

1 Altered structure and stability of bat-prey interaction networks in logged tropical forests
2 revealed by metabarcoding

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16

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23 embargo following publication. Specific analysis scripts are available on GitHub with links
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25
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27 undertook field collections and laboratory work, DHB analysed the data with input from EC,
28 and DHB wrote the manuscript with input from all authors.

29 **Abstract**

- 30 1. Habitat degradation is pervasive across the tropics and is particularly acute in Southeast
31 Asia, with major implications for biodiversity. Much research has addressed the impact
32 of degradation on species diversity; however, little is known about how ecological
33 interactions are altered, including those that constitute important ecosystem functions
34 such as pest consumption.
- 35 2. We examined how rainforest degradation alters trophic interaction networks linking
36 insectivorous bats and their prey. We used DNA metabarcoding to study the diets of
37 forest-dwelling insectivorous bat species, and compared bat-prey interaction networks
38 between old growth forest and forest degraded by logging in Sabah, Borneo.
- 39 3. We predicted that rainforest degradation would cause measurable reductions in the
40 numbers of prey consumed by individual bats, and that this degradation would yield
41 networks in logged forest with lower functional complementarity, modularity and
42 nestedness than those in old growth forest.
- 43 4. Compared to bats in old growth rainforest, bats in logged sites consumed a lower
44 diversity of prey. Their interaction networks were less nested and had a more modular
45 structure in which bat species had lower closeness centrality scores than in old growth
46 forest. These network structures were associated with reduced network redundancy and
47 thus increased vulnerability to perturbations in logged forests.
- 48 5. Our results show how ecological interactions change between old growth and logged
49 forests, with potentially negative implications for ecosystem function and network
50 stability. We also highlight the potential importance of insectivorous bats in consuming
51 invertebrate pests.

52 **Malay abstract**

- 53 1. Degradasi habitat merupakan suatu fenomena yang berleluasa dikawasan tropika,
54 terutamanya di Asia Tenggara dengan implikasi yang besar ke atas biodiversiti. Banyak
55 kajian telahpun meneliti impak degradasi habitat atas kepelbagaian spesis. Walau
56 bagaimanapun, dari segi mana interaksi ekologi diubah suai kurang diselidik, termasuk
57 interaksi yang membentuk fungsi ekosistem yang penting seperti pemakanan binatang
58 perosak.
- 59 2. Kami telah memeriksa bagaimana degradasi hutan hujan tropika dapat mengubah suai
60 interaksi antara tahap trofik yang menghubungkan kelawar yang memakan serangga
61 dan mangsa mereka. Kami telah menggunakan “DNA metabarcoding” untuk mengenal
62 pasti kandungan artropod dalam sampel najis kelawar and membandingkan jaringan
63 interaksi kelawar dan mangsa mereka diantara hutan dara dan hutan yang telah dibalak
64 di Sabah, Borneo.
- 65 3. Kami meramalkan bahawa degradasi hutan hujan akan menyebabkan kekurangan
66 dalam bilangan nod mangsa yang dimakan oleh setiap individu kelawar yang dapat
67 diukur. Degradasi ini pula boleh menghasilkan jaringan yang mempunyai fungsi saling
68 melengkapi dan modulariti yang rendah, dan lebih berkelompok atau “mempunyai
69 “nestedness” yang lebih tinggi di hutan yang dibalak berbanding hutan dara.
- 70 4. Kelawar di kawasan hutan yang dibalak memakan diversiti mangsa yang lebih rendah
71 dengan kelawar di habitat hutan hujan dara. Jaringan-jaringan interaksi mereka kurang
72 berkelompok dan mempunyai stuktur yang lebih modular dimana spesis kelawar
73 mempunyai pemarkahan kerapatan berpusat yang lebih rendah daripada sepesis
74 kelawar di hutan dara. Struktur-struktur jaringan ini berkait dengan lebih jaringan
75 atau “network redundancy” yang lebih rendah and ini membawa kepada kerentanan
76 yang meningkat terhadap gangguan luar di hutan yang telah dibalak.

77 5. Keputusan kami menunjukkan bagaimana interaksi ekologi berubah diantara hutan dara
78 dan hutan yang dibalak, dengan potensi implikasi negatif untuk fungsi ekosistem dan
79 kestabilan jaringan. Kami juga telah menunjukkan potensi kepentingan kelawar yang
80 memakan serangga dalam fungsi mereka untuk makan perosak invertebrat.

81 **Introduction**

82 Many tropical forests have been degraded by human activity, leading to biodiversity loss
83 (Barlow et al., 2016) and modifying the ecological processes fundamental to forest dynamics
84 (Ghazoul, Burivalova, Garcia-Ulloa, & King, 2015) such as the regeneration of plant
85 communities. Land-use change is responsible for 62% of habitat alteration in Asia (Song et al.,
86 2018), with degraded forests being of particular conservation interest; these habitats may retain
87 high biodiversity yet have minimal protection and are vulnerable to clearance for agriculture
88 and development (Meijaard et al., 2018).

89

90 The island of Borneo hosts high biodiversity but has lost much of its old growth forest, with
91 46% of its remaining forest classified as degraded by selective logging (Gaveau et al., 2014).

92 As a consequence, there is considerable interest in understanding the conservation value and
93 viability of these remaining forest areas (Meijaard & Sheil, 2007; Melo, Arroyo-Rodríguez,
94 Fahrig, Martínez-Ramos, & Tabarelli, 2013), especially given their minimal conservation
95 protection under current policies (Struebig et al., 2015). Mounting evidence suggests
96 selectively-logged forests can support a substantial proportion of the original biota, and are
97 generally more biodiverse than secondary forests (Gibson et al., 2011). Indeed, despite their
98 degradation, Borneo's logged forests retain potentially important communities of ground-
99 dwelling mammals (Deere et al., 2017), bats (Struebig et al., 2013), birds (Edwards et al., 2010)
100 and invertebrates (Slade, Mann, & Lewis, 2011). Much less is understood, however, about how
101 such habitat degradation impacts the ecological interactions among co-occurring species, such
102 as between predators and prey, hosts and parasites, and plants and their pollinators (Andresen,
103 Arroyo-Rodríguez, & Escobar, 2018).

104

105 A powerful approach for understanding ecological interactions is through network analyses, in
106 which interactions ('edges') are represented by links among biological 'nodes' (usually
107 species) (Cirtwill et al., 2018). These networks most commonly depict mutualisms such as
108 pollination and seed dispersal (Bascompte, 2009) or antagonisms such as parasitism and
109 predation (Lafferty, Dobson, & Kuris, 2006), quantifying aspects of the community's trophic
110 structure. Through measuring and comparing aspects of network structure, it is possible to
111 predict a system's resilience to perturbations (Memmott, Waser, & Price, 2004), the importance
112 of a species to a given network function (Freeman, 1978), and the potential for competition
113 between species and their conspecifics (Bastolla et al., 2009). Altered network structure may
114 thus reveal functionally important shifts within ecological communities.

115

116 Highly mobile predators may be important for stabilising numbers of prey throughout their
117 habitat (McCann, Rasmussen, & Umbanhowar, 2005; McCracken et al., 2012), by dampening
118 boom and bust cycles of insects (Kunz, Torrez, Bauer, Lobova, & Fleming, 2011). Previously,
119 lower bird abundance linked to forest degradation was shown to reduce top-down control of
120 phytophagous herbivores, thus increasing herbivory (Peter, Berens, Grieve, & Farwig, 2015)
121 and potentially affecting forest restoration (Böhm, Wells, & Kalko, 2011). Similarly, bats may
122 control herbivorous insects in rainforests (Kalka, Smith, & Kalko, 2008). Therefore, the loss
123 of bats may be expected to alter ecosystem functioning via trophic cascades.

124

125 Research in palaeotropical forests suggests logging affects bat community composition and
126 abundance by altering roost availability (Struebig et al., 2013), reflecting patterns seen in the
127 neotropics (Peters, Malcolm, & Zimmerman, 2006). While these communities might be
128 predicted to show altered network structures, studies from mutualistic neotropical systems of
129 bats dispersing seeds have shown little difference in network structure in fragmented forest,

130 despite a reduction in the number of food species consumed (Laurindo, Novaes, Vizentin-
131 Bugoni, & Gregorin, 2019), possibly as a result of highly resilient bat species which are core
132 to their networks. Bat-seed dispersal networks have been shown to be robust to secondary
133 extinctions (Mello et al., 2011), but parallels between mutualistic and antagonistic networks
134 may be limited due to known differences in their structure (Lewinsohn, Prado, Jordano,
135 Bascompte, & Olesen, 2006; Thébault & Fontaine, 2010). Therefore, given the key predation
136 roles of insectivorous bats in rainforests, an improved understanding of their feeding ecology
137 is a priority for the conservation of bats and their ecosystems (Meyer, Struebig, & Willig,
138 2016).

139
140 Genetic tools, particularly high throughput sequencing (HTS), are increasingly used for dietary
141 analyses (Aizpurua et al., 2018; Clare, Fraser, Braid, Fenton, & Hebert, 2009; Czenze et al.,
142 2018; Razgour et al., 2011). The application of DNA metabarcoding to bat and bird faeces
143 makes it possible to obtain detailed information on previously unknown species interactions
144 (Clare, 2014; Creer et al., 2016; Evans, Kitson, Lunt, Straw, & Pocock, 2016; Roslin &
145 Majaneva, 2016). While traditional approaches based solely on the morphological
146 identification of prey items in guano restricted the resolution of diet, metabarcoding approaches
147 can allow numerous prey species to be identified at genus- or family-level (Clare, 2014), so
148 providing the means to compare datasets of ecological interactions across networks.

149
150 Here we use DNA metabarcoding to assess the impact of rainforest degradation on predator-
151 prey interactions, focusing on insectivorous bats that forage under the forest canopy in Borneo.
152 We captured bats in old growth and logged rainforest and generated bipartite ecological
153 networks of their interactions with prey using metabarcoding of their guano. Comparing the
154 taxonomic composition, completeness and structure of these networks, we predicted that:

155 1. Disturbance causes the network in logged forest to have lower functional
156 complementarity, modularity and nestedness than networks in old growth forest.

157 2. Bats in logged forest consume fewer prey items than in old growth forest, leading to
158 higher closeness centrality in logged forests.

159

160 In addition, we screened the resulting sequence data for economically important pests of

161 forestry plantations and agricultural crops in modified tropical landscapes.

162 **Methods**

163 **Sample collection**

164 We sampled bats using six harp traps per night at three sites in lowland tropical rainforest in
165 Sabah, Malaysian Borneo, each <500m above sea level and experiencing a largely unseasonal
166 climate. In total we sampled at 636 unique trapping locations over 876 trap nights. We collected
167 faecal samples in two old growth sites: Danum Valley Conservation Area (hereafter ‘Danum’),
168 Maliau Basin Conservation Area (‘Maliau’), and a forest heavily disturbed by multiple rounds
169 of logging: the Stability of Altered Forest Ecosystems Project (‘SAFE’). Bats were captured
170 by placing harp traps at regular intervals (mean 37m SD 77m) along landscape features such
171 as streams and trails. The traps were erected in the morning, and then checked at approximately
172 8PM and 8AM. Bats were released at the points of capture, with pregnant, lactating or juvenile
173 bats being released instantly. Otherwise, captured bats were placed into individual cloth bags
174 for up to 12 hours, upon which any guano was removed and stored at -20°C. For full
175 information on fieldwork see Supplementary Information 1.

176

177 **Laboratory work**

178 To build a network of bat-insect interactions for each of the three forest sites studied (Danum,
179 Maliau and SAFE), we sequenced prey DNA from bat guano using metabarcoding. DNA
180 extraction, PCR, sequencing and quality-control took place following the methods outlined by
181 Czenze et al. (2018). Briefly, we extracted DNA using a Qiagen stool kit, then amplified it
182 using arthropod-specific primers (Zeale, Butlin, Barker, Lees, & Jones, 2011) and sequenced
183 the DNA on an Illumina MiSeq (Supplementary Information 2).

Table 1. Bat species and samples used to construct the ecological networks.

	Old growth forest		Logged forest
	Danum	Maliau	SAFE
<i>Hipposideros cervinus</i> (Fawn Roundleaf bat)	184	90	110
<i>Hipposideros diadema</i> (Diadem roundleaf bat)	2	10	3
<i>Hipposideros dyacorum</i> (Dayak roundleaf bat)	0	13	9
<i>Hipposideros ridleyi</i> (Ridley's roundleaf bat)	2	1	14
<i>Kerivoula hardwickii</i> (Hardwicke's woolly bat)	3	0	23
<i>Kerivoula intermedia</i> (Small woolly bat)	29	9	44
<i>Kerivoula papillosa</i> (Papillose wooly bat)	21	0	6
<i>Rhinolophus borneensis</i> (Bornean horseshoe bat)	1	26	10
<i>Rhinolophus sedulus</i> (Lesser woolly horseshoe bat)	10	4	14
<i>Rhinolophus trifoliatus</i> (Trefoil horseshoe bat)	14	19	28

184

185 **Bioinformatics**

186

187 The resulting sequences were merged into contiguous reads, the primers were removed, and
 188 the reads were length-filtered and collapsed to haplotype with any singletons excluded from
 189 the resulting dataset, before clustering sequences into Molecular Operational Taxonomic Units
 190 (MOTUs) using the Uclust algorithm (Edgar, 2010) in QIIME (Caporaso, Kuczynski,
 191 Stombaugh, Bittinger, & Bushman, 2010). To reduce costs, we restricted sequencing to the ten
 192 bat species for which we were able to obtain at least ten guano samples from one or more forest
 193 sites (see Table 1 for sample sizes). This approach was taken to ensure that, as much as is
 194 possible, networks contained the same sets of bat taxa. Removing rare or unevenly distributed
 195 species was suggested by Blüthgen (2010) to reduce the confounding impact of observation
 196 frequency. We only took this approach for bats and not for MOTUs due to the expected
 197 comparative rarity of most MOTUs consumed.

198

199 Where not otherwise stated, we generated the three networks by clustering sequences into
 200 MOTUs at 0.95 similarity, chosen to balance over- and under-splitting of MOTUs. We then

201 compared representative sequences of each MOTU to one another using BLAST+ (Camacho
202 et al., 2009), with the resulting data being filtered in LULU (Frøslev et al., 2017) to combine
203 suspected duplicate MOTUs. However as the choice of clustering threshold used to cluster the
204 sequence data into prey MOTUs can have a strong effect on the conclusions drawn (Clare et
205 al., 2016; Hemprich-Bennett et al., 2018), we examine a range of clustering thresholds for a
206 subset of the analyses in Prediction 1 to ensure that our conclusions are robust to our choice of
207 this key parameter.

208
209 For a subset of analyses indicated below, networks were generated for each site at every MOTU
210 clustering level from 0.91-0.98 similarity before quality control in LULU, allowing us to test
211 the robustness of conclusions to changes in clustering level used.

212

213 **Analysis**

214 We imported binary adjacency matrices generated into R version 3.4.4 (R Core Team, 2017)
215 for analysis. For network-level analyses these matrices were then summed by bat species (i.e.
216 a_{ij} denotes all instances of bat species i consuming MOTU j), giving weighting to the network.

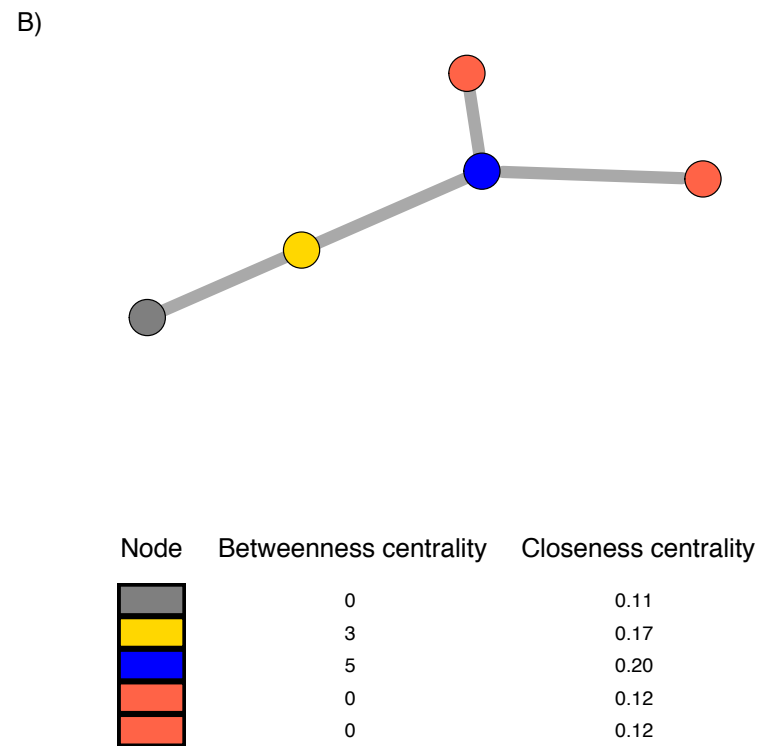
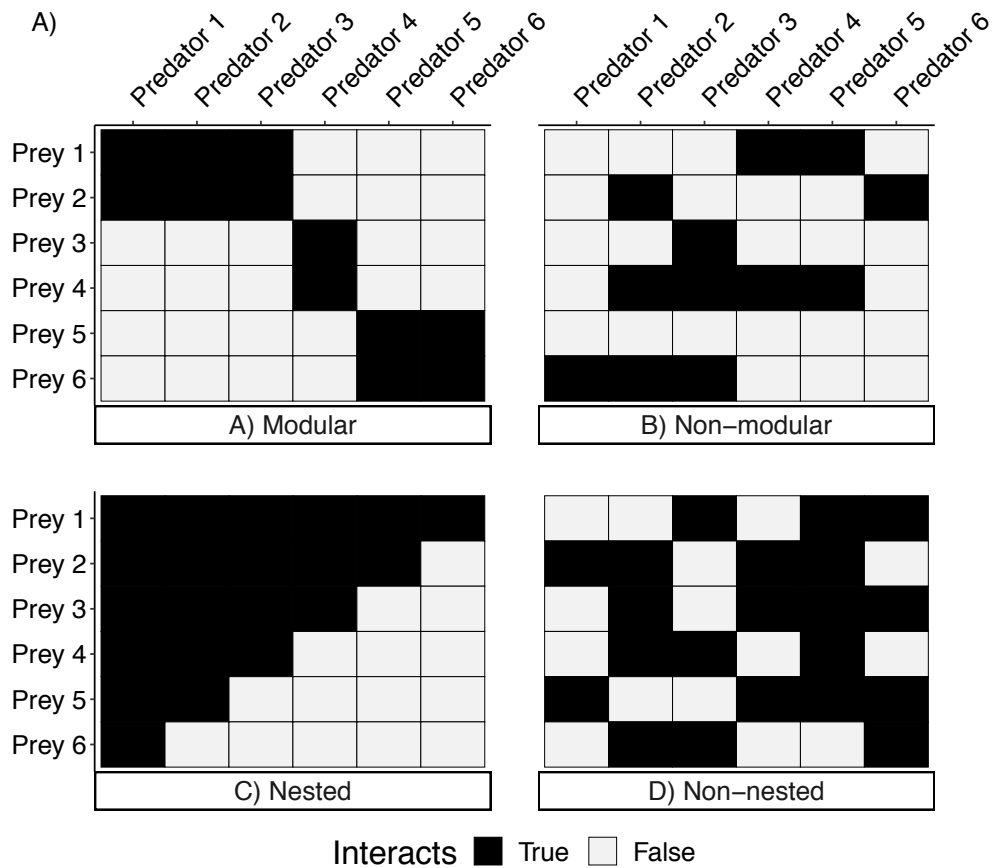
217

218 **Prediction 1: Disturbance causes the network in logged forest to have lower functional**
219 **complementarity, modularity and nestedness than networks in old growth forest.**

220

221 To compare networks we focus on three measured components of network structure:
222 nestedness, modularity and functional complementarity (Figure 1). Nestedness represents the
223 extent to which the interactions of specialist nodes are nested subsets of the interactions of the
224 generalist nodes (Almeida-Neto et al., 2008). Highly nested communities are more resilient to
225 perturbations (Memmott et al., 2004), as the generalists and specialists perform the same role,

226 conferring redundancy. Decreases in the nestedness of plant-pollinator communities following
227 disturbance leads to reduced functional redundancy (Soares, Ferreira, & Lopes, 2017). We here
228 calculate two metrics used to measure nestedness: discrepancy (Brualdi & Sanderson, 1999),
229 and weighted nestedness based on overlap and decreasing fill (WNODF) (Almeida-Neto,
230 Guimarães, Guimarães, Loyola, & Ulrich, 2008). Modularity is the extent to which a network's
231 interactions are partitioned into weakly-coupled 'modules' (Rezende, Albert, Fortuna, &
232 Bascompte, 2009), which can contain the negative effects of perturbation (Fortuna et al., 2010).
233 Modularity tends to decrease as prey availability is reduced (Oliveira, 2018), potentially
234 increasing susceptibility to adverse effects of future stressors. Functional complementarity
235 (Blüthgen & Klein, 2011; Devoto et al., 2012; Peralta, Frost, Rand, Didham, & Tylianakis,
236 2014), calculates the extent to which species have complementary non-overlapping diets by
237 measuring the branch lengths of a functional dendrogram of their dietary dissimilarity. These
238 metrics describe some of the most important elements of network structure and respond reliably
239 to alterations to MOTU clustering level (Hemprich-Bennett et al., 2018), while allowing us to
240 assess how phenomena such as habitat alteration affect ecosystem functioning.



241

242 Figure 1). Panel 1 shows networks characterised by extreme a) modularity, b) non-modularity, c) nestedness structures and d) non-nestedness in

243 bipartite networks. Panel 2 shows a simple network with values of betweenness centrality and closeness centrality for each node to 2 decimal

244 places.

245 To test whether each of these metrics differ significantly between habitats more than would be
246 expected by chance, we obtained null distributions for each metric, network and clustering
247 threshold using the swap algorithm (Dormann & Strauss, 2014) to randomize each network for
248 each MOTU clustering level 1,000 times, preserving the row and column sums. The observed
249 value was deemed to be significantly different from chance if it was outside of the range of
250 2.5-97.5% of the randomly generated values. Two networks were also deemed different from
251 one another if their ‘expected’ ranges did not overlap. Choice of MOTU clustering threshold
252 in ecological metabarcoding studies has been shown to alter measurements of most network
253 metrics (Hemprich-Bennett et al., 2018), and so to assess the impact of node resolution on the
254 networks analysed here, we performed this analysis on data generated at each MOTU clustering
255 threshold between 91-98% using the package ‘LOTUS’ (Hemprich-Bennett et al., 2018), which
256 acts as a wrapper for the bipartite package (Dormann, Gruber, & Fründ, 2008). A conclusion
257 can be considered to be robust if it is consistently found across all MOTU clustering thresholds
258 used.

259
260 As sample size varied greatly across species and site (Table 1), we checked the impact of
261 sample size and species diversity included in our analysed networks by using random
262 subsamples of the bats captured at each site to generate smaller networks ranging from 40
263 individuals to the full network dimension, with 1,000 iterations per increment. Each focal
264 metric other than modularity was calculated for the subnetworks, and the Shannon diversity
265 (Shannon, 1948) of nodes used to create the network was recorded. These values were plotted
266 to observe if network size (number of individuals used to make the network) or bat diversity
267 were important determinants of network structure. If the rank order of a measured metric was
268 not shown to be strongly determined by network size or bat diversity, then any conclusions
269 drawn from it can be considered robust to sampling effort.

270

271 To determine the contribution of a given bat species to the measured networks, we also
272 generated subnetworks by removing each species individually from the original networks and
273 calculating each network metric. The influence of the species was then calculated by
274 subtracting the subnetwork's measured value from the whole-network value. We then ranked
275 these calculated differences to show which species had the greatest and smallest impact on
276 each network metric per site.

277

278 To obtain information on the taxonomic composition of bat diets, we compared a representative
279 sequence for each MOTU using BLAST+ 2.7.1 (Camacho et al., 2009) against a database of
280 arthropod CO1 sequences from the Barcode Of Life Database (BOLD) (Ratnasingham &
281 Hebert, 2007), as accessed on 27/04/18. Using the program MEGAN 6.11.7 (Huson et al.,
282 2016) and the quality-control parameters outlined in Salinas-Ramos et al., (2015), we excluded
283 all sequences that could not be assigned to Order level, and used the BLAST assignments to
284 determine the taxonomic composition of each guano sample. For each bat species at each site,
285 we calculated the proportion of individuals that consumed a given Order of prey. We focussed
286 on taxonomic Order (rather than, e.g. Family or Genus) due to the greater success in sequence
287 assignment success at this level as sequence library completeness for Bornean arthropods is
288 low.

289 **Prediction 2: Bats in logged forest consume fewer discrete prey items than in old growth**
290 **forest, leading to higher closeness centrality in logged forests.**

291

292 We calculated the degree (number of prey MOTUs consumed) for each individual bat using
293 the R package 'bipartite' (Dormann et al., 2008) and analysed these data with a fixed effects
294 model, using species, habitat type (old growth or logged forest) and site as fixed effects, using

295 backwards model selection with the Akaike information criterion (AIC), to detect whether
296 models using habitat type or site were stronger predictors of bat degree. For each bat species
297 we also calculated two measures of centrality using bipartite. Measures of centrality identify
298 the influence of a node within a system or the distribution of its influences, often based on path
299 lengths between nodes (Delmas et al., 2019). We focus on closeness centrality and betweenness
300 centrality (Figure 1). Closeness centrality uses the shortest path lengths between all pairs of
301 nodes to measure the proximity of the nodes in the network to one another, providing a measure
302 of how rapidly a perturbation can spread (Freeman, 1978). If habitat degradation reduces the
303 diversity or richness of prey available to predators, network metrics such as closeness centrality
304 (Martín González, Dalsgaard, & Olesen, 2010) may increase as the nodes become ‘closer’
305 together. Betweenness centrality, in contrast, identifies the number of times a node is in the
306 shortest path-length between any two other nodes, and so quantifies the importance of the node
307 in connecting the overall network (Freeman, 1977). Using these measures of centrality,
308 researchers have attempted to quantify the concept of ‘keystone species’ within the context of
309 mutualistic networks (Martín González et al., 2010; Mello et al., 2015). In networks of
310 frugivory, high centrality is linked both to the taxonomic class of a node, and the node having
311 a high level of dietary specialisation (Mello et al., 2015), but in pollinators high centrality is
312 associated with generalism (Martín González et al., 2010).

313
314 In addition, to assess the potential presence of prey species in bat diets, we compared our
315 sequence data to publicly-available sequences on BOLD (Ratnasingham & Hebert, 2007) on
316 01/06/18 using the R package ‘bold’ (Chamberlain, 2019). We assigned sequences to species
317 level using the highest obtained ‘similarity’ score per sequence if it was >0.98. The output data
318 were then compared to a list of Malaysian crop pest species names obtained from Vun Khen
319 (1996).

320

321 All code used for analyses in this paper can be found at:

322 <https://github.com/hemprichbennett/bat-diet>; see Supplementary Information 2 for additional

323 detail on laboratory work and bioinformatic analyses.

324 **Results**

325 We captured 3,292 bats of 41 species, providing 700 faecal samples of 10 species that were
326 used to create ecological networks (see Table 1). In total the 700 faecal samples yielded
327 18,737,930 contiguous reads, which were used to assemble the paired-end files. After removing
328 adapters and primers, and any sequence with incomplete adapter or primer, this was reduced
329 to 10,064,815 sequences, which was further reduced to 932,459 unique haplotypes after
330 collapsing to haplotype, removing singletons, and discarding sequences outside of 2bp of the
331 expected read-length. At 95% clustering this was condensed to 14,623 MOTUs, which LULU
332 then reduced to 3,811 MOTUs (see Supplementary Information 3).

333

334 **Prediction 1: Disturbance causes networks in logged forest to have lower functional**
335 **complementarity, modularity and nestedness than in old growth forest.**

336

337 Null models (Figure 3) indicated that the logged site was consistently less nested than the old
338 growth sites (using the metrics discrepancy and WNODF). In an old growth forest site
339 (Danum), values for functional complementarity were almost always within the expected
340 range. Modularity was only significantly different from expectation in the logged forest, but it
341 was always more modular than the old growth sites. No metrics analysed showed alterations
342 in their rank order between the different MOTU clustering thresholds used, and so any
343 conclusions drawn are unaltered by this bioinformatic parameter. Low values of discrepancy
344 and high values of WNODF indicate a nested structure, a low value of modularity indicates a
345 lack of modular structure, and a low value of functional complementarity indicates no
346 complementarity between the predators.

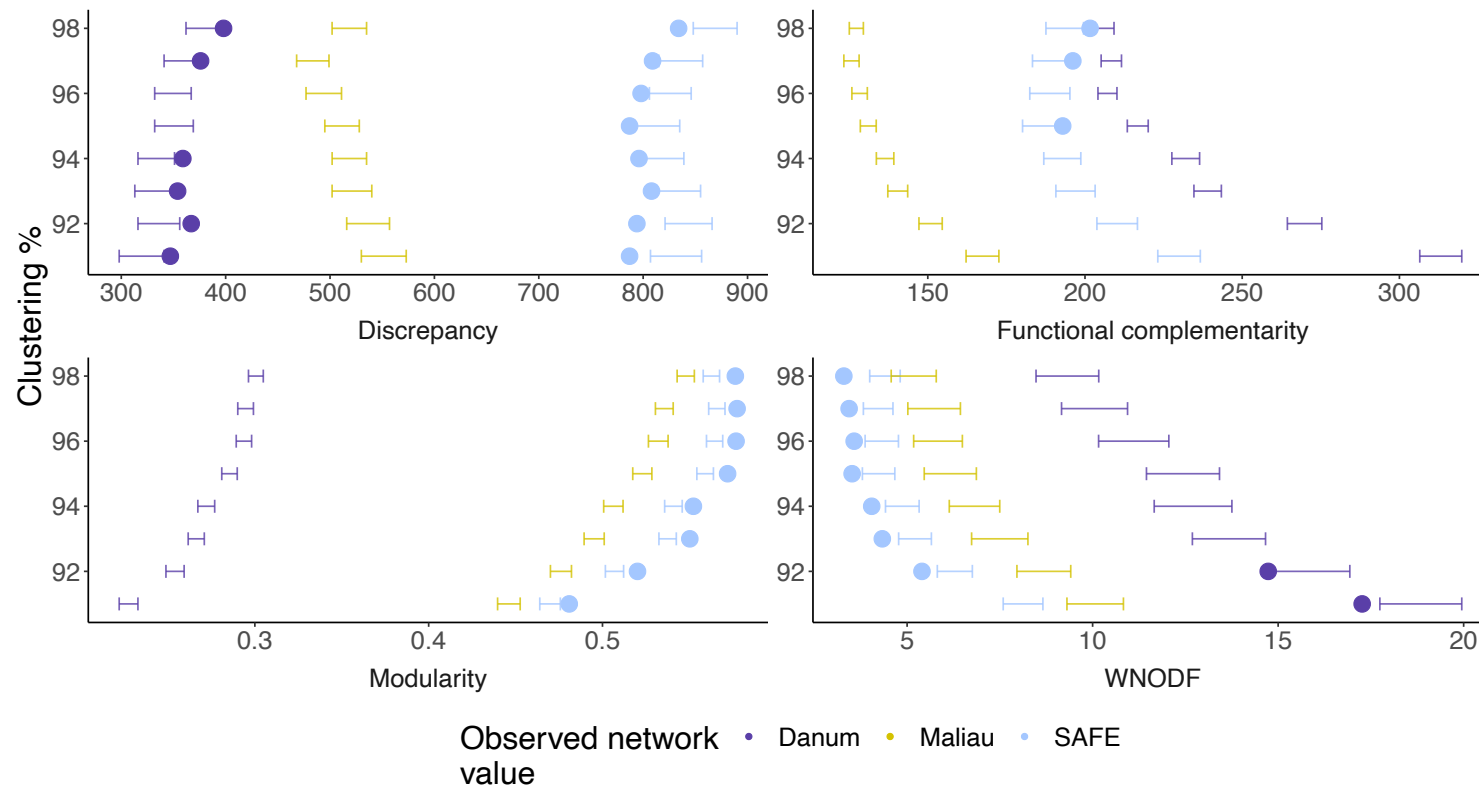
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348 Functional complementarity in logged forest was intermediate between the old growth sites,
349 and likely not impacted by habitat degradation. Contrary to previous suggestions (Fründ,
350 McCann, & Williams, 2016) we did not find that nestedness performed poorly with small
351 sample sizes.

352 Most network metrics were greatly altered by bat removal, with the common species *H.*
353 *cervinus* and *K. intermedia* causing the largest alteration to most metrics (see Supplementary
354 Information 6). *R. borneensis* was shown to be important for the discrepancy, functional
355 complementarity and modularity of an old growth site (Maliau).

356

357 Rarefaction revealed little impact of the diversity or richness of bats included in a network on
358 any observed metric, but strong effects of the number of samples used to generate a subnetwork
359 (see Supplementary Information 7). Discrepancy, functional complementarity and WNODF
360 showed distinctions between logged and old growth forest sites once sampling effort
361 approached completion.



362

363 Figure 2. Summary plot showing the observed values (circles) and 95% confidence intervals (bars) given by the random values generated for each
 364 metric studied at each MOTU clustering level, showing how conclusions drawn are altered by MOTU clustering level. The observed values for
 365 each network were only plotted for the networks and metrics where the observed values fell outside of the range of 95% of the random values. For
 366 most metrics studied, the 95% confidence intervals do not overlap at most clustering levels used, showing that the networks differ regardless of
 367 clustering level used. Danum and Maliau are the old growth sites, and SAFE the logged site.

368 **Prediction 2: Bats in logged forest consume fewer discrete prey items than in old growth**
369 **forest, leading to higher closeness centrality in logged forests.**

370 We found a significant difference in degree for bats in old growth versus logged forest (F:
371 84.84 on 11 and 688 DF, $p < 0.01$, adjusted $R^2 = 0.57$; see Table 2). The effect of habitat type
372 on the number of MOTU consumed by an individual bat (its degree) was greater than the effect
373 of species identity (Table 2, Figure 3), with bats in old growth forest consuming a greater
374 number of MOTUs than bats in logged forest. The difference was lowest in *Hipposideros*
375 species. This lower degree in logged forest shows that bats in this habitat generally consumed
376 a lower number of prey items than their conspecifics in old growth rainforest.

377

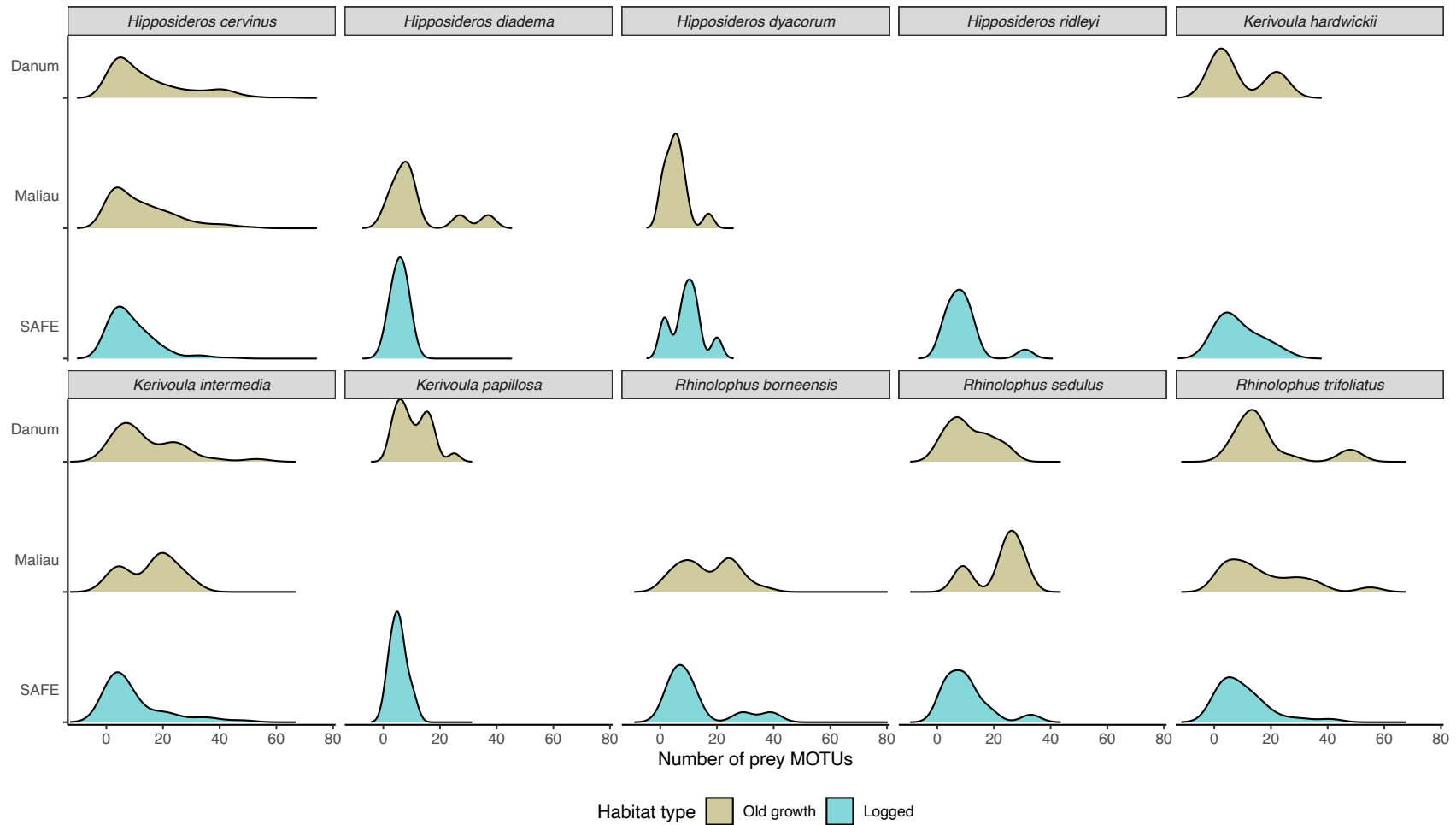
378 All bat species had comparably low closeness centrality within the logged forest (see
379 Supplementary Information 4), consistent with the observation that the logged forest had lower
380 connectance than at the old growth forest sites. This shows that the bat species nodes were
381 further from all other nodes in their network than in old growth rainforest. Rather than a
382 reduced number of dietary items generating homogenous diets, this indicates the interactions
383 of the network becoming more dispersed. At one of the old growth sites (Maliau) *Hipposideros*
384 *cervinus* and *Rhinolophus borneensis* were the only species to have non-zero betweenness
385 centrality scores (see Supplementary Information 5), indicating that every shortest path-length
386 between nodes at Maliau (old growth) went via one of this pair of species, as opposed to the
387 more diverse range of shortest path-lengths found in the other two networks.

388

Table 2. Degree model coefficients from fixed effects model, testing for the effects of habitat type (logged or old growth) and species identity on the degree of the individual bats studied.

Term	Estimate	Std error	Statistic	P value
Habitat: Logged	9.078	0.874	10.384	<0.001
Habitat: Old growth	14.330	0.630	22.740	<0.001
<i>Hipposideros diadema</i>	-2.680	2.948	-0.909	0.364
<i>Hipposideros dyacorum</i>	-5.045	2.458	-2.053	0.040
<i>Hipposideros ridleyi</i>	2.407	2.820	0.854	0.394
<i>Kerivoula hardwickii</i>	-0.915	2.336	-0.392	0.695
<i>Kerivoula intermedia</i>	0.708	1.382	0.512	0.609
<i>Kerivoula papillosa</i>	-3.681	2.230	-1.651	0.099
<i>Rhinolophus borneensis</i>	4.198	1.928	2.178	0.030
<i>Rhinolophus sedulus</i>	0.617	2.201	0.281	0.779
<i>Rhinolophus trifoliatus</i>	2.491	1.552	1.605	0.109

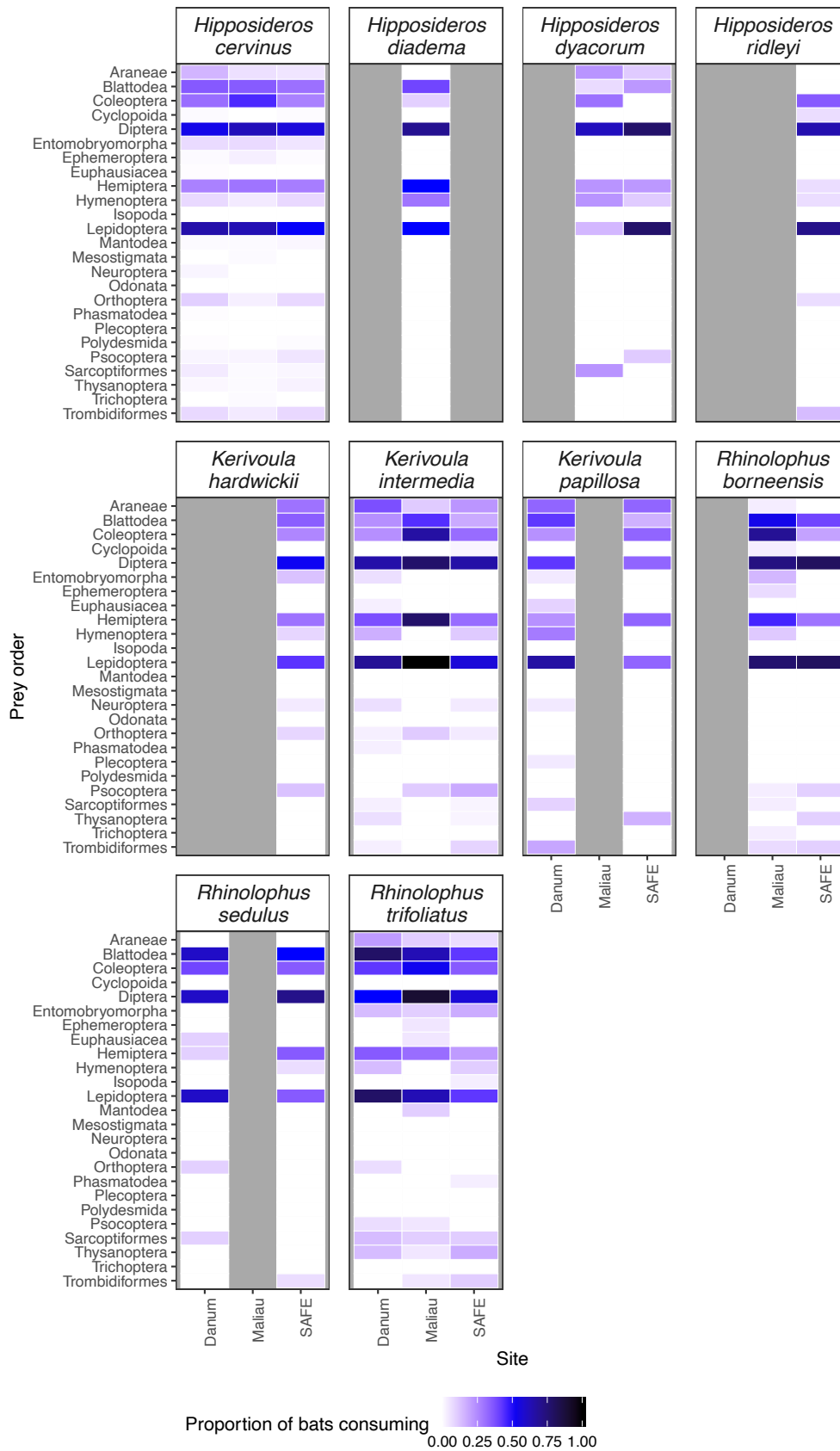
389



390

391 Figure 3. Smoothed histograms showing the number of MOTUs consumed by the individual bats for each focal bat species at each site. Species

392 on average consumed a greater number of MOTUs in old growth forest than in logged forest.



393

394 Figure 4. The proportion of individual bats of each species found to consume each taxonomic

395 Order at each site studied.

396 Lepidoptera, Diptera (especially Cecidomyiidae) and Blattodea (especially Ectobiidae) were
 397 the most common prey Orders consumed (Figure 4; Supplementary Information 8). The
 398 lepidopteran pest species *Pleuroptya balteata* was detected in the diet of several bat species
 399 (Table 3) and at each site sampled, and *Psilogramma menephron* was consumed by *H. cervinus*
 400 in the logged forest site. However relatively few individual bats were recorded as consuming
 401 these species.
 402

Table 3. The crop pest species detected in the diet of bats at each of the study sites in Sabah.

Pest species	Bat species	Site	Forest type	Number of detections / number of bats sampled at that site
<i>P. balteata</i>	<i>H. cervinus</i>	Danum	Old growth	3/184
<i>P. balteata</i>	<i>H. diadema</i>	Danum	Old growth	1/2
<i>P. balteata</i>	<i>R. trifoliatus</i>	Danum	Old growth	1/14
<i>P. balteata</i>	<i>H. cervinus</i>	Maliau	Old growth	2/90
<i>P. balteata</i>	<i>H. cervinus</i>	Maliau	Old growth	1/90
<i>P. menephron</i>	<i>H. cervinus</i>	SAFE	Logged	1/110
<i>P. balteata</i>	<i>H. cervinus</i>	SAFE	Logged	1/110
<i>P. balteata</i>	<i>K. intermedia</i>	SAFE	Logged	1/44
<i>P. balteata</i>	<i>R. sedulus</i>	SAFE	Logged	1/14
<i>P. balteata</i>	<i>R. trifoliatus</i>	SAFE	Logged	1/28

403 **Discussion**

404 We found substantial differences in bat-insect interactions across sites experiencing varying
405 degrees of habitat degradation. Bats consumed significantly fewer prey in logged forest sites
406 than old growth forest; indeed, habitat type had a stronger effect on the number of MOTUs
407 consumed by an individual bat than species identity.

408

409 Network structure also differed in several key aspects between the logged forest and old growth
410 sites. Structural differences in centrality, modularity and nestedness together indicate that
411 logged forest networks are more specialised than old growth rainforest networks. Systems that
412 are specialised in this manner have been shown to be more vulnerable to extinctions than those
413 with a more generalised structure (Memmott et al., 2004), such as the old growth rainforest
414 networks analysed. Rainforests in Southeast Asia are facing multiple stressors, including the
415 effects of disturbance, habitat fragmentation and climate change (Deere et al., 2020; Struebig
416 et al., 2015). Our findings of altered network structure in an area which has been selectively
417 logged indicate that such logged forests may be more sensitive to the effects of these future
418 perturbations.

419

420 Bats foraging within the logged forest site consistently consumed fewer prey MOTUs than
421 those within old growth forest. Indeed, the effect of habitat type was greater than that of the
422 bat species in question, showing a strong alteration to foraging activity within logged forest.
423 This was mirrored by the findings of reduced closeness centrality within the logged network,
424 as the positions of bats within the network shifted. The most abundant bat species were found
425 to have key roles in the structuring of their networks. Common predators will encounter a
426 greater richness of prey than rarer species, through the ecological sampling effect (Dormann,
427 Fründ, & Schaefer, 2017). While rare nodes are thought to have a stabilising effect on

428 ecological networks (McCann, 2000) and are of conservation interest, abundant species are
429 likely key to ecosystem functioning (Baker et al., 2018) as they are involved in a high
430 proportion of the trophic energy transfer within a system. A possible strategy for conservation
431 of ecological function could therefore be to find the species most important to a system and
432 target them (Montoya, Rogers, & Memmott, 2012). If using this framework, we find that the
433 most common bat (*Hipposideros cervinus*) is likely the species most key to the network, while
434 also being the species with the least reduction in the number of prey MOTUs it consumes in
435 the logged forest site (Figure 3).

436

437 Two species of moths known as crop or forestry pests were found in bats diets: *Pleuroptya*
438 *balteata* was consumed at all sites and *Psilogramma menephron* was consumed in the logged
439 forest. This is consistent with the potential role of tropical bats in pest control: although they
440 represented only a small percentage (0.4%) of the MOTUs consumed by the bats overall, they
441 were foraging in forest habitat and so the prey are likely occurring at lower densities than they
442 would be expected to in managed landscapes. Natural habitats are thought to be important
443 sources of pests to agricultural landscapes (Tscharntke et al., 2007) and so their consumption
444 by predators is potentially of some economic importance; in this case *P. menephron* is an
445 important pest of timber trees and *P. balteata* feeds on leaves of mango, tea and rambai (Vun
446 Khen, 1996). In the neotropics (Kalka & Kalko, 2006; Kalka et al., 2008; Morrison & Lindell,
447 2012; Williams-Guillén, Perfecto, & Vandermeer, 2008) and temperate Europe (Böhm et al.,
448 2011) bats are important agents controlling insect herbivory, but there are few examples from
449 Southeast Asia (cf. Maas, Clough, & Tscharntke, 2013). We here provide one of few examples
450 of bats in the region consuming pests, potentially reducing numbers of such species in natural
451 habitats.

452

453 **Limitations**

454 Due to the highly labour-intensive nature of capturing forest-interior bats it was only possible
455 to sample three ecological networks. With limited replication (only one logged forest site and
456 two old growth sites sampled), it is not possible to attribute differences between the sites
457 unambiguously to the effects of logging, rather than other site-specific differences.
458 Nonetheless, this work documents marked differences in network structure across the
459 landscape that are consistent with variations in forest management, and which is likely to have
460 implications for community stability and dynamics. It also highlights the utility of
461 metabarcoding-based approaches for more comprehensive investigation of between-habitat
462 differences in tropical forest predator-prey networks.

463

464 **Conclusions**

465 Through combining DNA metabarcoding and network analysis, we have been able to measure
466 how the ecological interactions which structure ecological communities differ between
467 communities in logged and old growth forest. We show that in a logged forest bats and their
468 prey exhibit altered network structures, which make them more prone to future local
469 extinctions, adding to the previous findings that logged forest bat communities have altered
470 composition and abundance (Struebig et al., 2013). Logged forests, although often heavily
471 degraded, comprise a large proportion of the remaining rainforest extent and support
472 considerable biodiversity, and so are highly important for conservation. However, our data also
473 indicate that such forests are potentially more fragile than their old growth counterparts, and
474 so efforts should be made to reduce future environmental perturbations where possible.

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