Malaysia, the diversity
86 of insectivorous bats was impacted by forest area, with species-specific responses
87 being modulated by their habitat affinity (Struebig et al., 2008). Insectivorous bats
88 emit echolocation calls to navigate their surroundings and locate food (Schnitzler et
89 al., 2003). The characteristics of the calls produced, e.g., call shape, are adapted to
90 a species' foraging preferences (Denzinger & Schnitzler, 2013; Schnitzler & Kalko,
91 2001). For example, species adapted to foraging in the forest interior (forest
92 foragers) use long constant frequency (CF) calls or very short, broadband, frequency
93 modulated (FM) calls, adapted to particularly cluttered environments. Edge foragers
94 use quasi-constant frequency (QCF) calls, or medium frequency calls (FMqCF)
95 composed of an FM component followed by a short and quasi constant element
96 (qCF), allowing them to locate and navigate between background features (medium
97 frequency FM component), and to locate prey at an intermediate distance (qCF
98 component). Open-space foragers use low frequency (LF) (<30 kHz) FMqCF calls
99 with a narrow FM component and a long QCF component, enabling prey detection in
100 vast empty spaces (Denzinger & Schnitzler, 2013; Schnitzler & Kalko, 2001). Within
101 foraging guilds, bat calls are not species specific: the calls of several species have
102 evolved in a convergent way to respond to analogous environmental pressures,
103 resulting in very similar calls in species facing analogous ecological conditions and
104 therefore preventing species-specific identification in certain instances (Gibb et al.,
105 2019; Russo et al., 2017). To overcome this issue, bat calls are commonly classified
106 into sonotypes, i.e., calls of similar shape and peak frequency (Roemer et al., 2021).

107 Owing to the role of their foraging habitat in modulating their calls, bats of
108 different foraging guilds are expected to respond antagonistically to habitat loss and
109 fragmentation (Denzinger & Schnitzler, 2013; Schnitzler & Kalko, 2001). In the
110 aftermath of damming, once continuous forests are lost to smaller insular forest
111 patches harbouring a gradient of vegetation structures: while cluttered forest
112 represent optimal conditions for supporting diverse assemblages of forest bats, the
113 water matrix can pose a serious obstacle to this guild's mobility, thus acting as a
114 morpho-ecological filter (Colombo et al., 2022). On the other hand, the newly created
115 edges and adjacent open water surface might constitute high-quality habitat for edge
116 and open-space foragers, as these vegetation structures are adapted to these guilds'
117 morphological and acoustical adaptations (Denzinger & Schnitzler, 2013; Schnitzler
118 & Kalko, 2001). In this sense, forest-dependent bats, which have been identified as
119 being of conservation priority in SE Asia due to the general decline of forested areas
120 in this region (Kingston, 2010), are expected to be restricted to continuous mainland
121 forest and large, well-connected islands. Differentiating the response of these three
122 guilds is therefore central to the implementation of adapted conservation measures.
123 Notwithstanding, the study of insectivorous bats in Southeast Asia, especially forest
124 and edge foragers, has been largely impaired by the ability of most insectivorous
125 species to avoid live trapping methods, such as harp traps and mist nets (Kingston,
126 2013). With the increasing affordability of low-cost acoustic devices, insectivorous

127 bat surveys are becoming more accessible and reliable, further allowing for high
128 replication (Gibb et al., 2019; Hill et al., 2018).

129 Utilising such technological advances, here we provide the first assessment of
130 the effects of habitat loss and insular fragmentation on insectivorous bats in a dam-
131 induced landscape in peninsular Malaysia. Using passive acoustic monitoring, we
132 surveyed insectivorous bats in 26 forest islands and two mainland continuous forest
133 sites. Across a gradient of habitat loss and insular fragmentation, we tested the
134 effect of island size, isolation, and habitat quality (island shape and NDVI), at the
135 following levels of bat diversity (1) overall assemblage, considering sonotype
136 richness, activity and assemblage composition, (2) foraging guild, separately
137 considering the activity of forest, edge and open-space foragers, and (3) sonotype,
138 given each sonotype activity. We hypothesise that increased forest size and canopy
139 density (i.e., higher NDVI values), and decreased isolation positively influence
140 sonotype richness and activity. Yet, the different foraging guilds are hypothesised to
141 show contrasting responses. In particular, forest foragers are expected to respond
142 positively to forest size, canopy density, and connectivity to the mainland and
143 surrounding forest patches, while open-space and edge foragers are expected to
144 show opposite responses.

145 **2. Material and methods**

146 **2.1 Study area**

147 This study was conducted within the insular fragmented landscape of the Kenyir
148 Lake and its surroundings in peninsular Malaysia. This artificial freshwater reservoir
149 was formed in 1986 by the damming of the Kenyir river. The novel insular landscape
150 occupies 260 000 ha and is composed of >340 islands ranging in size between 0.6
151 and 1428 ha embedded in the water matrix (Figure 1). Tropical humid forest on the
152 islands and the adjacent mainland continuous forest are characterised by lowland
153 and mid-elevation dipterocarp vegetation. The wide reservoir landscape, including
154 the islands and surrounding mainland continuous forest, was subject to selective
155 logging prior to damming (Muhammad Yusuf, 2005; Qie et al., 2011). This practice is
156 still allowed in some parts of the lake's catchment area, but not in Taman Negara
157 National Park, which borders its south-eastern side (Mariapan et al., 2017). This
158 region experiences a wet season between November and March, and a dry season
159 between May and October. Annual precipitation varies between 2700 and 4000 mm
160 annually (Qie et al., 2011).

161 **2.2 Study design and data collection**

163 We selected 26 islands covering a range of sizes (min-max: 0.45 – 167.3 ha) and
164 distances from the mainland (135 – 2748 m), in addition to two mainland sampling
165 sites. This sampling strategy was set up to study the effects of forest size and
166 isolation independently, i.e. maintaining a low correlation between these variables (r
167 = -0.36 when considering island size and distance to mainland, r = -0.49 when
168 considering log-transformed island size and distance to the mainland). Bat acoustic
169 surveys were carried out between September 8th and October 13th 2019, using
170 Audiomoth recorders (Hill et al., 2018) set on a sampling rate of 384 kHz and the
171 gain to the second setting (“med”). This sampling period has been selected to avoid

172 the severe monsoons typical of this region, and thus scaping any rain-induced
173 deterioration of the acoustic recording. We deployed one recorder in each sampling
174 site and recorded for six hours, a sampling effort deemed adequate when aiming to
175 detect bat populations' and assemblages' response to habitat modification (López-
176 Baucells et al., 2021). Recordings were divided into two time periods starting 30
177 minutes before sunset and ending 30 minutes after sunrise: from 18:00 to 22:00, and
178 from 04:00 to 06:00 (Hayes, 1997), covering the two peaks of bat activity at dusk and
179 dawn (Fenton, 1970). Each recorder was attached to a tree, positioned 2 metres
180 above the ground and, to minimise any uncontrolled impact from edge effects,
181 placed as inland as possible relative to island size, i.e., between 14 and 123 m from
182 the edge (median: 50 m).

183 **2.3 Acoustic analysis**

184 Using the software Kaleidoscope Version 5.4.7 (Wildlife Acoustics, 2019), we split
185 the recorded sequences into 5-second recordings (Torrent et al., 2018). The same
186 software was used to filter the sequences containing sounds with a minimum
187 frequency of 10 kHz and a maximum frequency of 250 kHz, and a pulse length
188 between 2 and 500 ms. Among these sequences, only those containing one bat
189 pass, i.e., at least two pulses of the same sonotype were kept for subsequent
190 analysis (Torrent et al., 2018).

191 Prior to the acoustic analysis, we first compiled a list of all species of
192 insectivorous bat known to occur in peninsular Malaysia (Lim et al., 2014; Nor
193 Zalipah et al., 2019). Secondly, we collated reference calls for these species. We did
194 so by conducting a literature survey using the Web of Science platform, between
195 September and November 2021. We searched for publications by each species'
196 name followed by the country name: we favoured reference calls obtained in our
197 study area in order to avoid any potential geographical variation in the call
198 parameters. For those species we could not find any reference calls, we used the
199 reference calls available in the bat call library Chirovox (Görföl et al., 2022)
200 (Supporting file 1). We therefore matched the call type of the species present in
201 peninsular Malaysia to one of the sonotypes described in Yoh et al. (2022) for bat
202 species in Malaysian Borneo, namely CF, FM, FMqCF1, FMqCF2, FMqCF3,
203 FMqCF4, FMqCF5, QCF and LF sonotypes. Using start and end frequency,
204 frequency of maximum energy, duration and interpulse interval as defined in Russo
205 & Jones (2002), we classified the calls into one of these nine sonotypes. Given their
206 very distinct echolocation parameters, the CF calls belonging to the genera
207 *Rhinolophus* and *Hipposideros* could be identified to the species level.

208 As the shape of the echolocation calls reflects the physical constraints
209 encountered by the bats, we were able to classify bat sonotypes into three foraging
210 guilds: (1) the constant-frequency and FM calls represent forest foragers, (2)
211 FMqCF4, FMqCF5 and QCF represent edge foragers, and (3) LF, FMqCF2 and
212 FMqCF3 calls represent open-space foragers (Yoh et al., 2022). Social calls could
213 not be identified to the sonotype level and were treated as assemblage-level activity.

214 **2.4 Patch variables**

215 Patch variables were obtained from a georeferenced LANDSAT 5 image which was
216 transformed into a land/water matrix using an unsupervised classification on the

217 software ArcGIS (ESRI, 2011). We then used the “landscapemetrics” R package
218 (Hesselbarth et al., 2019) to extract: (1) island size (*area*; ha), (2) shortest Euclidean
219 distance to the mainland (*dist.main*; m), (3) shortest Euclidean distance to the
220 nearest neighbour island or mainland (*dist.neigh*; m), (4) island shape (*shape*),
221 defined as the ratio between the patch perimeter and the hypothetical minimum
222 perimeter of this patch, i.e. the perimeter of a maximally compact patch (McGarigal &
223 Cushman, 2002), (5) the normalised difference vegetation index (*NDVI*), and (6)
224 distance between the recorder and the forest edge (*dist.edge*; m). Given that the
225 mainland continuous forest sites are characterised by an extensive forest coverage
226 non-isolated area, we attributed these sites with the closest possible values to
227 ‘reality’. This included area values of one order of magnitude higher than the largest
228 island (1670 ha) and zero distances to either the mainland or the nearest neighbour.
229 To streamline, we refer to the area of both islands and mainland size as ‘forest area’.
230 *NDVI* and *shape* were calculated as for the remaining sampling sites but considering
231 a 1000 m buffer centred in the sampling site and excluding water.

232 2.5 Data analysis

233 Assemblage-level metrics include sonotype richness, activity, and assemblage
234 composition. Sonotype richness was defined as the number of sonotypes: this
235 measure is representative of the diversity of call traits present at a site. Activity i.e.,
236 the number of bat passes, was used as a proxy for abundance. Although activity is
237 widely used as a surrogate for abundance when studying echolocating bats (see for
238 instance Charbonnier et al., 2016; Ellerbrok et al., 2022), this method may
239 overestimate abundance due to the possibility of multiple detection of a single
240 individual (Gibb et al., 2019; Kunz et al., 2009). Yet, it offers an effective tool for the
241 detection of damming effects (e.g., López-Bosch et al., 2021 and Colombo et al.,
242 2022), as well as other human-induced disturbances on bat communities (Mena et
243 al., 2022; Williams-Guillén & Perfecto, 2011). Assemblage composition was
244 summarised as a single variable using a Non-Metric Multi-Dimensional Scaling
245 (NMDS) ordination. This analysis was performed considering sonotype activity and
246 using a Bray-Curtis similarity matrix (stress = 0.130). The scores of the first axis of
247 the NMDS composed the assemblage composition metric. Guild activity was
248 calculated by summing the activity of the individual sonotypes respectively belonging
249 to the forest, open-space and edge guilds (Table 1). Sonotype-level responses were
250 examined for the sonotypes recorded in more than 10 sites and which had more than
251 50 bat passes. This threshold was intended to ensure a normal distribution of the
252 residuals, as well as homoscedasticity. Social and unidentified calls were only
253 included in the assemblage-level analysis. Among the sonotypes that met the
254 threshold to be analysed, namely FMqCF2, FMqCF3, FMqCF4, FMqCF5, LF, *R.*
255 *trifoliatum*, *H. diadema* and QCF, *H. diadema* and FMqCF2 had unequal error
256 variances and were therefore excluded from the analysis.

257 We first accounted for spatial autocorrelation by applying Mantel tests using
258 the R package “ade4” (Dray & Dufour, 2007). These tests correlate geographic
259 distance between sampling sites and each response variable as well as the residuals
260 of each model introduced in the subsequent section. We found no spatial
261 autocorrelation ($p > 0.05$) in all instances. We also examined the pairwise correlation
262 between patch variables using Pearson correlation coefficients. *Shape* and *area*
263 ($\log_{10} x$) ($r = 0.720$), as well as *area* ($\log_{10} x$) and *NDVI* were highly correlated ($r =$
264 0.800). Given the overall importance of area explaining biodiversity patterns in

265 insular forest fragments (Jones et al., 2021), we preferred to keep this metric to
266 enable comparisons with other studies, whereas *shape* was excluded from
267 subsequent analysis. Due to the lack of knowledge on the effects of canopy
268 closeness on bats in this region, we chose to also keep *NDVI* in subsequent
269 analyses. However, *area* ($\log_{10} x$) and *NDVI* were not included together in a model.
270 Collinearity between predictor variables was also examined using Variance Inflation
271 Factors (VIFs), with no variable showing substantial collinearity ($VIF > 5$) (Dormann et
272 al., 2013).

273 We then analysed the combined effects of patch variables – *area*, *dist.main*,
274 *dist.neigh* and *NDVI* – on (1) sonotype richness, activity and assemblage
275 composition; (2) activity of forest, edge, and open-space sonotypes, and (3) the
276 individual activity of eight sonotypes. To do so, we applied Linear Models (LMs) to
277 each of these response variables, whose distribution was scrutinised prior to the
278 analysis. The response variables regarding overall assemblage, guild and sonotype
279 level activity, as well as forest area were log-transformed. Although all models were
280 run with a gaussian error distribution, we initially considered a negative binomial
281 distribution for the overall, guild-level and sonotype-level activity responses. Given
282 that none of the models addressing individual sonotypes activity nor forest guild
283 activity converged with a negative binomial error distribution, and that the distribution
284 of these variables' residuals was closer to a normal distribution when using a log-
285 transformation with a gaussian error structure, we chose to retain that transformation
286 and error structure in the models. We further considered *dist.edge* as a covariate in
287 each model, aiming to control for any eventual effect of distance to the forest edge.

288 A candidate model set including all possible combinations of patch variables
289 (including the covariate *dist.edge*), except combinations involving *area* ($\log_{10} x$) and
290 *NDVI* in the same model, was generated using the dredge function of the “MuMIn” R
291 package (Barton, 2022). All models were ranked by Akaike Information Criteria
292 corrected for small sample sizes (AICc: Burnham & Anderson (2002). To account for
293 model uncertainty in multi-model inference, we used a model-averaging approach
294 considering the most parsimonious models, i.e. those having the lowest AICc within
295 a $\Delta AICc < 2$ ($\Delta AICc = AICc_i - AICc_{min}$, i being the i^{th} model derived from the dredge)
296 (Froidevaux et al., 2022). We report model average estimates along with their 95%
297 confidence intervals (CIs) which were considered significant if not overlapping zero
298 (Nakagawa & Cuthill, 2007). Assumptions about the normal distribution of the
299 variables and their residuals were verified using the R packages “performance”
300 (Lüdecke et al., 2021) and “Dharma” (Hartig, 2022). All data analyses were
301 performed using R (R Core Team, 2022).

302 **3. Results**

303 In total, we recorded 21 197 bat passes from 16 different sonotypes: 10 forest, three
304 edge and three open-space foragers (Table 1). Sonotype richness varied between 4
305 and 13 sonotypes per site, activity varied between 43 and 3351 bat passes per six
306 hours recording. Activity varied greatly across sampling sites ($43 - 3351$, $757.03 \pm$
307 744.18), and among foraging guilds ($0 - 689$, 101.89 ± 174.73 for forest foragers, 2
308 $- 2923$, 489.39 ± 698.75 for edge foragers, and $11 - 641$, 130.39 ± 144.01 for open-
309 space foragers). While the edge forager FMqCF4 and the open-space forager LF
310 were present at every site, the following forest foragers were found at only one site:
311 *Rhinolophus refulgens* (island 13), CF.46 (island 25), *Hipposideros cervinus*, *H.*
312 *kunzi* and *H. bicolor* (CF A) (Tables 1 and S1). According to the NMDS, low values in

313 the first axis were mostly associated with larger forest sites and forest foragers (*H.*
314 *cervinus*, *H. kunzi*, *H. bicolor*, FM), while high values were associated with smaller
315 islands, as well as with edge (FMqCF4, FMqCF5), open-space (FMqCF3), and forest
316 foragers (*R. refulgens*, *R. affinis*) (Figure 2). Overall, 988 bat passes could not be
317 identified to either the guild or to the sonotype level, including 981 bat passes
318 corresponding to social calls (Table 1). *R. trifoliatus* was likely greatly influential on
319 the response of the forest guild: being present in less than half the forest sites, it
320 accounted for nearly 80% of the forest guild's activity (Table 1). Most of the FM
321 sonotype activity (71.42%) was recorded on the mainland sites.

322 **3.1 Overall assemblage responses**

323 Sonotype richness increased with NDVI ($\beta = 0.819 \pm 0.409$, $p = 0.045$, $CI_{\min} = 0.017$,
324 $CI_{\max} = 1.620$), while total bat activity was unaffected by the patch variables
325 considered (Table S2). Assemblage composition varied among sites based on their
326 size ($\beta = -0.536 \pm 0.137$, $CI_{\min} = -0.817$, $CI_{\max} = -0.254$), $p < 0.001$) (Table S2,
327 Figure 3D, I and Figure 4).

328

329 **3.2 Guild-level responses**

330 Forest sonotypes were more active at sites with higher NDVI ($\beta = 1.476 \pm 0.439$, $p =$
331 0.002 , $CI_{\min} = 0.616$, $CI_{\max} = 2.335$). The activity of forest sonotypes also increased
332 with decreasing distance to the closest neighbouring forest site ($\beta = -1.468 \pm 0.439$,
333 $p = 0.002$, $CI_{\min} = -2.328$, $CI_{\max} = -0.608$), while edge sonotypes activity decreased
334 with increasing both island size ($\beta = -1.050 \pm 0.366$, $p = 0.004$, $CI_{\min} = -1.768$, CI
335 $_{\max} = -0.332$) and distances to edge ($\beta = -1.045 \pm 0.355$, $p = 0.003$, $CI_{\min} = -1.741$,
336 $CI_{\max} = -0.350$). None of the tested variables had a significant effect on open-space
337 sonotypes (Table S2, Figure 3O – Q and Figure 4). Unlike all other response
338 variables, only one model was selected for the activity of forest foragers (*Dist.neigh*,
339 *NDVI*, $AICc = 132.129$) (Table S3).

340 **3.3 Sonotype-level responses**

341 Among all the six individual sonotypes, only FMqCF4 and *R. trifoliatus* showed a
342 significant response to the tested patch variables. FMqCF4 sonotype showed higher
343 activity in smaller islands ($\beta = -1.127 \pm 0.365$, $p = 0.002$, $CI_{\min} = -1.841$, $CI_{\max} = -$
344 0.412), while *R. trifoliatus* was more active on larger forest sites ($\beta = 1.487 \pm 0.446$, p
345 $= 0.001$, $CI_{\min} = 0.614$, $CI_{\max} = 2.361$) (Table S2, Figure 4 and S1).

346 **4. Discussion**

347 A number of studies have demonstrated that habitat loss and insular fragmentation
348 cause species local extinctions across lowland tropical forests (Gibson et al., 2013;
349 Moore et al., 2022; Palmeirim et al., 2022; Pinto Henriques et al., 2021). Here, we
350 contribute to fill an important knowledge gap by accordingly demonstrating overall
351 negative bats response to dam-induced disturbance across an insular fragmented
352 landscape in Southeast Asia. Our results highlight the role of canopy density driving
353 the number of sonotypes, whereas forest area dictated which sonotypes were able to
354 persist. Our guild-level analysis revealed that forest foragers were associated with
355 denser forest structures, likely representing higher habitat quality for this guild, and
356 were negatively affected by increasing isolation from neighbouring landmasses. In

357 contrast, edge foragers seemed to benefit from island shrinkage. Fragmentation
358 effects were not so clearly observed at the sonotype-level, with only two of the six
359 sonotypes analysed responding to patch variables, namely to forest area which had
360 a positive effect on the forest forager *R. trifoliatus* and a negative effect on the edge
361 sonotype FMqCF4.

362 Effects of forest area

363 Forest area did not predict sonotype richness at our study site. Owing to their high
364 correlation, habitat quality and forest area were precluded from being combined in
365 models, and models including habitat quality were more parsimonious than those
366 including area: the absence of area effects is therefore more likely a consequence of
367 the study design rather than a proper lack of area effects. In fact, a large body of
368 evidence reports that area affects bat richness in fragmented insular (Luypaert et al.,
369 2023), and non-insular systems (Rocha et al., 2017). This pattern holds true for
370 several taxa on reservoir islands (Palmeirim et al., 2022), including dung-beetles
371 (Qie et al., 2011), primates and ungulates (Yong, 2015), and birds (Yong et al.,
372 2011) surveyed in nearly the same islands in Kenyir. Notwithstanding, bat
373 assemblage composition varied along the gradient of forest area, with edge foragers
374 being particularly active on smaller islands. This trend was further reflected at the
375 sonotype level by the edge forager FMqCF4 and the forest forager *R. trifoliatus*, both
376 of whom displayed contrasting responses to forest area, the former being negative,
377 and the latter being positive. These responses were expected given that small
378 islands tend to be edge-dominated. The extensive variation in species-specific
379 home-range size may have further influenced the ability of some species to use the
380 smaller fragments: while that of most edge foragers (5 – 210 ha) and *R. trifoliatus* (5
381 ha) are notably small, the majority of forest foragers have a vast home-ranges,
382 reaching up to 2199 ha for some species (Wilson et al., 2010). Given their tendency
383 to avoid flying across the water matrix (Meyer & Kalko, 2008), forest foraging
384 species, mostly belonging to the FM sonotype, were therefore rarely recorded on
385 smaller islands. Yet, as a caveat to this study, in small islands, detectors had to be
386 placed closer to edges given the lack of forest interior. It is therefore possible that the
387 detectors on small islands, being mechanically closer to forest edges, recorded a
388 higher activity of edge foragers. This is further supported by the negative relationship
389 between edge foragers activity and the *Dist.edge*. In any case, this would still
390 demonstrate the preferential use of edges by this bat guild (López-Bosch et al.,
391 2021). In contrast, our results show that the forest forager *R. trifoliatus* responds
392 positively to forest area, suggesting that this sonotype requires greater habitat
393 complexity associated with larger areas of forest (Benchimol & Peres, 2015a).

394 Effects of habitat quality

396 Despite the absence of clear effects of forest size, canopy closeness, as indicated by
397 the NDVI, promoted an increase in the number of bat sonotypes and forest foragers
398 activity across the Kenyir landscape. A bat species' response to habitat quality is
399 likely influenced by the intrinsic habitat characteristics such as 3D forest structure or
400 canopy ruggedness, ultimately impacting which species are able to use each site
401 (Froidevaux et al., 2016). Our study landscape has been subject to intensive
402 selective logging prior to the construction of the dam (Qie et al., 2011). Indeed,
403 evidence for previous logging is still noticeable in the area, with logging trails and
404 canopy holes being observed *in-situ*, resulting in a low but variable overall NDVI on
405 the islands and surrounding continuous forest sites. Whilst the effects of logging on

406 bat species richness seem to be limited both in the Neotropics (Meyer et al., 2016)
407 and in the Paleotropics (Struebig et al., 2013), logging appears to strongly influence
408 assemblage composition, edge species being indicative of repeatedly logged sites
409 (Peters et al., 2006). Yet, the effects of logging on biodiversity depend on the
410 intensity and extraction methods (Burivalova et al., 2014), and further investigations
411 regarding the effects of logging intensity in the context of insular forest fragments are
412 needed to further our understanding of how logging may drive bat sonotype richness.
413 Notwithstanding the potential effects of logging, forest insularisation led to the
414 creation of edges, whose deleterious effects on vegetation include increased
415 exposure to wind-throws, culminating in shifts towards disturbance-adapted pioneer
416 trees (Benchimol & Peres, 2015a; Santo-Silva et al., 2021). While sites with low
417 canopy closeness can be widely used by edge foragers, only those sites harbouring
418 increased NDVI may represent suitable habitat for manoeuvrable forest dependent
419 species that are further adapted to echolocate in more cluttered environments
420 (Froidevaux et al., 2016; Suarez-Rubio et al., 2018). By allowing forest foragers to
421 persist, habitat quality contributes to maintain bat diversity, as also observed for
422 other biological groups, e.g., large-sized mammals and reptiles (Oliveira et al., 2020;
423 Silva et al., 2022). This is further supported by the increase in forest bat activity we
424 observed in denser canopies. Higher NDVI values may also be associated with
425 higher availability of mature trees that provide roosting sites for species such as *R.*
426 *trifoliatus*, *R. sedulus*, *K. papillosa* and *K. pellucida*, all of which depend on these
427 structures to rest and thus to persist. For instance, in Malaysia, the absence of tree
428 cavities due to forest disturbance was associated with the decline of the forest
429 foragers *Kerivoula* sp. (Struebig et al., 2013). Our findings reiterate the importance of
430 habitat quality as a key driver of species diversity in fragmented landscapes
431 (Armstrong et al., 2022; Poniatowski et al., 2018).

432 Effects of isolation

433 Contrary to our expectations, isolation was not an important variable explaining bat
434 assemblage-level responses. These results contrast with an insular fragmented
435 landscape in Panama, where isolation to the mainland was the main predictor of bat
436 richness (Meyer & Kalko, 2008). However, our results are in agreement with findings
437 from a non-insular Malaysian fragmented landscape, where isolation has also been
438 found to be a poor prediction of bat richness (Brändel et al., 2020). The lack of
439 isolation effects may be related to the overall small distance separating most of the
440 sampling sites, and the overall size of the lake, as the home ranges for most local
441 species exceed the distance separating most of the study sites (Wilson et al., 2010).
442 Nevertheless, forest foragers were more active in sites less isolated from
443 neighbouring landmasses, which might be due to morphological constraints (Norberg
444 & Rayner, 1987). Indeed, forest foragers have a wing morphology characterised by a
445 low aspect ratio (wingspan²/wing area) and a low wing loading (body mass/wing
446 area) (Norberg & Rayner, 1987). Although this characteristic allows them to have a
447 slow and highly manoeuvrable flight, it also makes flight over open spaces
448 particularly energetically demanding (Altringham, 2011; Bader et al., 2015).
449 Furthermore, the absence of distance-to-mainland effects in favour of distance-to-
450 neighbour effects for forest foragers underlines the value of intermediary islands to
451 act as stepping-stones for forest bats to cross the water matrix and reach more
452 remote islands. This idea is supported by Saura et al. (2014) who also stress that
453 these intermediate islands need to be sufficiently large and of high quality in order to
454 act as stepping-stones.

455 Limitations and potential caveats

456 Our results emphasise the valuable use of passive acoustic monitoring techniques to
457 survey bat assemblages, further allowing us to examine bat responses at multiple
458 levels. However, the use of sonotype richness instead of species richness likely
459 biased the estimated sonotype richness towards forest species. Indeed, while the CF
460 calls produced by forest foragers could be identified to the species level, other
461 sonotypes including FMqCF, QCF and LF contained multiple species. Likewise,
462 given the similarity of the ecological constraints faced by edge foragers, the calls
463 produced by the species belonging to this guild can only be separated between three
464 sonotypes (FMqCF4, FMqCF5 and QCF). For this reason, our results might
465 underestimate the effects of habitat loss and insular fragmentation on insectivorous
466 bats, which is further enhanced by the fact that larger forest sites – expected to
467 harbour higher species diversity – were proportionally less sampled. In addition, as
468 species detectability is a function of call intensity (Hayes, 2000), forest bats
469 producing low-intensity FM calls such as Vespertilionidae (e.g., *Kerivoula* and *Myotis*
470 spp.) tend to be under-detected (Waters & Jones, 1995). This might further explain
471 the relatively weak responses observed at the sonotype-level, which should
472 therefore be interpreted with caution. Likewise, even the most commonly used
473 devices in bat detection, including Audiomoths, tend to lack the sensitivity required to
474 detect some of the high intensity calls emitted by smallest-bodied bats such as *H.*
475 *cervinus*, *H. larvatus* and *H. bicolor* (Kingston, 2010): although common in
476 Peninsular Malaysia (Lim et al., 2014), these species have probably been under
477 detected in our study. Live trapping remains the most efficient method to monitor
478 these species (Kingston, 2013), and still, studies using these trapping methods have
479 highlighted the high sensitivity of these forest genera to forest disturbance (Huang et
480 al., 2019).

481 Conservation implications

482 SE Asia may lose over 74% of its original forest cover by the end of the century,
483 putting forest-dependent species at tremendous risk (Sodhi et al., 2004). Forest
484 foragers from the Kenyir lake are no exception: being absent from the smallest
485 islands, they showed low activity in isolated and degraded forest patches, which
486 nevertheless make up the majority of the landscape of Lake Kenyir. Additionally,
487 three forest species, namely *H. bicolor*, *H. cervinus* and *H. kunzi*, were only found on
488 the mainland. Our results suggest that conservation efforts should target forest bats
489 which, given their forest-adapted morphology and the rapid vanishing of their
490 foraging habitat, are particularly extinction prone (Jones et al., 2003; Safi & Kerth,
491 2004). The FM sonotype, of which most potential representatives such as *Kerivoula*
492 *intermedia*, *K. pellucida* or *Nycteris tragata* are listed as near threatened (Senawi &
493 Ahmad, 2021), was mostly active in the mainland, and completely absent from 21
494 islands. We therefore stress that bats highly dependent on forest can only persist in
495 large undisturbed forest tracts. The independent presence of dense canopies and
496 connection to nearby landmasses does not guarantee the use by forest bats. Indeed,
497 only patches that are large, well connected to the mainland, and harbouring a high
498 habitat quality can serve as stepping-stones, and therefore allow less vagile species
499 to commute over the water matrix (Saura et al., 2014). In insular forest patches,
500 species are lost in a sustained and delayed manner according to the time elapsed
501 since isolation, a process referred to as an “extinction debt” (Jones et al., 2016).
502 Furthermore, these islands suffer an inevitable vegetation decay (Benchimol &

503 Peres, 2015a). In line with (Jones et al., 2016), our results suggest that islands
504 should not be used as conservation units for mitigation purposes due to the imminent
505 extinction debt. Instead, conservation efforts should prioritise maintaining mainland
506 habitat quality, for instance by minimising logging activity in these highly forested
507 areas (Hari Poudyal et al., 2018; Harvey & Brais, 2011). This can be achieved by
508 legally protecting the islands and surrounding mainland continuous forest/wider
509 reservoir landscape as to minimise disturbances. Such measures have successfully
510 helped minimising further human activities in a Brazilian Biological reserve
511 encompassing part of a mega-dam (Benchimol & Peres, 2015a, 2015b). In addition,
512 future hydropower developments should consider how dam placement is likely to
513 affect the creation of different island systems. These developments should aim to
514 reduce the creation of a myriad of small, isolated, and habitat-degraded forest
515 fragments, for instance by targeting craggy locations over flat areas, therefore
516 drastically minimising the flooded area. The biological impacts of damming tend to
517 be largely underestimated, as current environmental impact assessment methods
518 poorly predict the extent and location of dam-induced flooding, possibly leading to a
519 64.5 % increase of the flooded surface compared to initial predictions (Cochrane et
520 al., 2017). Working towards a more accurate planning is therefore essential to
521 minimise the flooding area, avoid the flooding of ecologically valuable zones, and
522 adequately locate future dams.

523 **5. Conclusions**

524 Hydropower development is set to massively expand across Southeast Asian
525 forests, with energy production expected to increase threefold by 2035 (Petinrin &
526 Shaaban, 2015; Tang et al., 2019). In Malaysia alone, at least four additional major
527 dams will soon be constructed (> 34 000 MW) (Foo, 2015). Coupled with a steadily
528 declining share of forest in this region, these threats put insectivorous bat
529 assemblages at risk, especially for forest-dependent species. Here, we showed that
530 canopy density played a central role in promoting both sonotype richness,
531 persistence and activity of forest foragers, while this guild was negatively impacted
532 by isolation to neighbouring forest patches. Forest area further affected the
533 assemblage composition, larger forest patches being associated with forest-
534 dominated assemblages, and smaller patches being associated with edge-foragers.
535 Large, dense, well connected forest fragments still supported a subset of the
536 mainlands' assemblage diversity. Yet, our results suggested that preserving a high
537 canopy density, especially in the mainland, is essential to serve the preservation of
538 forest-dependent species. Keeping forest disturbances such as logging minimum
539 and developing more efficient tools to predict the spatial extent of future dam's
540 effects is therefore a priority for the preservation of bat assemblages in SE Asia.

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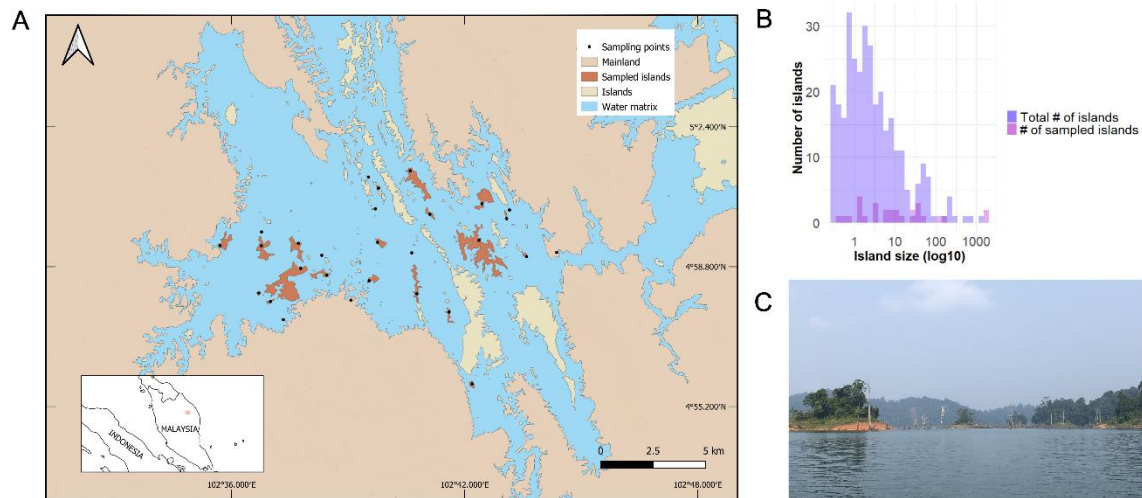
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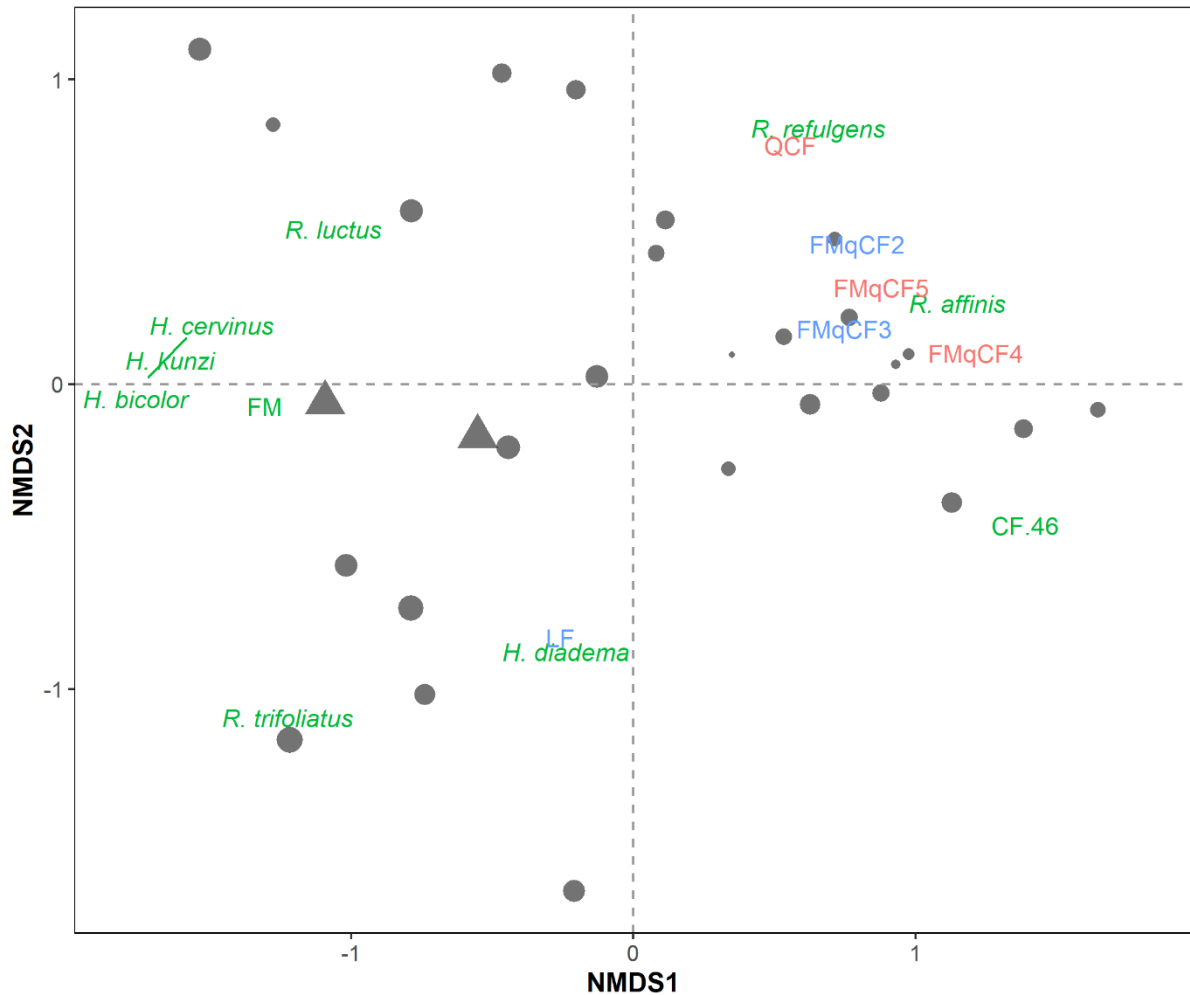
945 **Figures and Tables:**

946 *Colour should be used for figures 1, 2, 3, 4 and S1*



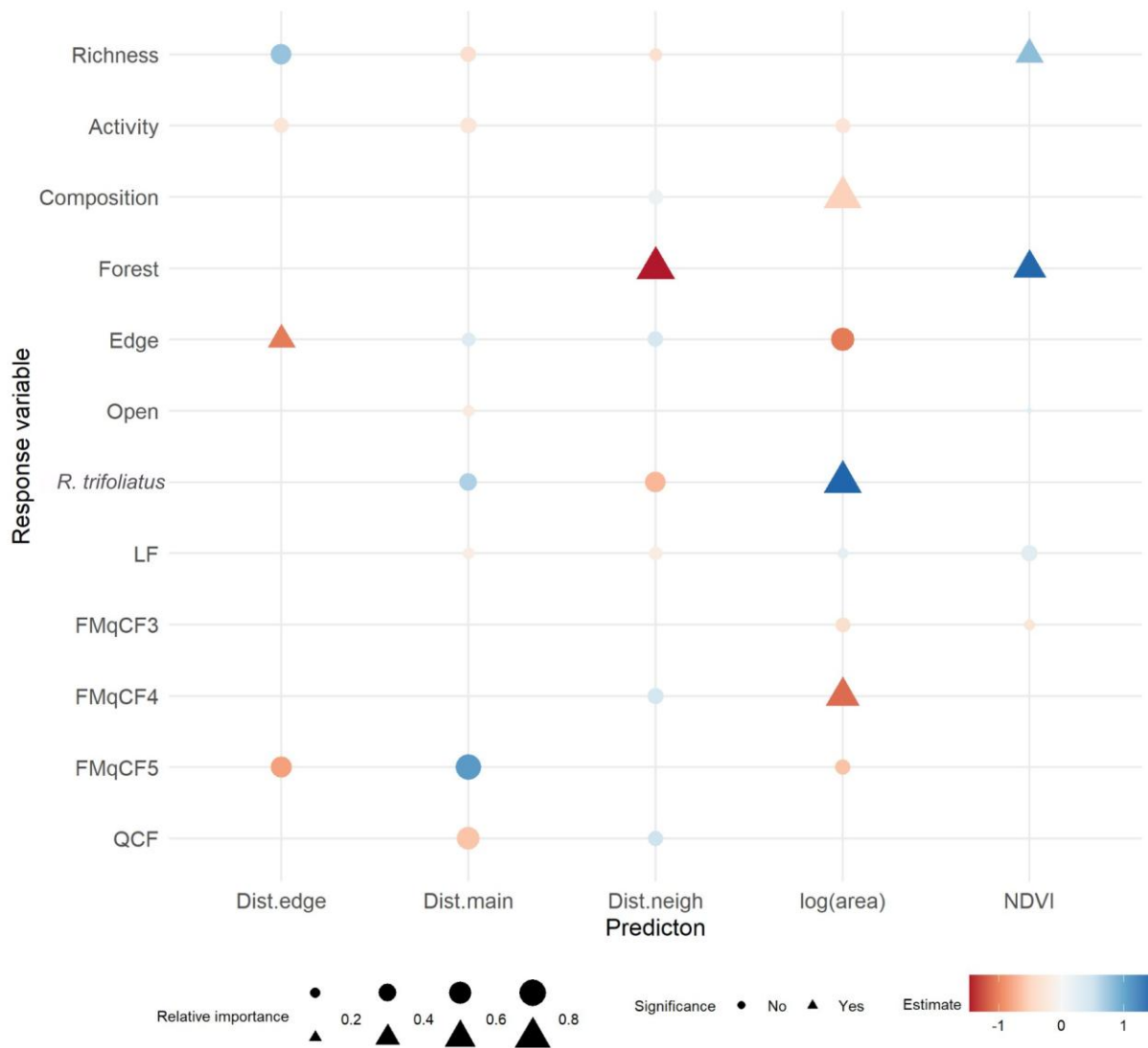
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948 **Figure 1.** Map of the Kenyir Lake (A) Location of the study area and sampling sites
949 in the Kenyir lake, peninsular Malaysia. The solid dots depict each of the 28
950 sampling sites. (B) Distribution of island sizes in Kenyir lake. (C) Photo of the Kenyir
951 Lake. *Two columns fitting image*

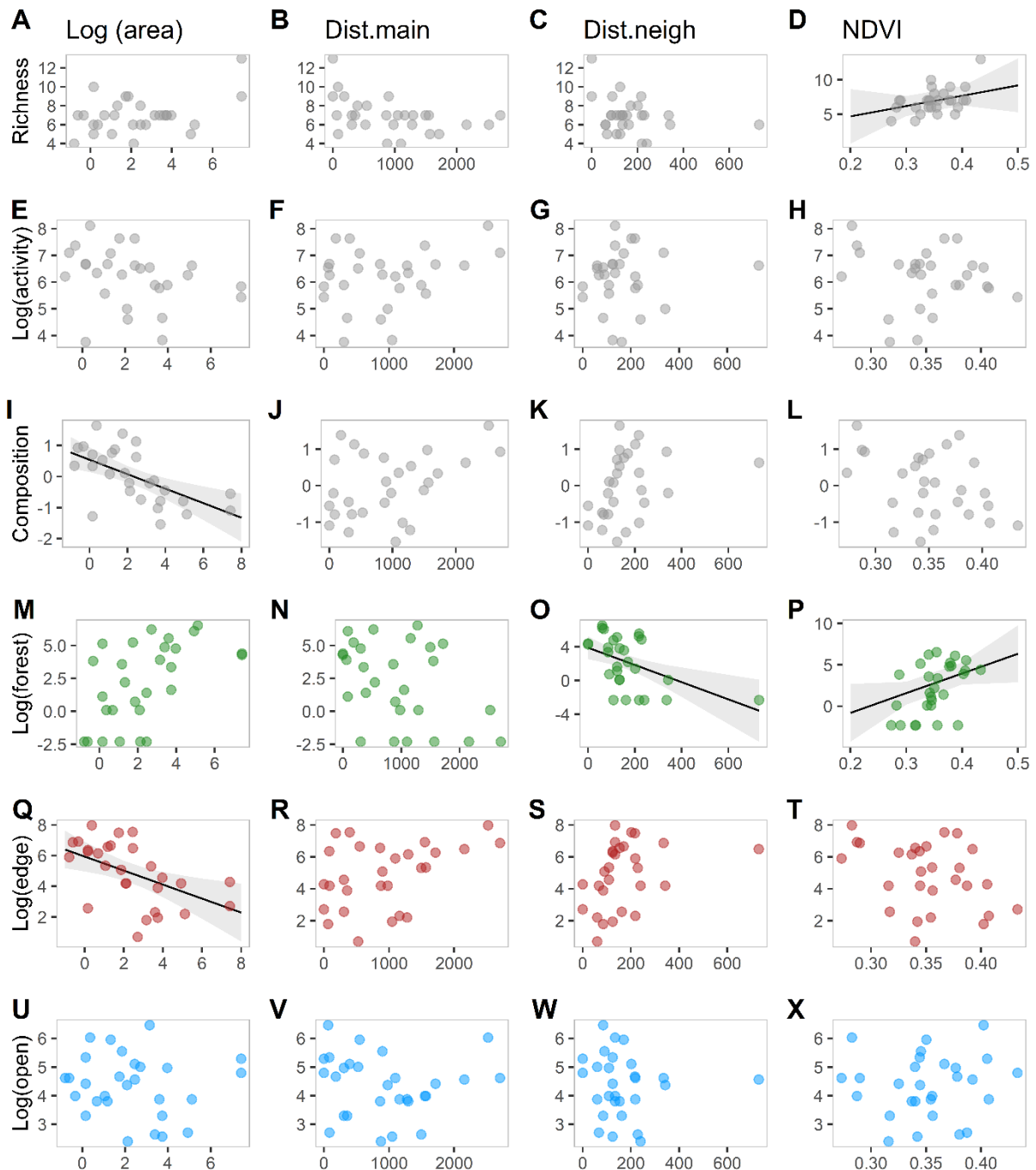


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953 **Figure 2.** Non-Metric Multi-Dimensional Scaling (NMDS) ordination plot denoting
 954 both sampling sites and sonotypes. Sampling sites are represented by circles,
 955 matching the islands which are sized proportionally to their size ($\log_{10} x$), and
 956 triangles correspond to the mainland continuous forest sites. Sonotypes are
 957 represented by their name and colour-coded according to the corresponding foraging
 958 guild: forest (in green), edge (red) and open-space (blue) (for further details
 959 regarding each sonotype, see Table 1). Given that the sonotypes *H. kunzi*, *H.*
 960 *cervinus* and *H. bicolor* are overlapping, for the sake of clarity, the position of these
 961 sonotypes is replaced by a green line and the sonotypes labels are separated.
 962 *Single column fitting image*



963
 964 **Figure 3.** Results of the model averaging procedure. Response variables are shown
 965 on the y axis, and predictor variables are shown on the x axis. The variables that
 966 were retained in the model selection and averaging appear at the intersection
 967 between response and predictor variables. The value of each estimate is depicted
 968 with a colour gradient, negative estimates being increasingly red, and positive
 969 estimates being increasingly blue. The significance of each selected variable is
 970 shown with point shape: significant variables are represented with a triangle, and
 971 non-significant variables are shown with a circle. The relative importance of each
 972 selected variable within the averaged model is shown with point size, smaller points
 973 having a lower relative importance than larger points.
 974 *Two columns fitting image*
 975



976
 977 **Figure 4.** Relationships between bat sonotype richness (A-D), activity ($\log_{10} x$) (E-H),
 978 assemblage composition (axis 1 of the NMDS) (I-L), and the activity of forest ($\log_{10} x$) (M-P),
 979 edge ($\log_{10} x$) (Q-T), and open-space foraging bats ($\log_{10} x$) (U-X) and Area
 980 ($\log_{10} x$) (A, E, I, M, Q, U), distance to the mainland (*Dist.main*) (B, F, J, N, R, V),
 981 Distance to neighbour (*Dist.neigh*) (C, G, K, O, S, W) and *NDVI* (D, H, L, P, T, X). In
 982 each panel, the solid black line is the prediction given by the averaged model
 983 obtained from the dredge, and the shaded area represents the 95% confidence
 984 interval. The predictions of the selected model were only shown for significant
 985 variables.

986 *Two columns fitting image*

987 **Table 1.** List of all sonotypes identified during the acoustic bat surveys across the
 988 insular fragmented landscape of the Kenyir Lake, peninsular Malaysia. For each
 989 sonotype, we indicate the potential species matching that sonotype, corresponding
 990 foraging guild, total activity (number of bat passes), and number of sampling sites in
 991 which each of the sonotypes was recorded. Bat passes that could not be identified
 992 were labelled as “unknown”.

Sonotype name	Potential species	Guild	# of bat passes	# of sites occupied (%)
<i>H. diadema</i>	<i>Hipposideros diadema</i>	Forest	392	11 (39.3%)
<i>R. affinis</i>	<i>Rhinolophus affinis</i>	Forest	146	7 (25%)
<i>R. trifoliatus</i>	<i>Rhinolophus trifoliatus</i>	Forest	2268	12 (42.8%)
<i>R. luctus</i>	<i>Rhinolophus luctus</i>	Forest	6	2 (7.1%)
<i>R. refulgens</i>	<i>Rhinolophus refulgens</i>	Forest	2	1 (3.6%)
<i>H. kunzi</i>	<i>Hipposideros kunzi</i>	Forest	1	1 (3.6%)
<i>H. cervinus</i>	<i>Hipposideros cervinus</i>	Forest	1	1 (3.6%)
<i>H. bicolor</i>	<i>Hipposideros bicolor</i>	Forest	2	1 (3.6%)
CF.46	<i>Hipposideros lekaguli</i> ²	Forest	1	1 (3.6%)
FM	Species from the subfamilies <i>Kerivoulinae</i> and <i>Murininae</i> , <i>Nycteris tragata</i> , <i>Coelops frithii</i> , <i>C. robinsoni</i> , <i>Lyroderma lyra</i> , <i>Megaderma spasma</i>	Forest	35	6 (21.4%)
LF	<i>Arielulus circumdatus</i> , <i>A. cuprosus</i> , <i>Chaerephon johorensis</i> , <i>Chaerephon plicata</i> , <i>Cheiromeles torquatus</i> , <i>Mops mops</i> ,	Open-space	2048	28 (100%)
FMqCF2	<i>Hesperoptenus blanfordi</i> , <i>H. doriae</i> , <i>H. tomesi</i>	Open-space	162	11 (39.3%)
FMqCF3	<i>Pipistrellus stenopterus</i>	Open-space	1441	27 (96.4%)
FMqCF4	<i>Tylonycteris robustula</i> , <i>Glischropus tylopus</i> , <i>Hesperoptenus blanfordi</i> , <i>P. tenuis</i> , <i>P. javanicus</i> , <i>Myotis adversus</i> , <i>M. horsfieldii</i> , <i>M. hasseltii</i> , <i>M. montivagus</i> , <i>Scotophilus kuhli</i> , <i>Miniopterus magnater</i> ,	Edge	13 195	28 (100%)
FMqCF5	<i>Glischropus tylopus</i> , <i>Tylonycteris pachypus</i> , <i>T. robustula</i> , <i>Myotis ridleyi</i> , <i>M. muricola</i> , <i>M.</i>	Edge	389	15 (53.6%)

² This species has not been sampled around our study site to our knowledge

QCF	<i>ater, M. siligronensis,</i> <i>Pipistrellus tenuis</i> <i>Emballonura monticola,</i>	Edge	119	16 (57.1%)
	<i>Taphozous melanopogon, T.</i> <i>longimanus,</i>			
Unknown	<i>Saccolaomius saccolamius,</i>		988	26 (92.8%)

993