

1 **Benign effects of logging on aerial insectivorous bats in Southeast**
2 **Asia revealed by remote sensing technologies**

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26 **Abstract**

27 1. Logging is the most widespread disturbance in tropical forests, altering ecological
28 communities and functions. However, many species can persist in logged forests,
29 particularly where disturbance is low. Despite a growing understanding of how
30 logging affects wildlife, there remains little information for Southeast Asia's bats
31 – in part due to major challenges in monitoring.

32 2. We integrated remote sensing data from passive acoustic bat detectors with
33 LiDAR-derived measures of forest structure from a human-modified landscape in
34 Sabah, Borneo. Our appraisal of logging effects benefitted from a semi-automated
35 classifier of bat calls that vastly speeds up the analysis of acoustic recording data.
36 We recorded 105,576 bat passes from 21 phonic groups across a habitat
37 disturbance gradient, comprising old-growth forest, repeatedly logged forest, and
38 tree plantations.

39 3. We show that logging pressure (as depicted by changes to habitat quality e.g.
40 canopy height or shape) had negligible impact on the acoustic activity of bats.
41 However, bat activity was higher in areas with a greater extent of high-biomass
42 forest, as well as areas with greater topographical ruggedness. Logged forest
43 supported higher levels of activity for several common bat phonic groups
44 compared to old-growth forest. Across the landscape, plantations supported the
45 lowest levels of bat activity, representing a three-fold decrease compared to old-
46 growth forest, and several species were not recorded in this habitat.

47 4. We found different call groups demonstrated different responses to forest
48 disturbance. Sheath-tailed bats (*Emballonura* spp.) were active across all habitat
49 types and were the most resilient to logging. Edge/open foragers were more
50 prevalent in highly forested and topographically-rugged areas. Horseshoe and

51 leaf-nosed bats (flutter clutter foragers) demonstrated idiosyncratic responses to
52 logging but were consistently absent from plantations.

53 5. *Synthesis and applications.* Logged forests can provide an important refuge for
54 many common bat species in Southeast Asia, but do not capture the full breadth
55 of forest-specialist species. Nevertheless, logged forests provide substantially
56 better habitat for bats than tree plantations. While aerial insectivorous bats
57 sampled via acoustic methods are poor indicators of forest disturbance overall,
58 several species that respond predictably to logging could be targeted for
59 biodiversity monitoring using acoustic and capture-based methods.

60

61 **Keywords:** Chiroptera; Southeast Asia; acoustic monitoring; land-use change, biodiversity;
62 remote sensing

65 **Introduction**

66 Tropical forests provide valuable habitat for some of the highest levels of biodiversity in the
67 world, while contributing to the livelihoods of millions of people (Edwards, Tobias, et al.,
68 2014; Meijaard et al., 2005; Putz et al., 2012). Logging is the most widespread disturbance in
69 these globally-important ecosystems (Blaser et al., 2011; Costantini et al., 2016). As tropical
70 forests continue to be logged, and often converted for other land-uses (primarily agriculture),
71 it is important to understand how these developments could impact biodiversity.

72 Logged forests are increasingly recognised for their ecological vibrancy and habitat value for
73 wildlife (Malhi et al., 2022). A pantropical meta-analysis comprising 48 studies showed
74 lightly logged forests (e.g. $< 10 \text{ m}^3 \text{ ha}^{-1}$) support more species of mammals, amphibians, and
75 invertebrates than old-growth forests (Burivalova et al., 2014). However, logging disturbance
76 is not uniform. The extent of disturbance - and hence impact on biodiversity - depends on the
77 number of logging cycles, logging intensity, and extraction techniques (Bicknell *et al.*, 2014).
78 Light Detection and Ranging (LiDAR) remote sensing provides valuable data that can be used
79 to study forest ecosystems and track the degradation caused by logging. Studies utilising
80 LiDAR-derived data have shown how logging impacts the structure of tropical forest by
81 reducing above-ground biomass and canopy height, while increasing canopy gap area
82 (d'Oliveira et al., 2012; Kent et al., 2015; Rangel Pinagé et al., 2019). While logging can be
83 much less detrimental to the ecosystem than the conversion of forest to other land uses (Malhi
84 et al., 2022), it can still cause substantial population declines among specialist taxa
85 (Burivalova et al., 2014; Thorn et al., 2018).

86 Despite an extensive literature on the effects of logging on biodiversity, there have been
87 relatively few studies on tropical bats (Meyer et al., 2016). This is important because bats
88 represent the second most diverse mammalian order, with over 1,400 species globally
89 (Simmons & Cirranello, 2021). In Borneo, bats represent 40% of the mammal diversity
90 (Payne, 2000). Bats also provide valuable ecosystem services as seed dispersers, pollinators,

91 and suppressors of insect populations (Kunz et al., 2011), and are considered important
92 bioindicators of ecosystem health (Jones *et al.* 2009). Presley *et al.* (2008) outlined three
93 potential demographic responses for bats in logged forests: (1) common species remain
94 common but decrease in abundance; (2) common species decline in abundance, becoming rare
95 in logged forests; or (3) rare species are locally absent from logged forest. To date, logging-
96 effect studies have found that bat responses to forest change are highly variable between
97 different ensembles of species, particularly dietary guilds (Bicknell *et al.*, 2015; Castro *et al.*,
98 2021; Castro-Arellano *et al.*, 2009; Clarke *et al.*, 2005; Presley *et al.*, 2008). Small, common
99 phytophagous species (i.e. frugivorous and nectarivorous species) that rely on pioneering
100 plants for foraging opportunities often respond positively to logging disturbance (Clarke et al.,
101 2005; Presley et al., 2008). On the other hand, larger, insectivorous or animalivorous
102 phyllostomid species are more vulnerable to logging, as well as habitat disturbance more
103 generally, and experience declines in diversity and abundance (Brändel *et al.*, 2020; Clarke *et*
104 *al.*, 2005; Farneda *et al.*, 2015).

105 The study of bats in tropical regions has been restricted by limitations in sampling techniques.
106 To fully sample a community and thus avoid biases in taxonomic and ecological coverage, bat
107 surveys require a combination of survey methods (Appel et al., 2021) – a challenge that is
108 amplified in species diverse tropical regions. Live-capture methods (e.g., mist-netting or harp
109 trapping) are most effective for sampling understorey bats, while acoustic methods tend to be
110 better for monitoring those foraging in less cluttered environments, which rely on echolocation
111 for navigation (e.g. above the canopy, in forest gaps). However, to date most logging-effect
112 studies involving tropical bats have relied on live-capture techniques (Meyer et al., 2016). The
113 majority have been undertaken in the American tropics where mist-netting is more effective
114 at capturing a larger portion of the overall bat community (e.g., Bicknell *et al.*, 2015; Castro
115 *et al.*, 2021; Castro-Arellano *et al.*, 2009; Clarke *et al.*, 2005). Far fewer studies have been
116 undertaken in the Asian and African tropics as the bat fauna is dominated by aerial
117 insectivorous species (i.e. those that use ultrasonic calls for orientation and foraging insect

118 prey), which are poorly represented using nets (Castro & Michalski, 2014; Meyer *et al.*, 2016).
119 Capture-based studies in Southeast Asia have demonstrated that logging affects bat
120 community composition, reduces species richness, and causes abundance declines (Danielsen
121 & Heegaard, 1995; Christine *et al.*, 2013; Zubaid, 1993). The most comprehensive logging
122 study involving bats in the region used harp traps to characterise bat assemblages across a
123 habitat disturbance gradient, comparing old-growth forest to logged forest areas that had
124 undergone various extraction cycles (Struebig *et al.* 2013). There was no discernible effect of
125 logging on bat species richness, but species composition differed between old-growth and
126 repeatedly logged forest sites – mirroring patterns observed in the American tropics (Castro-
127 Arellano *et al.*, 2009; Clarke *et al.*, 2005). Nevertheless, there remain large gaps in our
128 understanding of bat responses to logging simply because many species are poorly represented
129 in traps and nets. More research is needed to determine how different logging disturbances
130 impact echolocating aerial insectivorous species in tropical regions (Meyer *et al.*, 2016).

131 Here, we explore the effects of logging on bat activity and assemblage structure along a
132 disturbance gradient from old-growth forest through forest logged multiple times, and
133 plantations. Our study is based in Sabah, Malaysian Borneo, in a landscape with a long legacy
134 of logging (cumulative extraction rates between 150 and 179 m³ ha⁻¹) (Struebig *et al.*, 2013).
135 As 72% of Borneo's bat species are echolocating insectivores (Phillipps & Phillipps, 2016),
136 we use acoustic monitoring coupled with a new classification algorithm as an unintrusive
137 alternative to traditional capture methods. We examine how aerial insectivorous bats respond
138 to landscape changes using airborne LiDAR of forest metrics. Specifically, we sought to use
139 remote sensing technologies to characterise (i) community composition, and (ii) bat activity
140 in each disturbance type, while also (iii) assessing possible relationships between habitat
141 extent and quality and bat activity.

142

143 **Materials and methods**

144 Study area and sampling design

145 Fieldwork was undertaken within the Kalabakan and Ulu Segama Forest Reserves in and
146 around the Stability of Altered Forest Ecosystems Project (SAFE; www.safeproject.net)
147 (443°N, 117°35'E) in Sabah, Malaysian Borneo (Figure 1). The landscape is characterised by
148 lowland and hill dipterocarp forest, which was initially logged in the 1970s followed by two
149 rotations in the late 1990s and early 2000s. The Ulu Segama forest was left to recover ('twice-
150 logged forest'; 3 sampling blocks; LFE, LF2, LF3) (Supplementary Table S1). However, in
151 Kalabakan the forest was subject to salvage logging - the removal of all commercially valuable
152 trees - with the exception of some forest patches set aside for scientific research and
153 conservation purposes ('heavily logged forest'; 6 blocks; A-F). This highly disturbed forest
154 has a high density of roads and skids, few emergent trees, and is dominated by pioneer and
155 invasive vegetation (Struebig *et al.*, 2013). The landscape adjoins ca. 1 million ha of
156 continuous forest, including old-growth forest in Maliau Basin Conservation Area ('Old
157 Growth Forest'; 2 blocks; OG2, OG3). The forest is surrounded by a mosaic of tree plantations
158 – mostly oil palm *Elaeis guineensis* Jacq., but also *Acacia mangium* Willd. ('Tree
159 Plantation; 1 block; AC1) planted around the year 2000.

160

161 Defining the forest disturbance gradient

162 Logging activity varied substantially over the landscape. To characterise the resulting
163 structural disturbance to forests, we utilised airborne light detection and ranging (LiDAR)
164 products to quantify the extent (i.e., habitat quantity) and structure (i.e., habitat quality) of
165 forest, and hence define a disturbance gradient around our sampling sites. LiDAR metrics
166 were produced in November 2014 from a Leica ALS50-II sensor (Jucker *et al.*, 2018). The
167 LiDAR metrics were processed from raw point clouds by Swinfield *et al.* (2020), who
168 removed noise points, and delineated a digital terrain model from ground points. By

169 subtracting the terrain model, point clouds were normalised and a pit-free canopy height model
170 and plant area density profile was produced. Subsequent LiDAR metrics were then generated
171 from these two models at 30 m resolution.

172 To delineate forest extent, we utilised information on aboveground vegetation biomass
173 (AGB), which was calculated via a Borneo-specific model (see Jucker *et al.* 2018 for full
174 details). We applied a threshold to the AGB maps above which cells were classified as Forest,
175 and below which cells were classified as Non-Forest, to estimate *ForestExtent* around sample
176 sites (i.e. a measure of habitat quantity; binary; Forest vs Non-Forest). This definition of forest
177 excluded areas of plantation and highly degraded young regenerating forest, and was defined
178 as vegetation biomass $\geq 160 \text{ t ha}^{-1}$ (i.e. equivalent to above-ground carbon $\geq 75 \text{ tCha}^{-1}$; Martin
179 and Thomas, 2011) following the High Carbon Stock Approach (HCS; The HCS Approach
180 Toolkit, 2017). We chose a more conservative forest categorisation, as areas $< 160 \text{ t ha}^{-1}$
181 biomass were subject to salvage logging and therefore, more closely resemble areas of scrub.

182 We also extracted two measures of forest structure as proxies of habitat quality: mean canopy
183 height (*CanopyHeight*; a continuous variable) and shape (*Shape*; continuous; morphological
184 measurement of the ratio of canopy height to the maximum plant area density above ground),
185 an area with a low *Shape* value would be characterised by a dense upper canopy with little
186 understorey (Jucker et al., 2018; Swinfield et al., 2020). There is little research regarding bats
187 and LiDAR metrics, but *Shape* is known to be an important predictor of other forest-dependent
188 mammal species (Deere et al., 2020). In addition to *CanopyHeight*, average topographic
189 ruggedness (*Topography*; continuous) has been shown to be an important predictor for bat
190 occurrence in the project area (Mullin et al., 2020). Therefore, we also included *Topography*
191 using 1 arc-second (ca. 30 m resolution) Shuttle Radar Topography Mission digital elevation
192 model (Farr et al., 2007), converted using a topographic ruggedness index, according to
193 Wilson et al. (2007).

194

195 Acoustic sampling, processing, and bat identification

196 Bats were recorded using SongMeter-2 automated recorders (Wildlife Acoustics) fitted with
197 an omnidirectional ultrasonic SMX-US microphone between April and May 2011 and April
198 and June 2012 (Supplementary Table S1). Recorders were stationed across 47 sample points
199 at 1.5-2.0 m height above ground (one per site) and set to record nightly bat activity (18:15-
200 06:15) between one and three consecutive nights. These sample points were designed to target
201 the mid-storey, rather than the cluttered understorey. Each recorder was set to record by
202 triggers of high frequency sounds appropriate for echolocating bats in the region (sampling
203 rate 384 kHz, 16-bit resolution; high pass filter 12 kHz (fs/32); trigger level 18 signal to noise
204 ratio; gain 12 dB).

205 All pre-processing of recordings was undertaken using Kaleidoscope v.5.1.9g software
206 (Wildlife Acoustics, 2019-05-30) following procedures outlined in Yoh et al. (2022). Files
207 were divided into 5-second long sequences with a minimum of two individual pulses to define
208 a bat pass as a unit of activity, e.g. number of events per time interval (Torrent et al., 2018).
209 While this does not necessarily provide a measure of bat abundance (as it does not determine
210 the number of individual bats), it provides a discrete count of activity which can be compared
211 across sites (Plan, 2014). Calls were automatically assigned to call type, phonic group (a group
212 of species with indistinguishable calls; López-Baucells et al., 2021), or species, and any calls
213 that failed to meet specific confidence thresholds were manually verified (Yoh et al., 2022).
214 Through this process, calls were first identified to one of four call types (Supplementary Figure
215 1): frequency modulated (hereafter referred to as ‘active clutter foragers’; FM), constant
216 frequency (‘flutter clutter foragers’; CF), frequency modulated quasi constant frequency
217 (‘edge/open foragers’; FMqCF), and quasi-constant frequency (‘*Emballonura*
218 *alecto/monticola*’; QCF; Simmons & Cirranello, 2021). Those identified as an edge/open
219 foragers were automatically classified further to one of six phonic groups. Calls classified as
220 flutter clutter foragers were further differentiated to 17 species or phonic groups.

221 The classifier identified 158,563 files containing bat passes. Of these files, 71,482 included
222 bat passes that required manual verification. All bat passes that did not meet the specified
223 confidence thresholds (26351 out of 71482), excluding those for active clutter foragers, were
224 manually identified in Kaleidoscope Viewer by a single researcher (NY) to reduce potential
225 bias. Active clutter foragers represented the largest proportion of files to be manually verified
226 (45131 files). We checked 50% of active clutter forager bat passes and found this call type
227 was easily mistaken for environmental noise at low confidence and fewer than 1% contained
228 true bat passes. Therefore, we discarded active clutter forager calls that did not meet the
229 confidence threshold. Activity (the sum of bat passes per phonic group/species) was averaged
230 by sampling effort (number of nights per site).

231

232 Statistical analysis

233 *Bat community composition and habitat association*

234 We used non-metric multidimensional scaling (NMDS) ordinations based on Bray-Curtis
235 dissimilarity coefficients of log₁₀-transformed bat activity data to determine whether the
236 structure of bat communities reflected the various habitat type or the disturbance gradient.
237 Data were log-transformed to prevent skew from more active species. One phonic group
238 (*Hipposideros cineraceus/dyacorum*) was removed from the analysis as it was only recorded
239 on a single occasion. Ordinations were based on 9999 permutations in the R package “vegan”
240 (Oksanen et al., 2020) specifying two dimensions. We used PERMANOVA from the package
241 “RVAideMemoire” (Hervé, 2021) to test for differences in bat community composition
242 between habitats.

243 To determine if there were differences in bat activity between forest sites and tree plantations,
244 we first compared activity between habitats using Kruskal-Wallis tests followed by Dunn post-
245 hoc tests (Dinno, 2015). Tests were implemented separately for each call type and also for

246 overall levels of bat activity, and all p -values were adjusted using the Benjamini-Hochberg
247 method to account for the risk of false positives in call detection (Haynes, 2013).

248 To determine if there was a relationship between habitat covariates and bat activity, we
249 constructed Generalized Additive Models for Location, Scale and Shape (GAMLSS) –
250 appropriate for the Weibull distribution of the data (Goodness-of-fit test for the Weibull
251 distribution correlation = 0.984, $p = 0.069$) (Stasinopoulos et al., 2020) - using the “GAMLSS”
252 package. We also chose GAMLSS over other models as we expected the response variable to
253 exhibit a non-linear relationship in response to predictor variables (Stasinopoulos et al., 2020).
254 LiDAR datasets were not available for tree plantation sites and so were omitted from these
255 analyses. All covariates (*ForestExtent*, *CanopyHeight*, *Shape* and *Topography*) were extracted
256 from a 100m circular buffer around each site location. Habitat type (*HabitatType*; categorical;
257 three levels) was also included to assess if there were differences in activity not explained by
258 the other measures of habitat quality or extent. We centred and scaled continuous covariates
259 to one unit standard deviation and assessed for collinearity using Pearson correlation
260 coefficient. This revealed a high level of correlation among covariates (Pearson $r = \geq 0.7$),
261 and we therefore excluded highly-correlated covariates from appearing in the same model.
262 We specified GAMLSS with an effect parameterisation, specifying old-growth forest as the
263 fixed intercept and reference class from which to compare twice-logged forest and heavily
264 logged forest. We fitted separate global models for total bat activity, call type, and the four
265 dominant phonic types. We then used the dredge function from the “MumIn” package to fit
266 all possible model combinations. After inspecting the final models for goodness of fit using
267 residual diagnostics (Burnham & Anderson, 2002), we then model-averaged coefficient values
268 across the best performing models ($\Delta AIC < 2$; Supplementary Table S2). All analysis was
269 performed using R version 4.1.1 (2021-08-10) statistical software (R Core Team, 2017).

270

271 **Results**

272 From our data of remotely-sensed bat activity, we identified 105576 bat passes from 21 phonic
273 types across the landscape. More than 76% of all bat activity was represented by five phonic
274 groups: *Emballonura alecto/monticola* (18.6% of calls), Sonotype 6 (17.3%), *Rhinolophus*
275 *sedulus* (15.1%), Sonotype 5 (13.2%), and *Rhinolophus trifolius* (12.2%; Table 1). Two
276 phonic groups (*H. cineraceus/dyacorum* and *Rhinolophus philippinensis*) were only recorded
277 in heavily logged forest, once and on three occasions respectively. For activity, the
278 composition of the top five phonic groups were similar across habitats, consisting mostly of
279 common generalist species. Sonotype 6 and *E. alecto/monticola* were among the top five most
280 active phonic groups across all habitat types (Table 1).

281 **Table 1.** Total bat passes per sonotype or species in each habitat along the disturbance gradient. For each habitat type, relative bat passes (total bat passes/total
 282 nights surveyed) are provided in brackets for comparison. Detection range represents the distance at which a bat pass is likely to be detected and is represented
 283 by three classes, Short (1-3m), Intermediate (3-10m), or Long (10-20m). Detection range is determined by call shape, call frequency, and call intensity.

	Detection range	Bat Activity			
		Old-growth forest	Twice-logged forest	Heavily logged forest	Tree Plantation
Total nights surveyed		23	36	73	12
Total detector sites		8	12	23	4
Active clutter foragers (FM) (e.g., <i>Kerivoula</i> spp.)	Short	628 (27.3)	1988 (55.2)	2556 (35.0)	49 (4.1)
Flutter clutter bats (CF)					
<i>Hipposideros cineraceus/dyacorum</i>	Short	0	0	1 (< 0.1)	0
<i>Hipposideros cervinus</i>	Short	5 (0.2)	54 (1.5)	9 (0.1)	22 (1.8)
<i>Hipposideros diadema</i>	Short	248 (10.8)	36 (1.0)	33 (0.5)	7 (0.6)

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<i>Hipposideros galeritus</i>	Short	37 (1.6)	162 (4.5)	36 (0.5)	5 (0.4)
<i>Hipposideros ridleyi</i>	Intermediate	3 (0.1)	3 (0.1)	0	0
<i>Rhinolophus acuminatus</i>	Intermediate	229 (10.0)	165 (4.6)	262 (3.6)	91 (7.6)
<i>Rhinolophus affinis</i>	Intermediate	0	0	2 (< 0.1)	2 (0.2)
<i>Rhinolophus borneensis</i>	Intermediate	68 (3.0)	822 (22.8)	143 (2.0)	1 (0.1)
<i>Rhinolophus creaghi</i>	Intermediate	1 (< 0.1)	443 (12.3)	4 (0.1)	8 (0.1)
<i>Rhinolophus luctus</i>	Intermediate	503 (21.9)	80 (2.2)	181 (2.5)	5 (0.4)
<i>Rhinolophus philippinensis</i>	Intermediate	0	0	3 (< 0.1)	0
<i>Rhinolophus sedulous</i>	Intermediate	196 (8.5)	9558 (265.5)	6069 (83.1)	86 (7.2)
<i>Rhinolophus trifoliatus</i>	Intermediate	1703 (74.0)	1611 (44.8)	9542 (130.7)	42 (3.5)

Edge/open foragers (FMqCF)

Sonotype 1	Intermediate	10 (0.4)	39 (1.1)	271 (3.7)	95 (7.9)
Sonotype 2 (e.g., <i>Hesperoptenus blanfordi</i>)	Intermediate	241 (10.5)	6151 (170.9)	980 (1.3)	108 (9.0)
Sonotype 3 (e.g., <i>Pipistrellus stenopterus</i>)	Long	2373 (103.2)	504 (14.0)	2053 (28.1)	100 (8.3)
Sonotype 4 (e.g., <i>Glischropus tylopus</i>)	Intermediate	770 (3.3)	302 (8.9)	499 (6.8)	534 (44.5)
Sonotype 5 (e.g., <i>Myotis muricola</i>)	Intermediate	3911 (170.0)	2883 (80.1)	6180 (84.7)	961 (80.1)
Sonotype 6 (e.g., <i>Chaerephon plicatus</i>)	Long	9249 (402.1)	775 (21.5)	7019 (96.2)	1256 (104.7)
<i>Emballonura alecto/monticola</i> (QCF)	Intermediate	2590 (112.6)	4634 (128.7)	12410 (170.0)	463 (38.6)

285 Bat community composition and association with habitats

286 The NMDS ordination of bat activity revealed substantial variation in taxonomic composition
287 across the landscape and overlap between the various habitat types (Figure 2). The greatest
288 variation occurred among twice-logged sites and the least among tree plantation sites. Across
289 the landscape, there was a significant difference in bat community composition between
290 habitats (PERMANOVA: $R^2 = 0.17$, $p = 0.003$), driven by differences between the heavily
291 logged forest and the twice-logged forest (pairwise comparisons $p = 0.02$).

292 We found significant differences in bat activity between habitats, for total activity ($H(3) =$
293 10.126 , $p = 0.018$) and for each call type (active clutter foragers - $H(3) = 25.483$, $p < 0.001$;
294 flutter clutter foragers - $H(3) = 45.251$, $p < 0.001$; edge/open foragers - $H(3) = 15.763$, $p =$
295 0.001 ; *Emballonura* spp. activity - $H(3) = 10.039$, $p = 0.018$) (Figure 3). Activity for all call
296 types was lower in the plantations compared to forest (Supplementary Table S3; Figure 3).
297 GAMLSS analyses revealed that bat activity levels were similar amongst the three forest types
298 (old-growth forest, twice-logged forest, heavily logged forest; Figures 3-4). Overall bat
299 activity was positively associated with *ForestExtent* but was not associated with any measure
300 of habitat quality or *Topography* (Figure 4). The activity of edge/open foragers was also
301 positively associated with *ForestExtent* as well as *Topography*. Both edge/open foragers and
302 active clutter foragers were positively associated with *Topography*. Active clutter foragers
303 were the only call type to show a significant difference between habitat types, and neither
304 flutter clutter forager activity nor *Emballonura* spp. activity exhibited a response to any habitat
305 covariate. We found differences between the responses of individual phonic groups and these
306 did not reflect responses at the call type level (Figure 5).

307

308 **Discussion**

309 Pairing a semi-automated classifier of bat calls with LiDAR-derived forest structural metrics,
310 we found little evidence that logging disturbance negatively affected the composition of aerial
311 insectivorous bat communities. Although we observed some differences in the bat community
312 between twice-logged forest and heavily logged forest, neither of these disturbed forests
313 differed significantly from old-growth forest in terms of bat composition. Although bats
314 persisted in highly disturbed logged forests, bat activity declined in tree plantations and several
315 species/phonic groups were not recorded in this habitat. These findings support previous
316 studies of other vertebrate groups that show logged forests support many forest species
317 compared to tree plantations, such as oil palm and acacia (Edwards, et al., 2014; Gibson et al.,
318 2011). Species most adversely affected by logging tend to have narrow niche breadth and are
319 adapted to the stable conditions usually found in the forest interior – as exemplified for
320 animalivorous bats (Presley et al., 2008) and understory birds (Hamer et al., 2014). These
321 include species dependent on old-growth trees for feeding or nesting (including cavity-nesting
322 birds and saproxylic insects), large-bodied/long-lived species with low fecundity,
323 insectivorous/animalivorous species, or target species for poachers (Bicknell & Peres, 2010;
324 Costantini *et al.*, 2016; Edwards *et al.*, 2014; Thorn *et al.*, 2018).

325 Logging pressure (e.g. as reflected by timber extraction rate) is an important determinant of
326 logging impacts on biodiversity (Bicknell et al., 2014; Burivalova et al., 2014). Although high
327 numbers of species are reported from twice-logged tropical forests (Putz et al., 2012), further
328 logging deteriorates habitat conditions to such an extent that forest-specialist species decline
329 and taxa associated with forest edges or gaps proliferate to take their place (Cleary *et al.*, 2007;
330 Edwards *et al.*, 2014). In contrast, we found no relationship between the forest quality (*Shape*,
331 *CanopyHeight*) and bat activity, suggesting that the logging pressure in our study system did
332 not reduce habitat value, at least for common bat phonic groups. Unlike previous studies of
333 riparian forest remnants in the landscape (Mullin et al., 2020), we found habitat extent was
334 more important than measures of habitat quality for determining bat activity. However, we
335 utilised a more conservative measure of forest extent based on LiDAR data that represents

336 high-quality forest and as such, excludes young regenerating forests in the landscape.
337 Therefore, our findings suggest forest management should aim to maintain forest with above-
338 ground carbon ≥ 75 tCha-1 to ensure sufficient habitat quality to support Southeast Asian bat
339 communities. More fine-scale research is needed to better assess the relationship between
340 changes to understorey structure and bat activity, particularly for forest-specialists.

341 Species adapted to foraging in more open spaces, such as sheath-tailed bats (*E.*
342 *alecto/monticola*), were the most resilient to disturbance, as reflected by comparable levels of
343 activity within plantations and old-growth forest. Edge/open foragers also maintained similar
344 activity levels in plantations, but this was positively associated with the availability of good
345 quality habitat, as determined by greater forest extent. Bats of all other call types declined
346 substantially in tree plantations or were not detected at all in this habitat. We observed one of
347 the demographic responses outlined by Presley *et al.* (2008) – the decline of rare species in
348 logged forests. For example, *H. ridleyi* (a forest-specialist species classified as Vulnerable by
349 the IUCN, 2022) was absent from both the heavily logged forest and tree plantations, though
350 persisted in twice-logged forest. However, we also observed positive demographic responses
351 to logging. Several common phonic groups were recorded much more frequently and at higher
352 activity levels in logged forest compared to old growth, in line with findings from peninsular
353 Malaysia (Christine *et al.*, 2013). Positive responses to logging have also been observed for
354 terrestrial mammals in the same study system (Wearn *et al.*, 2017). We, therefore, suggest an
355 additional demographic response – namely that common species remain common and increase
356 in abundance.

357 Overall levels of bat activity provided a poor representation of how each call type and taxon
358 responded to habitat disturbance. Edge/open forager activity was dominated by two phonic
359 groups (Sonotype 5 and 6) which together constitute 67% of activity for this call type. Overall,
360 edge/open forager activity was positively associated with increased habitat extent and
361 topography ruggedness. However, it is unclear which phonic group drives the relationship at
362 the call type level as neither phonic group exhibited a relationship between habitat extent or

363 topography. Different flutter clutter forager species indicated different susceptibility to
364 logging disturbance, as indicated by changes in their activity. This aligns with the known
365 ecology of this group. Unlike edge/open foragers, flutter clutter foragers include forest
366 specialist taxa, as well as species adapted to more disturbed areas, such as forest edge/gaps
367 (Furey & Racey, 2016; Kingston, 2013; Table S4). Therefore, it is to be expected that there
368 would be more heterogeneity between the responses of species in this call type compared to
369 more ecologically similar species in the other call types. *Rhinolopus sedulus* and *R. trifolius*
370 collectively represented 89% of activity for this call type and exhibited contrasting responses
371 to logging, consistent with those observed by Struebig et al. (2013). Repeated logging cycles
372 reduce roosting opportunities for some forest species, such as woodpeckers, squirrels and bats.
373 As such, forest-roosting species are considered to be more susceptible to logging disturbance
374 than those that dwell elsewhere (Costantini, Edwards and Simons 2016; Struebig *et al.* 2013).
375 When interpreting the results of our study it is important to consider that there are several
376 factors that can influence the likelihood of detecting species acoustically. These include
377 differences in environmental conditions (e.g., structural clutter, microclimate) and call
378 characteristics between species (e.g., call intensity, peak frequency) (Russo et al., 2018; Table
379 1). Therefore, the relative sampling area will differ between sites and species. Low-intensity,
380 high-frequency calls typical of active clutter foragers (e.g., woolly bats *Kerivoula* spp.) remain
381 difficult to detect and record, particularly in complex, understory vegetation (Kingston, 2013;
382 Russo *et al.*, 2018). Considering only acoustic surveys, we found that logging appeared to
383 positively influence the activity of forest-specialist, active clutter foragers. However, capture
384 studies using harp traps demonstrate these same taxa are highly sensitive to logging and forest
385 fragmentation (Kingston *et al.* 2003; Struebig *et al.* 2008; Struebig *et al.* 2013). We are
386 therefore mindful that our study alone does not fully capture the responses of all bats in the
387 study system to habitat change. However, we demonstrate acoustic monitoring and semi-
388 automated classification of calls to be effective at surveying a large subset of the overall bat
389 community that cannot be reliably sampled with capture methods, but ultimately data from

390 both trapping and acoustic monitoring should be used to account for biases across survey
391 methods.

392 Logging intensity across our logged sites was highly variable (e.g., the cumulative extraction
393 rate for the twice logged forest = $150 \text{ m}^3 \text{ ha}^{-1}$ and heavily logged forest = $179 \text{ m}^3 \text{ ha}^{-1}$; Struebig
394 et al., 2013). However, these rates are very high compared to those found in logging impact
395 studies from the African and American tropics (Burivalova et al., 2014). Therefore, both
396 logging categories represent high intensity logging regimes. Further research could investigate
397 the potential for conservation initiatives, such as reduced-impact logging, to benefit forest-
398 specialist bats in these landscapes. While there were 2-3 years between the acoustic sampling
399 (2011/2012) and the LiDAR coverage (2014), there was no logging disturbance in the forests
400 in that period. So, while we cannot rule out other potential influences to the forest or bat
401 community in that interval (e.g. inter-annual climatic variation), we assume that structural
402 changes (e.g. through plant growth etc.) were experienced at broadly consistent rates across
403 the landscape. Even if this assumption was not fully met, we should expect the potential
404 influence of forest changes due to logging to be greater than any changes over 2-3 years of
405 forest recovery. Nevertheless, future survey efforts could use time-series analyses to
406 investigate how forest recovery over time impacts bat activity and species' long-term
407 persistence following logging disturbance.

408 **Conclusions**

409 Logging continues to be the most extensive disturbance affecting tropical forests worldwide.
410 Using remote sensing technologies, we show that even heavily logged forest areas can support
411 comparable levels of Southeast Asian bat activity to old-growth forest. However, old-growth
412 forest remains an important habitat for several rarer, forest-specialist species, which do not
413 persist in disturbed habitats. Neighbouring old-growth forests are also likely to provide
414 resources to more mobile species, e.g., roost sites, that would otherwise be absent from logging
415 concessions. Therefore, our results suggest heterogeneity is key to maintaining bat diversity

416 in human-modified tropical landscapes (Malhi et al., 2022). We demonstrate how acoustic
417 monitoring methods can be used to incorporate aerial insectivores into bat biodiversity studies
418 and help identify species for monitoring. Combining acoustic data with live-trapping
419 information could help better evaluate the more subtle, species-specific impacts of logging
420 disturbance.

421

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434

435 **Data availability statement**

436 Bat count data to be made publicly available through Zenodo upon acceptance for publication
437 (doi XXXX). LiDAR structural data are available at <https://doi.org/10.5281/zenodo.4020697>

438 **Author contributions**

439 MS, HB, and JB conceived and designed the study. MS led the fieldwork. NY processed the
440 bat calls. NY, DS, and NJD performed the statistical analysis. NY, JB, and MS wrote the
441 manuscript. All authors contributed to manuscript revision, read, and approved the submitted
442 version.

443 **Conflict of interest**

444 The authors declare that the research was conducted in the absence of any commercial or
445 financial relationships that could be construed as a potential conflict of interest.

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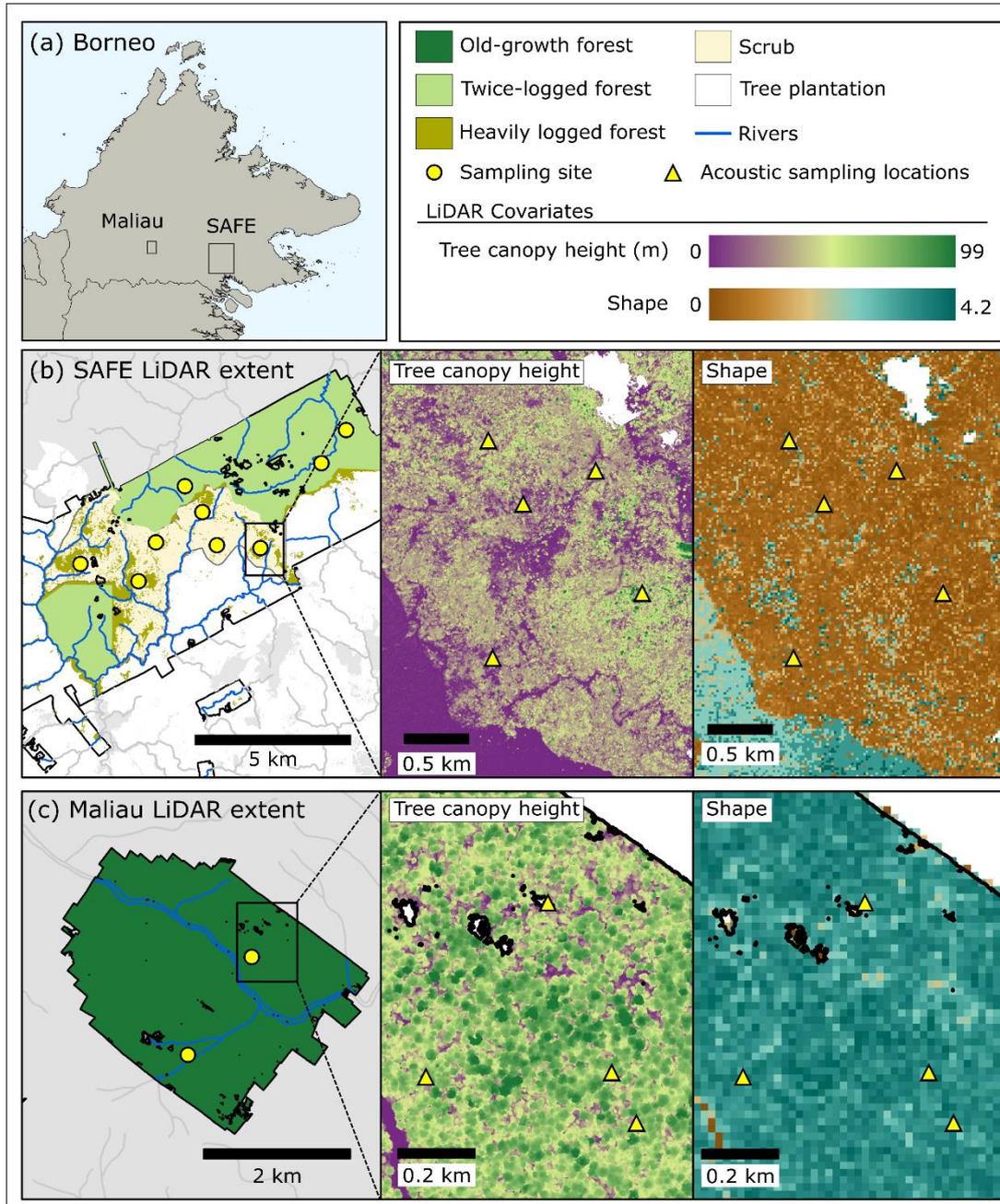


Figure 1. Map of the Stability of Altered Forest Ecosystem Project (SAFE) and sampling sites in Maliau Basin, Malaysian Borneo. (a) Location of SAFE and Maliau in Malaysian Borneo, (b) sample blocks across SAFE and examples of two LiDAR variables across multiple survey sites, and (c) the two sampling blocks in Maliau with the corresponding LiDAR coverage.

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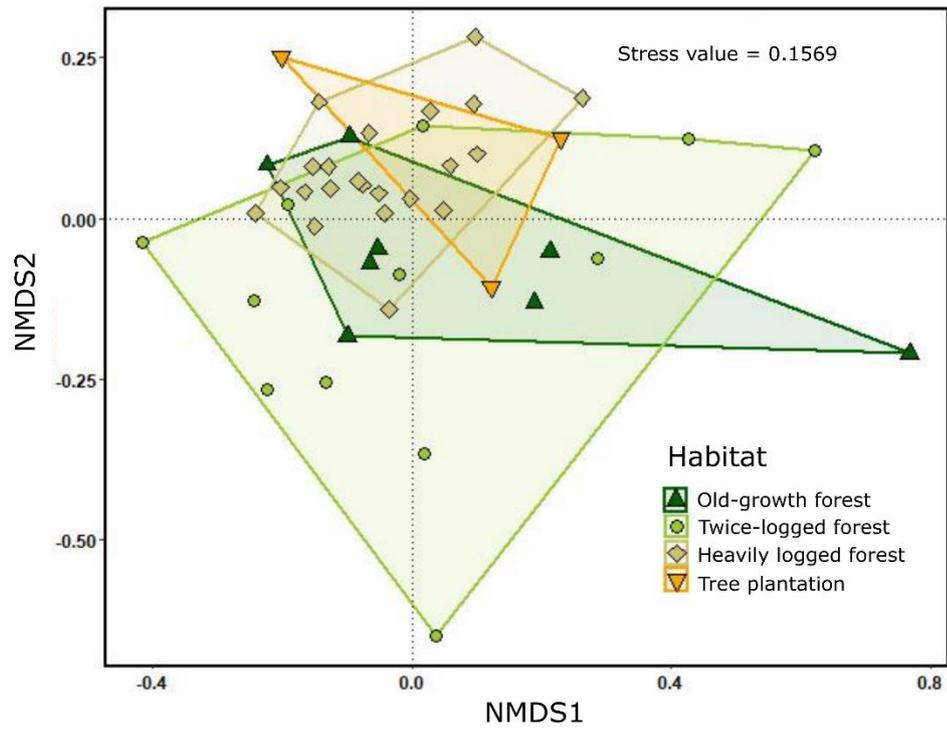
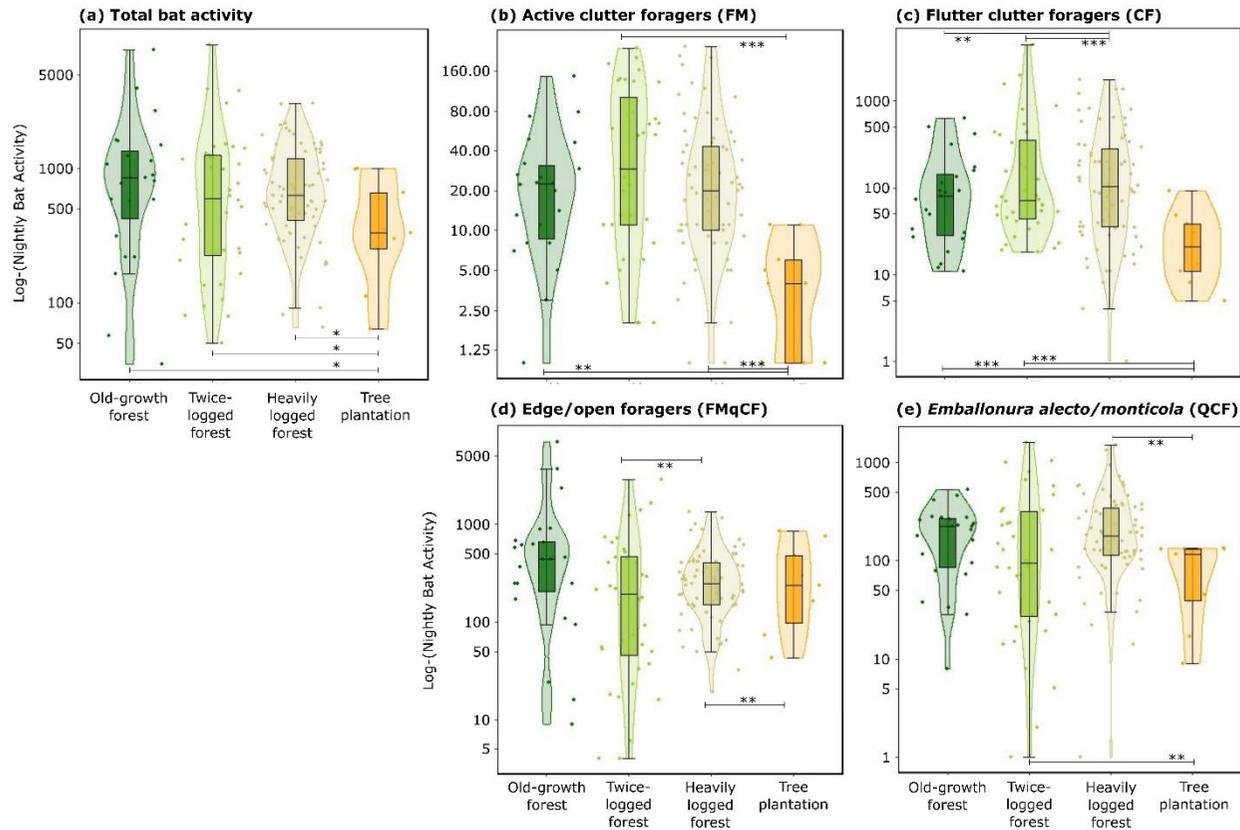
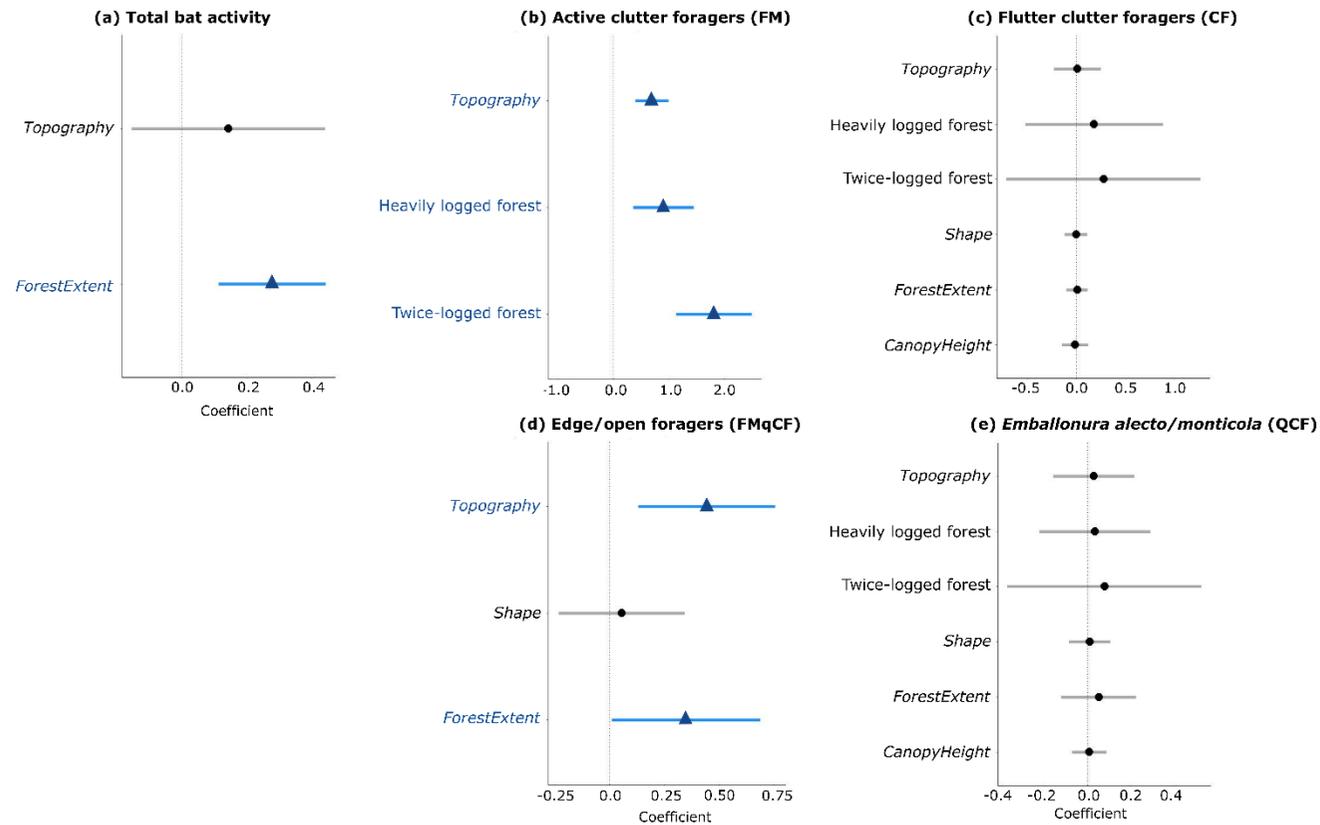


Figure 2. Nonmetric multi-dimensional scaling showing the (dis)similarities between bat communities across the four habitat types.

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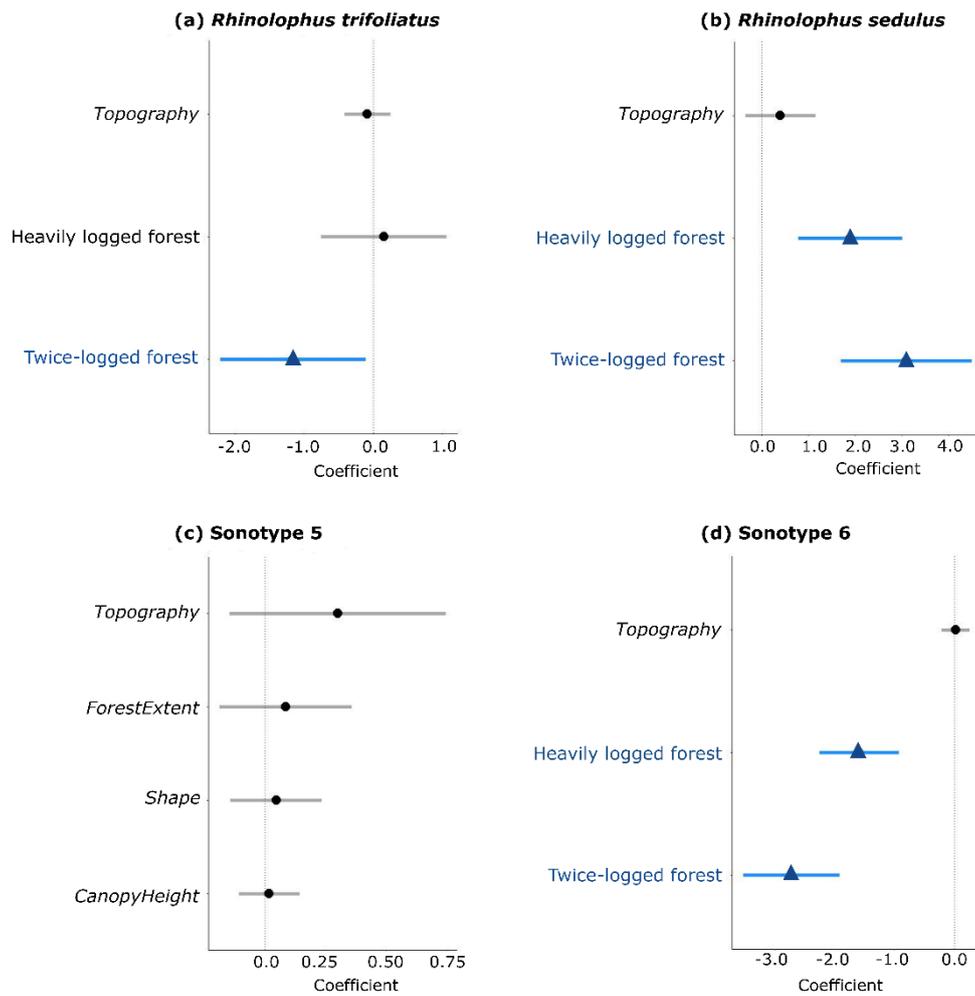


682 **Figure 3.** A comparison of overall nightly bat activity across each of the four habitat types. Each point represents an individual recording location. (a) Total bat
 683 activity, (b) active clutter forager activity, (b) flutter clutter forager activity, (c) edge/open forager activity, and (d) *Emballonura alecto/monticola* activity.
 684 Horizontal lines are median values, the boxes are between the 25th and 75th percentiles, and the whiskers represent the interquartile range. Statistical significance
 685 of the comparisons is according to the Dunn test results - * < 0.05, ** < 0.01, *** < 0.001.



686

687 **Figure 4.** Caterpillar plots from the General Additive Models for Location, Shape, and Space (including 95% confidence interval) for each call type. (a) Total
 688 activity, (b) active clutter forager activity, (b) flutter clutter forager activity, (c) edge/open forager activity, and (d) *Emballonura alecto/monticola* activity.
 689 Significant associations are shown with a triangle point and highlighted in blue. Models are listed in Supplementary Table S2.



690

691 **Figure 5.** Caterpillar plots from the General Additive Models for Location, Shape, and Space
 692 (including 95% confidence interval) for the dominant phonic group/species (*Emballonura* spp.
 693 represented in Figure 5). Significant associations are highlighted in blue. Models are listed in
 694 Supplementary Table S2.

695 **Supplementary information**

Table S1. Site descriptions for each of the acoustic survey points in Sabah, Borneo. Block refers to the Stability of Altered Forest Ecosystem’s (SAFE) site codes during 2011-2012.

Habitat type	Site Description	Block	Point	No. of nights	Total minutes	Latitude	Longitude	Start Date	End date
Old-growth forest	The OG2 block of control sites consists of old-growth forest which has undergone no logging	OG2	1	2	1480	4.746902	116.9683	2012-Jun-01	2012-Jun-03
			2	2	1480	4.751981	116.9663	2011-Apr-15	2011-Apr-17
			3	2	1480	4.751261	116.9662	2011-Apr-19	2011-Apr-21
			4	2	1480	4.748933	116.9661	2011-Apr-21	2011-Apr-23
	The OG3 block of control sites in Maliau Basin has	OG3	1	1	740	4.735662	116.9546	2011-May-24	2011-May-25

undergone limited selective logging to increase access

2	2	1480	4.734725	116.9542	2011-Apr-26	2011-Apr-28
3	2	1480	4.735012	116.9548	2011-Apr-28	2011-Apr-30
4	2	1480	4.735926	116.9568	2011-Apr-30	2011-May-02
5	1	740	4.735926	116.9568	2011-May-03	2011-May-04

Twice-logged forest	Twice logged forest to the Northeast of the SAFE experimental area. Forest has been recovering since the early 2000's.	LF2	1	2	1480	4.77019	117.698	2012-May-05	2012-May-07
			2	2	1480	4.768901	117.6982	2012-May-07	2012-May-09

		3	2	1480	4.769667	117.6983	2012-May-09	2012-May-11
		4	2	1480	4.768477	117.7001	2012-May-11	2012-May-13
	LF3	1	2	1480	4.753733	117.691	2012-May-05	2012-May-07
		2	2	1480	4.756727	117.6903	2012-May-07	2012-May-09
		3	2	1480	4.758399	117.6913	2012-May-09	2012-May-11
		4	1	740	4.757936	117.6932	2012-May-11	2012-May-12
Twice logged forest to the north of the SAFE experimental area and at the edge of the continuous forest. Forest has been	LFE	1	2	1480	4.724952	117.5969	2012-Jun-12	2012-Jun-14

		recovering since the early 2000's.								
				2	2	1480	4.726703	117.5962	2012-Jun-14	2012-Jun-16
				3	4	2960	4.724116	117.597	2012-May-29	2012-Jun-02
				4	2	1480	4.724393	117.5971	2012-Jun-02	2012-Jun-04
Heavily forest	logged	Fragment of forest in a matrix of repeatedly logged forest.	Frag. A	1	2	1480	4.709926	117.6463	2012-May-22	2012-May-24
				2	2	1480	4.710397	117.6538	2012-May-20	2012-May-22
				3	2	1480	4.708927	117.653	2011-May-24	2011-May-26
				4	3	2220	4.710989	117.6508	2011-May-19	2011-May-22

Running title: The effects of logging on bats in Southeast Asia

				5	1	740	4.709926	117.6463	2011- May-26	2011-May- 27
Heavily logged forest	logged	Fragment of forest in a matrix of repeatedly logged forest.	Frag. B	1	2	1480	4.72994	117.6197	2012- Apr-26	2012-Apr- 28
				2	2	1480	4.729936	117.6197	2012- Apr-21	2012-Apr- 23
				3	2	1480	4.73543	117.6182	2012- Jun-13	2012-Jun- 15
				4	2	1480	4.730977	117.6185	2012- Apr-23	2012-Apr- 25
			Frag. C	1	1.5	930	4.709915	117.6249	2011- May-17	2011-May- 19
				2	4	2960	4.709754	117.623	2011- May-12	2011-May- 17
				3	2	1480	4.708323	117.6241	2012- Apr-20	2012-Apr- 22

	4	2	1480	4.708793	117.6238	2012- Apr-22	2012-Apr- 24
Frag. D	1	2	1480	4.71509	117.584	2011- May-07	2011-May- 09
	2	2	1480	4.71169	117.5926	2011- May-09	2011-May- 11
Frag. E							
Frag. F	3	2	1480	4.71107	117.5875	2012- Apr-19	2012-Apr- 21
	4	1	740	4.71234	117.5859	2011- May-11	2011-May- 12
	1	2	1480	4.693655	117.5814	2012- Apr-26	2012-Apr- 28
	2	2.5	1551	4.690838	117.5759	2012- Apr-23	2012-Apr- 26
	3	2	1480	4.687996	117.5904	2012- Apr-19	2012-Apr- 21

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4	2	1480	4.695058	117.5783	2012-Apr-21	2012-Apr-23
1	2	1480	4.694425	117.5412	2012-May-21	2012-May-23
2	2	1480	4.697215	117.5432	2012-May-24	2012-May-26
3	2	1480	4.697581	117.5372	2012-May-16	2012-May-18
4	2	1480	4.696135	117.5401	2012-May-27	2012-May-29

Tree plantation	Acacia plantations	Acacia	1	2	1480	4.66408	117.6519	2012-May-20	2012-May-22
			2	2	1480	NA	NA	2012-May-22	2012-May-24
			3	2	1480	NA	NA	2012-Jun-12	2012-Jun-14

	4	2	1480	NA	NA	2012- May-24	2012-May- 26
	5	2	1480	NA	NA	2012- Jun-14	2012-Jun- 16

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697

698 **Table S2.** Candidate models used to characterize bat activity at the 100m scale.

699 Shading represents top models ($\Delta AICc < 2$).

700

Model	df	logLik‡	AICc§	$\Delta AICc¶$	wt¥
Total Bat Activity ~					
ForestExtent + Topography	4	-870.36	1748.70	0.00	0.47
ForestExtent	3	-871.91	1749.80	1.10	0.27
Shape	3	-873.38	1752.80	4.03	0.06
Shape + Topography	4	-872.56	1753.10	4.40	0.05
HabitatType + Topography	5	-871.59	1753.20	4.46	0.05
CanopyHeight	3	-874.11	1754.20	5.49	0.03
HabitatType	4	-873.20	1754.40	5.67	0.03
CanopyHeight + Topography	4	-873.37	1754.70	6.02	0.02
Topography	3	-875.53	1757.10	8.34	0.01
Null Model	2	-876.84	1757.70	8.95	0.01
Active Clutter Forager Activity ~					
HabitatType + Topography	5	-508.75	1027.50	7.21	1
Treatment	4	-518.43	1044.90	24.55	0
Topography	3	-520.42	1046.80	26.54	0
CanopyHeight + Topography	4	-519.67	1047.30	27.03	0
Null model	2	-521.91	1047.80	27.51	0
ForestExtent + Topography	4	-519.91	1047.80	27.52	0
Shape + Topography	4	-520.39	1048.80	28.47	0
CanopyHeight	3	-521.41	1048.80	28.52	0
ForestExtent	3	-521.72	1049.40	29.13	0
Shape	3	-521.89	1049.80	29.48	0
Flutter Clutter Forager Activity ~					
Null model	2	-714.39	1432.80	0.00	0.23
HabitatType	4	-712.57	1433.10	0.36	0.19
CanopyHeight	3	-714.16	1434.30	1.53	0.11
HabitatType + Topography	5	-712.26	1434.50	1.73	0.10
ForestExtent	3	-714.28	1434.60	1.77	0.10
Shape	3	-714.36	1434.70	1.93	0.09
Topography	3	-714.37	1434.70	1.95	0.09
CanopyHeight + Topography	4	-714.16	1436.30	3.52	0.04
ForestExtent + Topography	4	-714.26	1436.50	3.73	0.04
Shape + Topography	4	-714.34	1436.70	3.90	0.03
Edge/Open Forager Activity ~					
ForestExtent + Topography	4	-757.62	1523.20	0.00	0.64
Shape + Topography	4	-759.37	1526.70	3.50	0.11
Topography	4	-759.74	1527.50	4.25	0.08
HabitatType + Topography	5	-758.79	1527.60	4.33	0.07
ForestExtent	3	-761.73	1529.50	6.22	0.03
HabitatType	4	-760.73	1529.50	6.23	0.03
CanopyHeight	3	-762.03	1530.10	6.82	0.02
Shape	3	-762.06	1530.10	6.88	0.02
Topography	3	-765.21	1536.40	13.17	0.00
Null model	2	-769.00	1542.00	18.76	0.00

***Emballonura alecto/monticola* Activity ~**

ForestExtent	3	-707.94	1421.90	0.00	0.24
Null model	2	-709.21	1422.40	0.54	0.18
ForestExtent + Topography	4	-707.78	1423.60	1.68	0.10
Shape	3	-708.87	1423.70	1.87	0.10
CanopyHeight	3	-708.98	1424.00	2.09	0.09
HabitatType	4	-708.05	1424.10	2.23	0.08
Topography	3	-709.14	1424.30	2.40	0.07
HabitatType + Topography	5	-707.21	1424.40	2.54	0.07
Shape + Topography	4	-708.81	1425.60	3.74	0.04
CanopyHeight + Topography	4	-708.93	1425.90	3.99	0.03
<i>Rhinolophus trifolius</i> Activity ~					
HabitatType	4	-569.04	1146.10	3.98	0.59
HabitatType + Topography	5	-568.58	1147.20	5.06	0.34
Null model	2	-574.31	1152.60	10.52	0.02
Shape	3	-574.18	1154.40	12.26	0.01
Topography	3	-574.20	1154.40	12.29	0.01
ForestExtent	3	-574.24	1154.50	12.37	0.01
CanopyHeight	3	-574.27	1154.50	12.44	0.01
CanopyHeight + Topography	4	-574.09	1156.20	14.07	0.00
Shape + Topography	4	-574.13	1156.30	14.15	0.00
ForestExtent + Topography	4	-574.15	1156.30	14.20	0.00
<i>Rhinolophus sedulus</i> Activity ~					
HabitatType + Topography	5	-527.53	1065.10	0.78	0.68
HabitatType	4	-529.31	1066.60	2.33	0.31
CanopyHeight	3	-535.46	1076.90	12.65	0.00
Null model	2	-536.66	1077.30	13.04	0.00
Shape	3	-536.12	1078.20	13.95	0.00
CanopyHeight + Topography	4	-535.45	1078.90	14.62	0.00
ForestExtent	3	-536.58	1079.20	14.88	0.00
Topography	3	-536.66	1079.30	15.04	0.00
Shape + Topography	4	-536.11	1080.20	15.94	0.00
ForestExtent + Topography	4	-536.58	1081.20	16.87	0.00
Sonotype 5 Activity ~					
Shape + Topography	4	-628.49	1265.00	5.15	0.27
ForestExtent + Topography	4	-628.76	1265.50	5.69	0.21
Topography	3	-630.01	1266.00	6.18	0.16
CanopyHeight + Topography	4	-629.46	1266.90	7.10	0.10
Shape	3	-630.66	1267.30	7.50	0.08
ForestExtent	3	-631.21	1268.40	8.59	0.05
Null model	2	-632.31	1268.60	8.79	0.04
CanopyHeight	3	-631.48	1269.00	9.12	0.04
HabitatType + Topography	5	-629.66	1269.30	9.50	0.03
HabitatType	4	-630.98	1270.00	10.13	0.02
Sonotype 6 Activity ~					
HabitatType	4	-629.11	1266.20	0.00	0.71
HabitatType + Topography	5	-628.99	1268.00	1.76	0.29
CanopyHeight + Topography	4	-641.32	1290.60	24.43	0.00
Topography	3	-643.11	1292.20	26.02	0.00
Shape + Topography	4	-642.39	1292.80	26.57	0.00

ForestExtent + Topography	4	-642.92	1293.80	27.63	0.00
CanopyHeight	3	-645.23	1296.50	30.25	0.00
Shape	3	-646.83	1299.70	33.45	0.00
Null model	2	-648.84	1301.70	35.46	0.00
ForestExtent	3	-648.06	1302.10	35.90	0.00

701 ‡ The log-likelihood value, an alternative measure of model performance and denotes the plausibility
702 of the model. § Akaike's Information Criterion AICc. ¶ Delta AICc score, the difference between the
703 AICc score of each model against the best performing model. ¥ Akaike weight.

704

705 **Table S3.** Table outlining the results of the post-hoc Dunn test comparing bat activity between the four
 706 habitat types for overall activity and for each of the call types. Significance - * < 0.05, ** < 0.01, ***
 707 < 0.001.

Habitat	Z	p-value	
Total activity			
Heavily logged forest - Old-growth forest	-0.526	0.599	
Heavily logged forest - Tree plantation	2.956	0.019	*
Old-growth forest - Tree plantation	2.946	0.010	*
Heavily logged forest - Twice-logged forest	0.766	0.533	
Old-growth forest - Twice-logged forest	1.060	0.434	
Tree plantation - Twice-logged forest	-2.298	0.043	*
Active clutter foragers (FM)			
Heavily logged forest - Old-growth forest	-1.767	0.116	
Heavily logged forest - Tree plantation	3.818	< 0.001	***
Old-growth forest - Tree plantation	3.548	0.001	**
Heavily logged forest - Twice-logged forest	-1.526	0.152	
Old-growth forest - Twice-logged forest	1.139	0.255	
Tree plantation - Twice-logged forest	-4.659	< 0.001	***
Flutter clutter foragers (CF)			
Heavily logged forest - Old-growth forest	-3.280	0.002	**
Heavily logged forest - Tree plantation	1.909	0.068	
Old-growth forest - Tree plantation	3.987	< 0.001	***
Heavily logged forest - Twice-logged forest	-5.035	< 0.001	***
Old-growth forest - Twice-logged forest	1.254	0.210	
Tree plantation - Twice-logged forest	-5.281	< 0.001	***
Edge/open foragers (FMqCF)			
Heavily logged forest - Old-growth forest	0.563	0.574	
Heavily logged forest - Tree plantation	3.137	0.005	**
Old-growth forest - Tree plantation	1.056	0.582	
Heavily logged forest - Twice-logged forest	3.219	0.008	**
Old-growth forest - Twice-logged forest	0.706	0.576	
Tree plantation - Twice-logged forest	-0.739	0.690	
<i>Emballonura alecto/monticola</i> (QCF)			
Heavily logged forest - Old-growth forest	-0.532	0.595	
Heavily logged forest - Tree plantation	3.003	0.016	**
Old-growth forest - Tree plantation	1.999	0.137	
Heavily logged forest - Twice-logged forest	1.222	0.332	
Old-growth forest - Twice-logged forest	1.000	0.381	
Tree plantation - Twice-logged forest	-1.992	0.093	**

708

709 **Table S4.** Table outlining the results of the similarity percentages in bat activity between the four habitat
 710 types. Significance - * < 0.05, ** < 0.01, *** < 0.001.

	Avg. contribution to dissimilarity (SD)	Avg. abundance group A	Avg. abundance group B	Ordered cumulative contribution	<i>p</i> -value	
(A) Heavily logged forest vs (B) Old-growth forest						
Sonotype 2	0.029 (±0.018)	1.526	0.662	0.110	0.111	
Sonotype 3	0.028 (±0.020)	1.795	1.681	0.216	0.024	*
Sonotype 4	0.027 (±0.019)	1.071	1.122	0.315	0.132	
<i>Rhinolophus trifoliatus</i>	0.021 (±0.021)	2.295	2.010	0.394	0.693	
Sonotype 1	0.019 (±0.014)	0.813	0.157	0.464	0.203	
<i>Rhinolophus luctus</i>	0.019 (±0.017)	0.515	0.613	0.533	0.081	
<i>Rhinolophus sedulus</i>	0.018 (±0.017)	1.754	1.365	0.602	0.954	
<i>Rhinolophus acuminatus</i>	0.018 (±0.015)	0.798	1.142	0.670	0.291	
Sonotype 5	0.015 (±0.014)	2.363	2.545	0.728	0.517	
Sonotype 6	0.015 (±0.011)	2.434	2.514	0.782	0.787	
Active clutter foragers	0.014 (±0.013)	1.854	1.689	0.836	0.783	
<i>Rhinolophus borneensis</i>	0.014 (±0.011)	0.471	0.699	0.889	0.956	
<i>Hipposideros galeritus</i>	0.011 (±0.011)	0.177	0.438	0.931	0.859	
<i>Emballonura alecto/monticola</i>	0.011 (±0.012)	2.825	2.651	0.971	0.858	
<i>Hipposideros ridleyi</i>	0.006 (±0.007)	0.013	0.217	0.993	0.001	***
<i>Rhinolophus philippinensis</i>	0.001 (±0.003)	0.034	0.000	0.997	0.394	
<i>Rhinolophus creaghi</i>	0.001 (±0.002)	0.026	0.000	0.999	1.000	
<i>Rhinolophus affinis</i>	0.000 (±0.002)	0.013	0.000	1.000	0.700	
(A) Heavily logged forest vs (B) Twice-logged forest						
Sonotype 2	0.032 (±0.018)	1.526	1.273	0.105	0.003	**
<i>Rhinolophus sedulus</i>	0.025 (±0.017)	1.754	2.001	0.188	0.069	
<i>Rhinolophus trifoliatus</i>	0.024 (±0.019)	2.295	1.669	0.268	0.349	
<i>Rhinolophus borneensis</i>	0.022 (±0.018)	0.471	1.078	0.341	0.006	**
Sonotype 4	0.022 (±0.015)	1.071	0.927	0.412	0.967	
Sonotype 6	0.021 (±0.016)	2.434	1.711	0.482	0.005	**
<i>Rhinolophus creaghi</i>	0.021 (±0.019)	0.026	0.918	0.552	0.001	***

Sonotype 3	0.021 (± 0.017)	1.795	1.399	0.621	0.869	
Sonotype 1	0.018 (± 0.014)	0.813	0.289	0.682	0.136	
<i>Hipposideros galeritus</i>	0.017 (± 0.013)	0.177	0.794	0.739	0.004	**
<i>Emballonura alecto/monticola</i>	0.016 (± 0.013)	2.825	2.533	0.791	0.011	*
Active clutter foragers	0.016 (± 0.012)	1.854	1.967	0.843	0.585	
<i>Rhinolophus acuminatus</i>	0.016 (± 0.012)	0.798	0.832	0.895	0.934	
Sonotype 5	0.016 (± 0.014)	2.363	2.249	0.946	0.583	
<i>Rhinolophus luctus</i>	0.014 (± 0.011)	0.515	0.445	0.993	0.733	
<i>Rhinolophus philippinensis</i>	0.001 (± 0.003)	0.034	0.000	0.996	0.463	
<i>Hipposideros ridleyi</i>	0.001 (± 0.002)	0.013	0.025	0.999	0.992	
<i>Rhinolophus affinis</i>	0.000 (± 0.002)	0.013	0.000	1.000	0.852	

(A) Heavily logged forest vs (B) Tree plantation

<i>Rhinolophus trifoliatus</i>	0.033 (± 0.017)	2.295	1.063	0.121	0.055	
Sonotype 4	0.027 (± 0.021)	1.071	1.903	0.222	0.197	
Sonotype 1	0.024 (± 0.017)	0.813	0.668	0.313	0.030	*
<i>Rhinolophus acuminatus</i>	0.021 (± 0.015)	0.798	0.876	0.392	0.133	
Sonotype 3	0.021 (± 0.014)	1.795	1.131	0.471	0.561	
Active clutter foragers	0.021 (± 0.012)	1.854	1.082	0.548	0.097	
<i>Rhinolophus sedulus</i>	0.021 (± 0.015)	1.754	1.297	0.625	0.608	
Sonotype 5	0.016 (± 0.012)	2.363	2.448	0.684	0.411	
Sonotype 2	0.016 (± 0.010)	1.526	1.309	0.743	0.998	
<i>Rhinolophus luctus</i>	0.012 (± 0.011)	0.515	0.100	0.789	0.795	
<i>Rhinolophus creaghi</i>	0.012 (± 0.009)	0.026	0.434	0.832	0.402	
<i>Rhinolophus borneensis</i>	0.012 (± 0.011)	0.471	0.000	0.875	0.995	
Sonotype 6	0.011 (± 0.007)	2.434	2.130	0.917	0.948	
<i>Emballonura alecto/monticola</i>	0.011 (± 0.007)	2.825	2.397	0.957	0.645	
<i>Hipposideros galeritus</i>	0.008 (± 0.006)	0.177	0.259	0.986	0.976	
<i>Rhinolophus affinis</i>	0.003 (± 0.004)	0.013	0.100	0.995	0.022	*
<i>Rhinolophus philippinensis</i>	0.001 (± 0.003)	0.034	0.000	0.999	0.157	
<i>Hipposideros ridleyi</i>	0.000 (± 0.002)	0.013	0.000	1.000	0.982	

(A) Old-growth forest vs (B) Twice-logged forest

Sonotype 3	0.031 (± 0.022)	1.681	1.399	0.093	0.018	*
Sonotype 2	0.030 (± 0.027)	0.662	1.273	0.186	0.100	

Sonotype 4	0.028 (± 0.022)	1.122	0.927	0.269	0.128	
<i>Rhinolophus trifoliatus</i>	0.025 (±0.021)	2.010	1.669	0.345	0.293	
Sonotype 6	0.025 (±0.019)	2.514	1.711	0.420	0.002	**
<i>Rhinolophus sedulus</i>	0.024 (±0.019)	1.365	2.001	0.495	0.277	
<i>Rhinolophus creaghi</i>	0.022 (±0.021)	0.000	0.918	0.561	0.001	***
<i>Rhinolophus borneensis</i>	0.022 (±0.016)	0.699	1.078	0.627	0.086	
<i>Rhinolophus acuminatus</i>	0.019 (±0.016)	1.142	0.832	0.684	0.279	
Sonotype 5	0.019 (±0.017)	2.545	2.249	0.741	0.174	
Active clutter foragers	0.019 (±0.016)	1.689	1.967	0.797	0.124	
<i>Rhinolophus luctus</i>	0.018 (±0.020)	0.613	0.445	0.853	0.121	
<i>Hipposideros galeritus</i>	0.017 (±0.012)	0.438	0.794	0.905	0.012	*
<i>Emballonura alecto/monticola</i>	0.017 (±0.013)	2.651	2.533	0.956	0.068	
Sonotype 1	0.008 (±0.010)	0.157	0.289	0.981	1.000	
<i>Hipposideros ridleyi</i>	0.006 (±0.007)	0.217	0.025	1.000	0.001	***
<i>Rhinolophus affinis</i>	0.000 (-)	0.000	0.000	1.000	0.676	
<i>Rhinolophus philippinensis</i>	0.000 (-)	0.000	0.000	1.000	0.699	
(A) Old-growth forest vs (B) Tree plantation						
Sonotype 4	0.037 (±0.026)	1.122	1.903	0.116	0.017	*
Sonotype 3	0.032 (±0.018)	1.681	1.131	0.216	0.072	
<i>Rhinolophus trifoliatus</i>	0.031 (±0.015)	2.010	1.063	0.312	0.120	
Sonotype 2	0.029 (±0.017)	0.662	1.309	0.402	0.291	
<i>Rhinolophus acuminatus</i>	0.024 (±0.019)	1.142	0.876	0.479	0.057	
Active clutter foragers	0.019 (±0.011)	1.689	1.082	0.540	0.184	
<i>Rhinolophus borneensis</i>	0.019 (±0.013)	0.699	0.000	0.600	0.348	
Sonotype 1	0.019 (±0.024)	0.157	0.668	0.659	0.335	
Sonotype 5	0.018 (±0.015)	2.545	2.448	0.716	0.308	
Sonotype 6	0.016 (±0.012)	2.514	2.130	0.766	0.462	
<i>Rhinolophus luctus</i>	0.016 (±0.022)	0.613	0.100	0.816	0.347	
<i>Rhinolophus sedulus</i>	0.013 (±0.014)	1.365	1.297	0.858	0.945	
<i>Rhinolophus creaghi</i>	0.013 (±0.010)	0.000	0.434	0.898	0.429	
<i>Emballonura alecto/monticola</i>	0.012 (±0.008)	2.651	2.397	0.937	0.452	
<i>Hipposideros galeritus</i>	0.011 (±0.010)	0.438	0.259	0.971	0.718	
<i>Hipposideros ridleyi</i>	0.007 (±0.007)	0.217	0.000	0.992	0.015	*

<i>Rhinolophus affinis</i>	0.004 (± 0.004)	0.000	0.100	1.000	0.038	*
<i>Rhinolophus philippinensis</i>	0.000 (-)	0.000	0.000	1.000	0.420	
(A) Twice-logged forest vs (B) Tree plantation						
Sonotype 4	0.034 (± 0.025)	0.927	1.903	0.102	0.037	*
Sonotype 2	0.033 (± 0.018)	1.273	1.309	0.198	0.126	
<i>Rhinolophus borneensis</i>	0.028 (± 0.022)	1.078	0.000	0.280	0.044	*
<i>Rhinolophus sedulus</i>	0.027 (± 0.017)	2.001	1.297	0.358	0.241	
Active clutter foragers	0.025 (± 0.015)	1.967	1.082	0.432	0.028	*
<i>Rhinolophus trifoliatu</i> s	0.024 (± 0.015)	1.669	1.063	0.503	0.358	
<i>Rhinolophus acuminatus</i>	0.023 (± 0.017)	0.832	0.876	0.570	0.110	
<i>Rhinolophus creaghi</i>	0.022 (± 0.014)	0.918	0.434	0.635	0.038	*
Sonotype 3	0.021 (± 0.013)	1.399	1.131	0.697	0.635	
Sonotype 1	0.020 (± 0.022)	0.289	0.668	0.755	0.222	
Sonotype 5	0.019 (± 0.016)	2.249	2.448	0.811	0.282	
Sonotype 6	0.017 (± 0.016)	1.711	2.130	0.863	0.391	
<i>Hipposideros galeritus</i>	0.017 (± 0.012)	0.794	0.259	0.914	0.105	
<i>Emballonura</i>	0.015 (± 0.009)	2.533	2.397	0.958	0.301	
<i>alecto/monticola</i>						
<i>Rhinolophus luctus</i>	0.011 (± 0.012)	0.445	0.100	0.990	0.855	
<i>Rhinolophus affinis</i>	0.003 (± 0.004)	0.000	0.100	0.998	0.057	
<i>Hipposideros ridleyi</i>	0.001 (± 0.002)	0.025	0.000	1.000	0.834	
<i>Rhinolophus philippinensis</i>	0.000 (-)	0.000	0.000	1.000	0.562	

712 **Table S5.** Morphological and ecological characteristics species known to be included in the Borneo Bat
 713 Classifier used for processing the acoustic data. Adult body mass and adult forearm represent averages
 714 across sexes. Roost specialism^{C,D} includes three classes (forest, flexible, cave). Vertical stratification^D
 715 includes two classes (U – understory; C – canopy).

	Adult body mass (g)	Adult forearm length (mm)	Roost specialism	Vertical stratification
Active clutter foragers (FM)				
<i>Kerivoula hardwickii</i>	4.55 ^A	35.0 ^A	Forest	U
<i>Kerivoula intermedia</i>	3.50 ^C	28.5 ^A	Forest	U
<i>Kerivoula lenis</i>	8.00	39.0	Forest	U
<i>Kerivoula minuta</i>	2.03 ^A	27.0 ^A	Forest	U
<i>Kerivoula papillosa</i>	10.21 ^A	41.0 ^A	Forest	U
<i>Kerivoula pellucida</i>	4.14 ^A	31.5 ^A	Forest	U
<i>Megaderma spasma</i>	24.71 ^A	56.5 ^A	Flexible	U
<i>Murina peninsularis</i>	11.5 ^C	54.5 ^C	Forest	U
<i>Murina suilla</i>	4.00 ^A	30.0 ^A	Forest	U
<i>Nycteris tragata</i>	14.40 ^A	49.5 ^A	Flexible	U
<i>Phoniscus atrox</i>	4.81 ^A	33.0 ^A	Forest	U
<i>Phoniscus jagorii</i>	4.70 ^A	37.8 ^A	Forest	U
Flutter clutter foragers (CF)				
<i>Hipposideros cervinus</i>	9.30 ^B	45.0 ^E	Flexible	U
<i>Hipposideros cineraceus</i>	3.84 ^A	34.9 ^A	Cave	-
<i>Hipposideros diadema</i>	43.80 ^B	90.4 ^E	Cave	U
<i>Hipposideros dyacorum</i>	6.10 ^B	40.5 ^A	Cave	U
<i>Hipposideros galeritus</i>	8.2 ^B	49.5 ^C	Cave	U
<i>Hipposideros ridleyi</i>	8.80 ^B	48.0 ^E	Forest	U
<i>Rhinolophus acuminatus</i>	12.10 ^B	49.0 ^C	Cave	U
<i>Rhinolophus affinis</i>	13.60 ^B	51.5 ^C	Cave	U
<i>Rhinolophus borneensis</i>	7.90 ^B	42.0 ^C	Flexible	U
<i>Rhinolophus creaghi</i>	12.00 ^B	48.5 ^C	Cave	U
<i>Rhinolophus luctus</i>	33.50 ^B	63.4 ^E	Flexible	U
<i>Rhinolophus philippinensis</i>	10.30 ^B	51.0 ^C	Cave	U

<i>Rhinolophus sedulus</i>	8.80 ^B	40.3 ^E	Forest	U
<i>Rhinolophus trifolius</i>	12.30 ^E	52.0 ^E	Forest	U

Edge/open foragers (FMqCF)

Sonotype 1	-	-	-	-
Sonotype 2	-	-	-	-
Sonotype 3	-	-	-	-
Sonotype 4	-	-	-	-
<i>Glischropus tylopus</i>	4.59 ^A	29.0 ^A	Forest	-
<i>Myotis horsfieldii</i>	6.05 ^A	38.3 ^A	Flexible	-
<i>Tylonycteris robustula</i>	7.89 ^A	28.0 ^A	Forest	-
Sonotype 5				
<i>Miniopterus australis</i>	7.40 ^A	40.5 ^A	-	
<i>Myotis muricola</i>	4.80 ^A	34.7 ^A	Flexible	U
<i>Myotis ridleyi</i>	4.06 ^A	30.0 ^A	Flexible	U
<i>Tylonycteris pachypus</i>	4.10 ^A	26.2 ^A	Forest	-
Sonotype 6				
<i>Arielulus cuprosus</i>	5.40 ^C	35.5 ^A	-	C
<i>Chaerephon plicatus</i>	21.83 ^A	46.4 ^A	Flexible	C
<i>Saccolaimus saccolaimus</i>	43.00 ^A	71.2 ^A	Flexible	C

Emballonura alecto/monticola

(QCF)

<i>Emballonura alecto</i>	5.25 ^A	46.0 ^A	Flexible	C
<i>Emballonura monticola</i>	5.35 ^A	44.0 ^A	Flexible	C

716 ^A Jones et al. (2009), ^B Tanalgo et al. (2022), ^C Phillipps & Phillipps (2016), ^D IUCN (2022), ^E Jung &
 717 Threlfall (2018), ^F Crane et al. (2020)

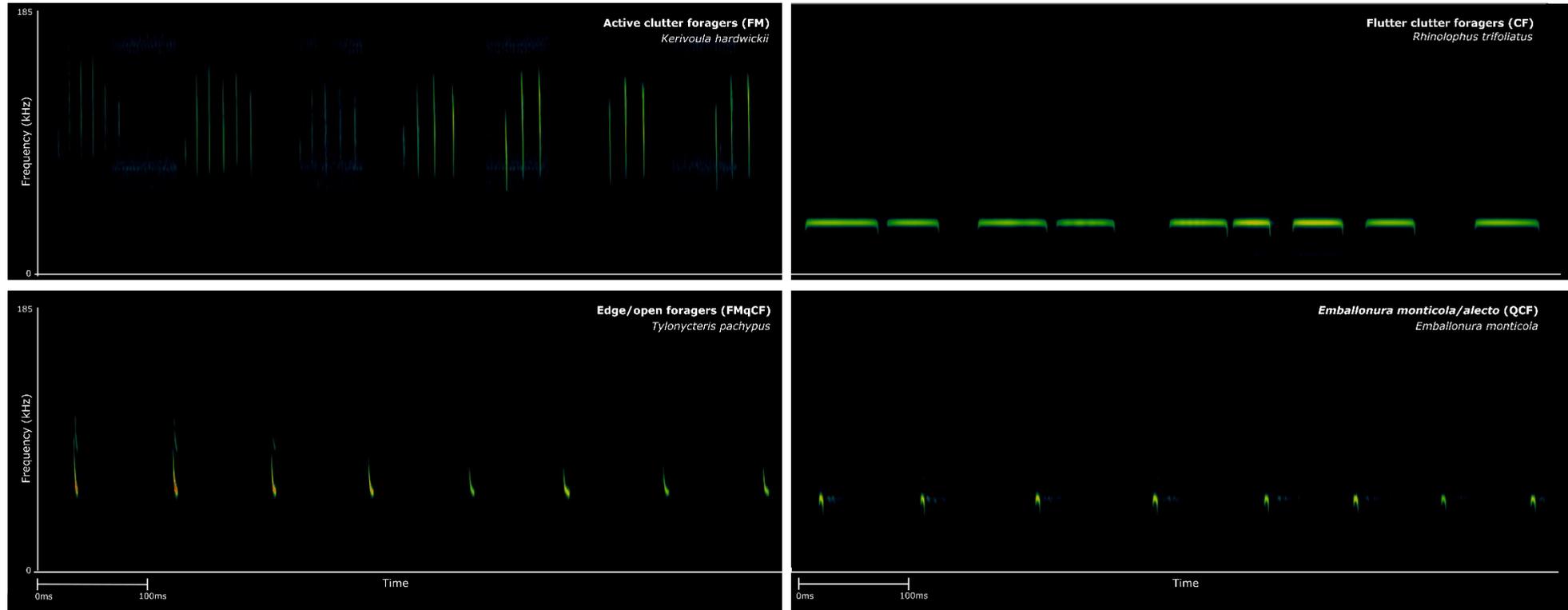


Figure S1. Example sonograms for each of the four call types used in the study. Call amplitude has not been standardized between species and therefore this image is for illustrative purposes only and should not be used for call identification.