

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

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

5 **Highlights:**

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

14 **Abstract**

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

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 activity increased in smaller islands. Of the six sonotypes analysed, the activity of
31 one forest sonotype increased with forest area, while that of one edge sonotype
32 decreased. Ensuring habitat quality within insular forest remnants, in addition to their
33 functional connectivity, maximises bat diversity, including the persistence of forest
34 foraging species. Future hydropower development should therefore avoid the
35 creation of a myriad of small, isolated, and habitat-degraded islands further
36 characterised by altered levels of bat diversity and guild-level activity.

37 **1. Introduction**

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

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

61 Species responses to habitat loss and insular fragmentation may further vary
62 between (Palmeirim et al., 2022) and within biological groups (Brändel et al., 2020;
63 Meyer & Kalko, 2008), as influenced by particular species traits (Meyer et al., 2008;
64 Palmeirim et al., 2021). For instance, the persistence of mid-sized mammal species
65 on islands can be related to their swimming capacity (Benchimol & Peres, 2015b),
66 while that of lizard species is dictated by their thermoregulation mode (Palmeirim et
67 al., 2017). Yet, even persisting taxa show general decreases in abundance in insular
68 forest fragments compared to surrounding mainland (e.g., bats: Gorresen & Willig
69 (2004), birds: Yong et al. (2011,)) and terrestrial and arboreal mammals: Benchimol &
70 Peres (2021)). As such, while certain species able to use non-forest habitats might
71 become overabundant (Moore et al., 2022), forest-dependent species become rarer
72 or locally extinct (Palmeirim et al., 2018). Understanding the drivers of species
73 response to forest insularisation – considering both environmental and intrinsic
74 species characteristics – allows more efficient management actions to be proposed,
75 which is not trivial given the expansion of the hydropower sector across lowland
76 tropical forests (Couto & Olden, 2018).

77 Although habitat loss and insular fragmentation have been reported as
78 important drivers of bat species' local extinction in the Neotropics (Colombo et al.,
79 2022; Meyer & Kalko, 2008), little is known for Asia. In fact, the only study targeting
80 such effects on insectivorous bats in this region highlighted the importance of island
81 area especially for forest-dependent species in East China (López-Bosch et al.,
82 2021). In addition, in a non-insular matrix setting in peninsular Malaysia, the diversity
83 of insectivorous bats was impacted by forest area, with species-specific responses
84 being modulated by their habitat affinity (Struebig et al., 2008). Insectivorous bats
85 emit echolocation calls to navigate their surroundings and locate food (Schnitzler et
86 al., 2003). The characteristics of the calls produced, e.g., call shape, are adapted to
87 a species' foraging preferences (Denzinger & Schnitzler, 2013; Schnitzler & Kalko,
88 2001). For example, species adapted to foraging in the forest interior (forest
89 foragers) use long constant frequency (CF) calls or very short, broadband, frequency
90 modulated (FM) calls, adapted to particularly cluttered environments. Edge foragers
91 use quasi-constant frequency (QCF) calls, or medium frequency calls (FMqCF)
92 composed of an FM component followed by a short and quasi constant element
93 (qCF), allowing them to locate and navigate between background features (medium
94 frequency FM component), and to locate prey at an intermediate distance (qCF
95 component). Open-space foragers use low frequency (LF) (<30 kHz) FMqCF calls
96 with a narrow FM component and a long QCF component, enabling prey detection in
97 vast empty spaces (Denzinger & Schnitzler, 2013; Schnitzler & Kalko, 2001). Within
98 foraging guilds, bat calls are not species specific: the calls of several species have
99 evolved in a convergent way to respond to analogous environmental pressures,
100 resulting in very similar calls in species facing analogous ecological conditions and
101 therefore preventing species-specific identification in certain instances (Gibb et al.,
102 2019; Russo et al., 2017). To overcome this issue, bat calls are commonly classified
103 into sonotypes, i.e., calls of similar shape and peak frequency (Roemer et al., 2021).

104 Owing to the role of their foraging habitat in modulating their calls, bats of
105 different foraging guilds are expected to respond antagonistically to habitat loss and
106 fragmentation (Denzinger & Schnitzler, 2013; Schnitzler & Kalko, 2001). In the
107 aftermath of damming, once continuous forests are lost to smaller insular forest
108 patches harbouring a gradient of vegetation structures: while cluttered forest
109 represent optimal conditions for supporting diverse assemblages of forest bats, the
110 water matrix can pose a serious obstacle to this guild's mobility, thus acting as a
111 morpho-ecological filter (Colombo et al., 2022). On the other hand, the newly created
112 edges and adjacent open water surface might constitute high-quality habitat for edge
113 and open-space foragers, as these vegetation structures are adapted to these guilds'
114 morphological and acoustical adaptations (Denzinger & Schnitzler, 2013; Schnitzler
115 & Kalko, 2001). In this sense, forest-dependent bats, which have been identified as
116 being of conservation priority in SE Asia due to the general decline of forested areas
117 in this region (Kingston, 2010), are expected to be restricted to continuous mainland
118 forest and large, well-connected islands. Differentiating the response of these three
119 guilds is therefore central to the implementation of adapted conservation measures.
120 Notwithstanding, the study of insectivorous bats in Southeast Asia, especially forest
121 and edge foragers, has been largely impaired by the ability of most insectivorous
122 species to avoid live trapping methods, such as harp traps and mist nets (Kingston,
123 2013). With the increasing affordability of low-cost acoustic devices, insectivorous
124 bat surveys are becoming more accessible and reliable, further allowing for high
125 replication (Gibb et al., 2019; Hill et al., 2018).

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

142 **2. Material and methods**

143 **2.1 Study area**

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

158 **2.2 Study design and data collection**

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

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

180 **2.3 Acoustic analysis**

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

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

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

211 **2.4 Patch variables**

212 Patch variables were obtained from a georeferenced LANDSAT 5 image which was
213 transformed into a land/water matrix using an unsupervised classification on the
214 software ArcGIS (ESRI, 2011). We then used the "landscapemetrics" R package
215 (Hesselbarth et al., 2019) to extract: (1) island size (*area*; ha), (2) shortest Euclidean

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

229 **2.5 Data analysis**

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

254 We first accounted for spatial autocorrelation by applying Mantel tests using
255 the R package "ade4" (Dray & Dufour, 2007). These tests correlate geographic
256 distance between sampling sites and each response variable as well as the residuals
257 of each model introduced in the subsequent section. We found no spatial
258 autocorrelation ($p > 0.05$) in all instances. We also examined the pairwise correlation
259 between patch variables using Pearson correlation coefficients. *Shape* and *area*
260 ($\log_{10} x$) ($r = 0.720$), as well as *area* ($\log_{10} x$) and *NDVI* were highly correlated ($r =$
261 0.800). Given the overall importance of area explaining biodiversity patterns in
262 insular forest fragments (Jones et al., 2021), we preferred to keep this metric to
263 enable comparisons with other studies, whereas *shape* was excluded from

264 subsequent analysis. Due to the lack of knowledge on the effects of canopy
265 closeness on bats in this region, we chose to also keep *NDVI* in subsequent
266 analyses. However, *area* ($\log_{10} x$) and *NDVI* were not included together in a model.
267 Collinearity between predictor variables was also examined using Variance Inflation
268 Factors (VIFs), with no variable showing substantial collinearity ($VIF > 5$) (Dormann et
269 al., 2013).

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

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

299 3. Results

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

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

319 **3.1 Overall assemblage responses**

320 Sonotype richness increased with NDVI ($\beta = 0.819 \pm 0.409$, $p = 0.045$, $CI_{\min} = 0.017$,
321 $CI_{\max} = 1.620$), while total bat activity was unaffected by the patch variables
322 considered (Table S2). Assemblage composition varied among sites based on their
323 size ($\beta = -0.536 \pm 0.137$, $CI_{\min} = -0.817$, $CI_{\max} = -0.254$), $p < 0.001$) (Table S2,
324 Figure 3D, I and Figure 4).

325

326 **3.2 Guild-level responses**

327 Forest sonotypes were more active at sites with higher NDVI ($\beta = 1.476 \pm 0.439$, $p =$
328 0.002 , $CI_{\min} = 0.616$, $CI_{\max} = 2.335$). The activity of forest sonotypes also increased
329 with decreasing distance to the closest neighbouring forest site ($\beta = -1.468 \pm 0.439$,
330 $p = 0.002$, $CI_{\min} = -2.328$, $CI_{\max} = -0.608$), while edge sonotypes activity decreased
331 with increasing both island size ($\beta = -1.050 \pm 0.366$, $p = 0.004$, $CI_{\min} = -1.768$, CI
332 $_{\max} = -0.332$) and distances to edge ($\beta = -1.045 \pm 0.355$, $p = 0.003$, $CI_{\min} = -1.741$,
333 $CI_{\max} = -0.350$). None of the tested variables had a significant effect on open-space
334 sonotypes (Table S2, Figure 3O – Q and Figure 4). Unlike all other response
335 variables, only one model was selected for the activity of forest foragers (*Dist.neigh*,
336 *NDVI*, $AIC_c = 132.129$) (Table S3).

337 **3.3 Sonotype-level responses**

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

343 **4. Discussion**

344 A number of studies have demonstrated that habitat loss and insular fragmentation
345 cause species local extinctions across lowland tropical forests (Gibson et al., 2013;
346 Moore et al., 2022; Palmeirim et al., 2022; Pinto Henriques et al., 2021). Here, we
347 contribute to fill an important knowledge gap by accordingly demonstrating overall
348 negative bats response to dam-induced disturbance across an insular fragmented
349 landscape in Southeast Asia. Our results highlight the role of canopy density driving
350 the number of sonotypes, whereas forest area dictated which sonotypes were able to
351 persist. Our guild-level analysis revealed that forest foragers were associated with
352 denser forest structures, likely representing higher habitat quality for this guild, and
353 were negatively affected by increasing isolation from neighbouring landmasses. In
354 contrast, edge foragers seemed to benefit from island shrinkage. Fragmentation
355 effects were not so clearly observed at the sonotype-level, with only two of the six

356 sonotypes analysed responding to patch variables, namely to forest area which had
357 a positive effect on the forest forager *R. trifoliatum* and a negative effect on the edge
358 sonotype FMqCF4.

359 Effects of forest area

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

391 Effects of habitat quality

393 Despite the absence of clear effects of forest size, canopy closeness, as indicated by
394 the NDVI, promoted an increase in the number of bat sonotypes and forest foragers
395 activity across the Kenyir landscape. A bat species' response to habitat quality is
396 likely influenced by the intrinsic habitat characteristics such as 3D forest structure or
397 canopy ruggedness, ultimately impacting which species are able to use each site
398 (Froidevaux et al., 2016). Our study landscape has been subject to intensive
399 selective logging prior to the construction of the dam (Qie et al., 2011). Indeed,
400 evidence for previous logging is still noticeable in the area, with logging trails and
401 canopy holes being observed *in-situ*, resulting in a low but variable overall NDVI on
402 the islands and surrounding continuous forest sites. Whilst the effects of logging on
403 bat species richness seem to be limited both in the Neotropics (Meyer et al., 2016)
404 and in the Paleotropics (Struebig et al., 2013), logging appears to strongly influence

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

429 Effects of isolation

430 Contrary to our expectations, isolation was not an important variable explaining bat
431 assemblage-level responses. These results contrast with an insular fragmented
432 landscape in Panama, where isolation to the mainland was the main predictor of bat
433 richness (Meyer & Kalko, 2008). However, our results are in agreement with findings
434 from a non-insular Malaysian fragmented landscape, where isolation has also been
435 found to be a poor prediction of bat richness (Brändel et al., 2020). The lack of
436 isolation effects may be related to the overall small distance separating most of the
437 sampling sites, and the overall size of the lake, as the home ranges for most local
438 species exceed the distance separating most of the study sites (Wilson et al., 2010).
439 Nevertheless, forest foragers were more active in sites less isolated from
440 neighbouring landmasses, which might be due to morphological constraints (Norberg
441 & Rayner, 1987). Indeed, forest foragers have a wing morphology characterised by a
442 low aspect ratio ($\text{wingspan}^2/\text{wing area}$) and a low wing loading ($\text{body mass}/\text{wing}$
443 area) (Norberg & Rayner, 1987). Although this characteristic allows them to have a
444 slow and highly manoeuvrable flight, it also makes flight over open spaces
445 particularly energetically demanding (Altringham, 2011; Bader et al., 2015).
446 Furthermore, the absence of distance-to-mainland effects in favour of distance-to-
447 neighbour effects for forest foragers underlines the value of intermediary islands to
448 act as stepping-stones for forest bats to cross the water matrix and reach more
449 remote islands. This idea is supported by Saura et al. (2014) who also stress that
450 these intermediate islands need to be sufficiently large and of high quality in order to
451 act as stepping-stones.

452 Limitations and potential caveats

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

478 Conservation implications

479 SE Asia may lose over 74% of its original forest cover by the end of the century,
480 putting forest-dependent species at tremendous risk (Sodhi et al., 2004). Forest
481 foragers from the Kenyir lake are no exception: being absent from the smallest
482 islands, they showed low activity in isolated and degraded forest patches, which
483 nevertheless make up the majority of the landscape of Lake Kenyir. Additionally,
484 three forest species, namely *H. bicolor*, *H. cervinus* and *H. kunzi*, were only found on
485 the mainland. Our results suggest that conservation efforts should target forest bats
486 which, given their forest-adapted morphology and the rapid vanishing of their
487 foraging habitat, are particularly extinction prone (Jones et al., 2003; Safi & Kerth,
488 2004). The FM sonotype, of which most potential representatives such as *Kerivoula*
489 *intermedia*, *K. pellucida* or *Nycteris tragata* are listed as near threatened (Senawi &
490 Ahmad, 2021), was mostly active in the mainland, and completely absent from 21
491 islands. We therefore stress that bats highly dependent on forest can only persist in
492 large undisturbed forest tracts. The independent presence of dense canopies and
493 connection to nearby landmasses does not guarantee the use by forest bats. Indeed,
494 only patches that are large, well connected to the mainland, and harbouring a high
495 habitat quality can serve as stepping-stones, and therefore allow less vagile species
496 to commute over the water matrix (Saura et al., 2014). In insular forest patches,
497 species are lost in a sustained and delayed manner according to the time elapsed
498 since isolation, a process referred to as an “extinction debt” (Jones et al., 2016).
499 Furthermore, these islands suffer an inevitable vegetation decay (Benchimol &
500 Peres, 2015a). In line with (Jones et al., 2016), our results suggest that islands

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

520 **5. Conclusions**

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

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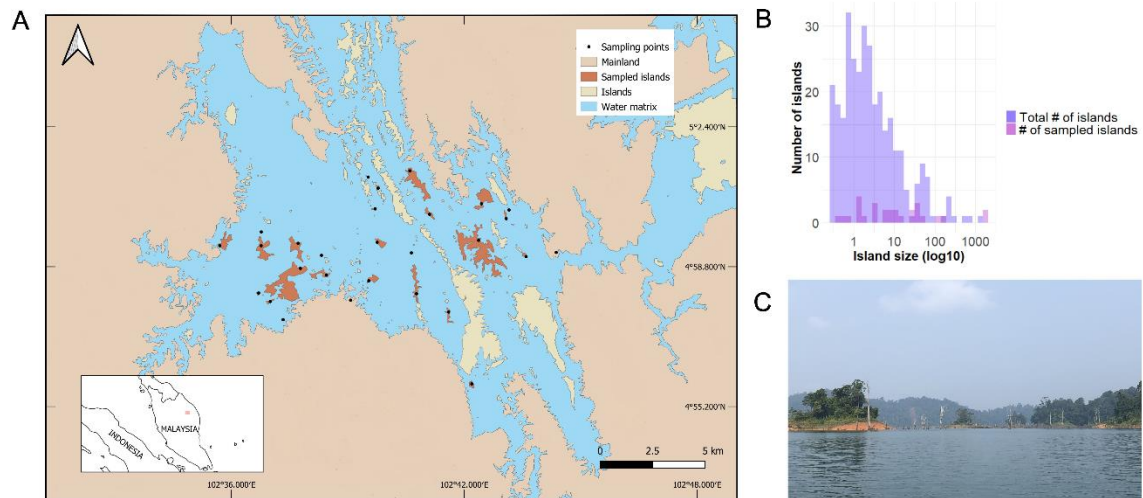
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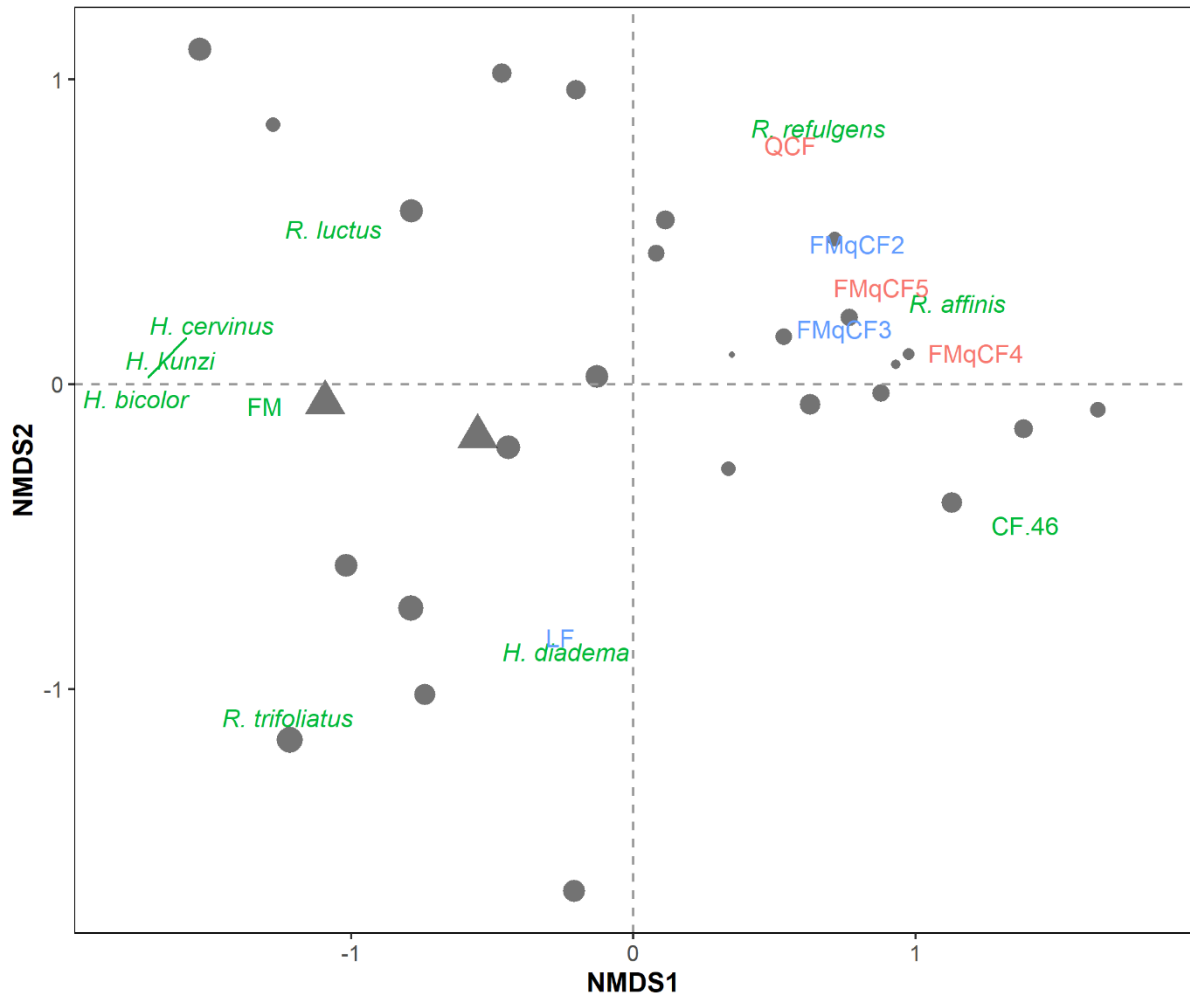
942 **Figures and Tables:**

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



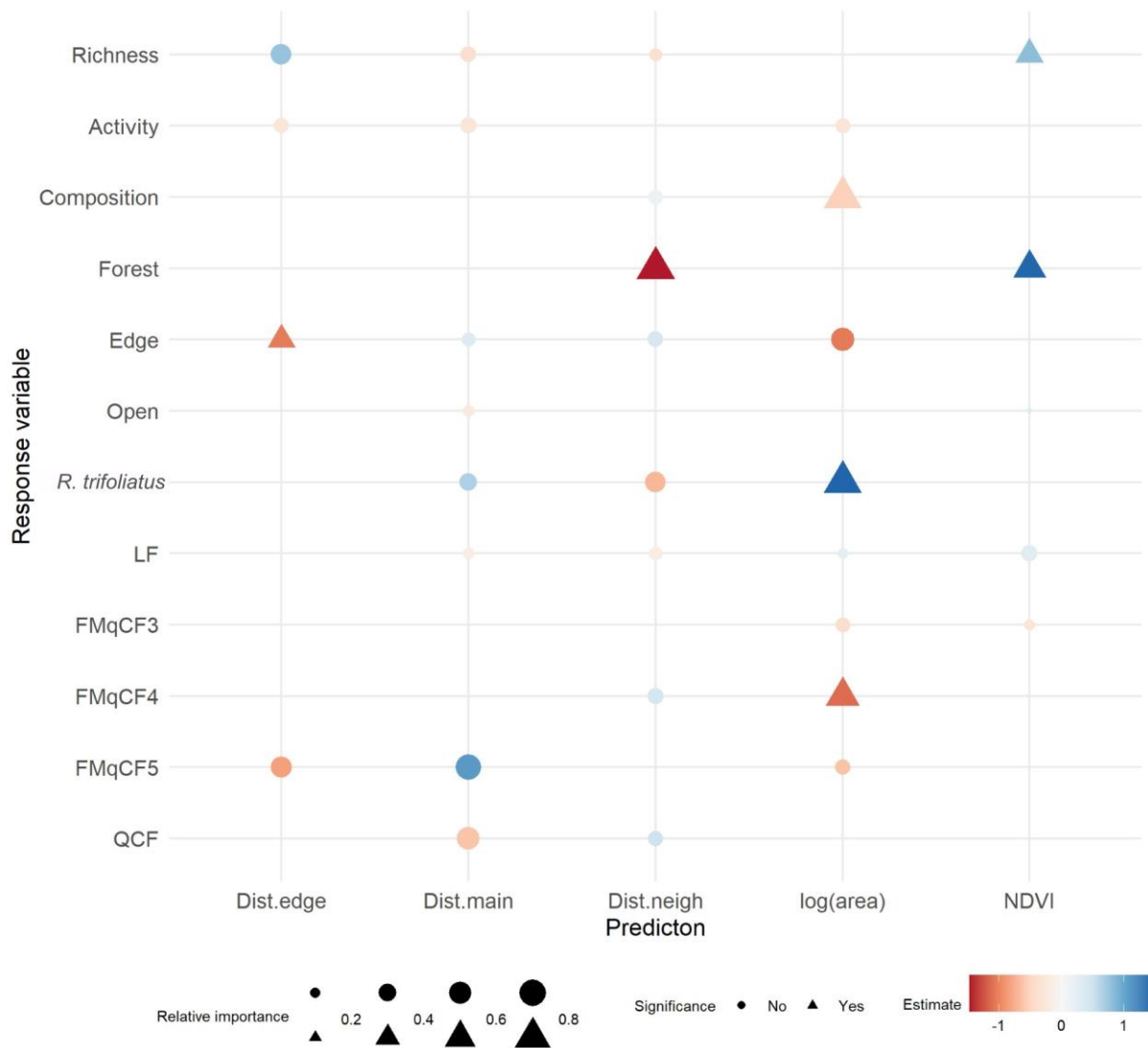
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945 **Figure 1.** Map of the Kenyir Lake (A) Location of the study area and sampling sites
946 in the Kenyir lake, peninsular Malaysia. The solid dots depict each of the 28
947 sampling sites. (B) Distribution of island sizes in Kenyir lake. (C) Photo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

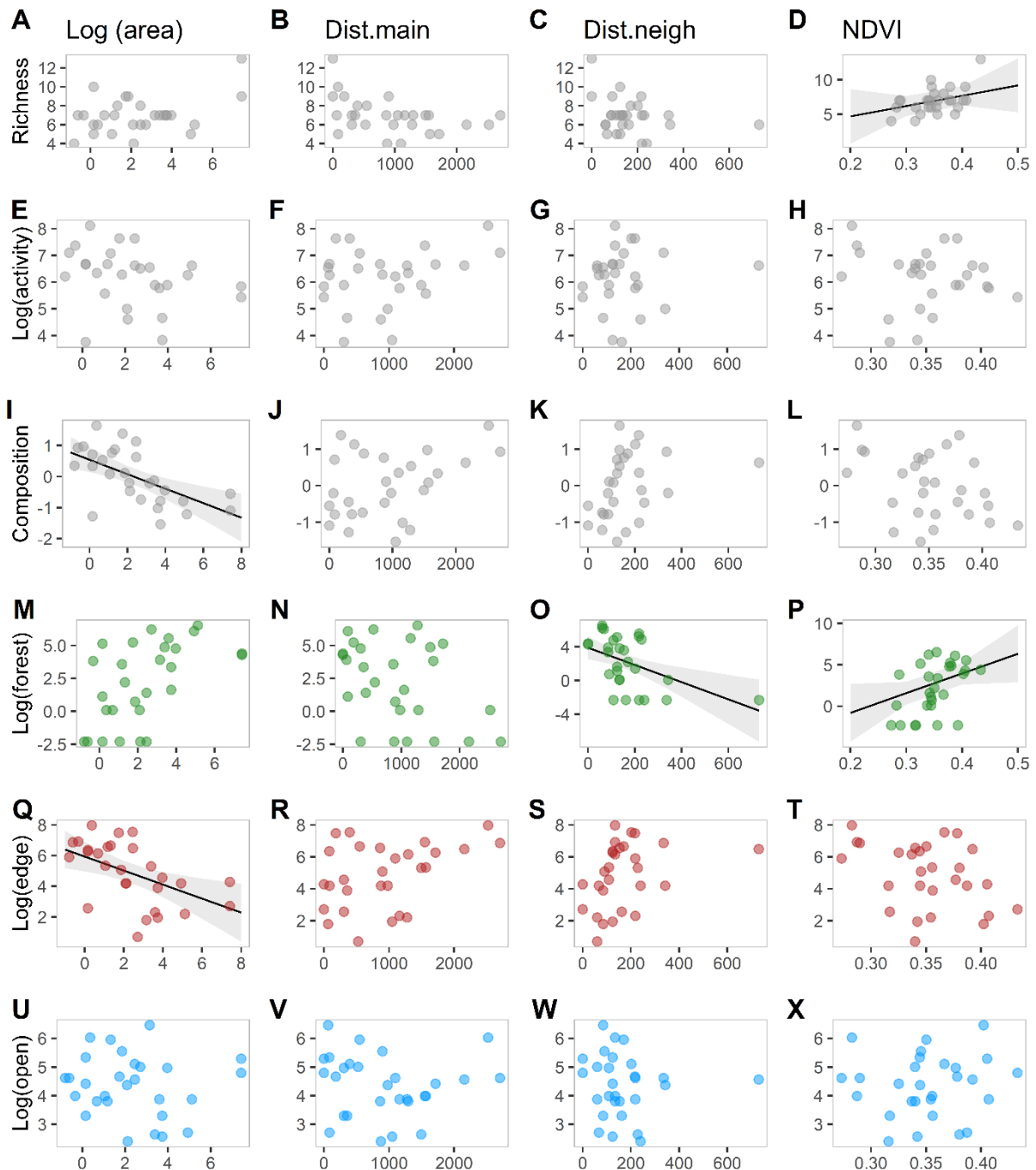


949

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



960
 961 **Figure 3.** Results of the model averaging procedure. Response variables are shown
 962 on the y axis, and predictor variables are shown on the x axis. The variables that
 963 were retained in the model selection and averaging appear at the intersection
 964 between response and predictor variables. The value of each estimate is depicted
 965 with a colour gradient, negative estimates being increasingly red, and positive
 966 estimates being increasingly blue. The significance of each selected variable is
 967 shown with point shape: significant variables are represented with a triangle, and
 968 non-significant variables are shown with a circle. The relative importance of each
 969 selected variable within the averaged model is shown with point size, smaller points
 970 having a lower relative importance than larger points.
 971 *Two columns fitting image*
 972



973
 974 **Figure 4.** Relationships between bat sonotype richness (A-D), activity ($\log_{10} x$) (E-H),
 975 assemblage composition (axis 1 of the NMDS) (I-L), and the activity of forest ($\log_{10} x$) (M-P),
 976 edge ($\log_{10} x$) (Q-T), and open-space foraging bats ($\log_{10} x$) (U-X) and Area
 977 ($\log_{10} x$) (A, E, I, M, Q, U), distance to the mainland (*Dist.main*) (B, F, J, N, R, V),
 978 Distance to neighbour (*Dist.neigh*) (C, G, K, O, S, W) and *NDVI* (D, H, L, P, T, X). In
 979 each panel, the solid black line is the prediction given by the averaged model
 980 obtained from the dredge, and the shaded area represents the 95% confidence
 981 interval. The predictions of the selected model were only shown for significant
 982 variables.

983 *Two columns fitting image*

984 **Table 1.** List of all sonotypes identified during the acoustic bat surveys across the
 985 insular fragmented landscape of the Kenyir Lake, peninsular Malaysia. For each
 986 sonotype, we indicate the potential species matching that sonotype, corresponding
 987 foraging guild, total activity (number of bat passes), and number of sampling sites in
 988 which each of the sonotypes was recorded. Bat passes that could not be identified
 989 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> ,	Edge	389	15 (53.6%)

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

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

990