1   Altered structure and stability of bat-prey interaction networks in logged tropical forests

2   revealed by metabarcoding

3

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20   **Data Accessibility Statement:** Data are currently archived at the Centre for Ecology and

21   Hydrology Environmental Information Data Centre

22   (https://doi.org/10.5285/8b106445-d8e0-482c-b517-5a372a09dc91) and will be released from

23   embargo following publication. Specific analysis scripts are available on GitHub with links

24   given in the manuscript and will be archived on Zenodo prior to publication.

25

26   Statement of authorship: SR, EC, DHB, MS and OTL conceived the project, DHB, VK and JB

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.

Abstract

29

30   1. Habitat degradation is pervasive across the tropics and is particularly acute in Southeast Asia, with major implications for biodiversity. Much research has addressed the impact of degradation on species diversity; however, little is known about how ecological interactions are altered, including those that constitute important ecosystem functions such as pest consumption.

35   2. We examined how rainforest degradation alters trophic interaction networks linking insectivorous bats and their prey. We used DNA metabarcoding to study the diets of forest-dwelling insectivorous bat species, and compared bat-prey interaction networks 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 numbers of prey consumed by individual bats, and that this degradation would yield networks in logged forest with lower functional complementarity, modularity and nestedness than those in old growth forest.

43   4. Compared to bats in old growth rainforest, bats in logged sites consumed a lower diversity of prey. Their interaction networks were less nested and had a more modular structure in which bat species had lower closeness centrality scores than in old growth forest. These network structures were associated with reduced network redundancy and thus increased vulnerability to perturbations in logged forests.

48   5. Our results show how ecological interactions change between old growth and logged forests, with potentially negative implications for ecosystem function and network stability. We also highlight the potential importance of insectivorous bats in consuming invertebrate pests.

Malay abstract

1. Degradasi habitat merupakan suatu fenomena yang berleluasa dikawasan tropika, terutamanya di Asia Tenggara dengan implikasi yang besar ke atas biodiversiti. Banyak kajian telahpun meneliti impak degradasi habitat atas kepelbagaian spesis. Walau bagaimanapun, dari segi mana interaksi ekologi diubah suai kurang diselidik, termasuk interaksi yang membentuk fungsi ekosistem yang penting seperti pemakanan binatang perosak.

2. Kami telah memeriksa bagaimana degradasi hutan hujan tropika dapat mengubah suai interaksi antara tahap trofik yang menghubungkan kelawar yang memakan serangga dan mangsa mereka. Kami telah menggunakan "DNA metabarcoding" untuk mengenal pasti kandungan artropod dalam sampel najis kelawar and membandingkan jaringan interaksi kelawar dan mangsa mereka diantara hutan dara dan hutan yang telah dibalak di Sabah, Borneo.

3. Kami meramalkan bahawa degradasi hutan hujan akan menyebabkan kekurangan dalam bilangan nod mangsa yang dimakan oleh setiap individu kelawar yang dapat diukur. Degradasi ini pula boleh menghasilkan jaringan yang mempunyai fungsi saling melengkapi dan modulariti yang rendah, dan lebih berkelompok atau "mempunyai "nestedness" yang lebih tinggi di hutan yang dibalak berbanding hutan dara.

4. Kelawar di kawasan hutan yang dibalak memakan diversiti mangsa yang lebih rendah dengan kelawar di habitat hutan hujan dara. Jaringan-jaringan interaksi mereka kurang berkelompok dan mempunyai stuktur yang lebih modular dimana spesis kelawar mempunyai pemarkahan kerapatan berpusat yang lebih rendah daripada sepesis kelawar di hutan dara. Struktur-struktur jaringan ini berkait dengan lebihan jaringan atau "network redundancy" yang lebih rendah and ini membawa kepada kerentantan yang meningkat terhadap gangguan luar di hutan yang telah dibalak.

4

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-Rodriguez, & 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,

7

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.

9

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
Hipposideros cervinus (Fawn Roundleaf bat)	184	90	110
Hipposideros diadema (Diadem roundleaf bat)	2	10	3
Hipposideros dyacorum (Dayak roundleaf bat)	0	13	9
Hipposideros ridleyi (Ridley's roundleaf bat)	2	1	14
Kerivoula hardwickii (Hardwicke's woolly bat)	3	0	23
Kerivoula intermedia (Small woolly bat)	29	9	44
Kerivoula papillosa (Papillose wooly bat)	21	0	6
Rhinolophus borneensis (Bornean horseshoe bat)	1	26	10
Rhinolophus sedulus (Lesser woolly horseshoe bat)	10	4	14
Rhinolophus trifoliatus (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

11

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,

12

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.

13
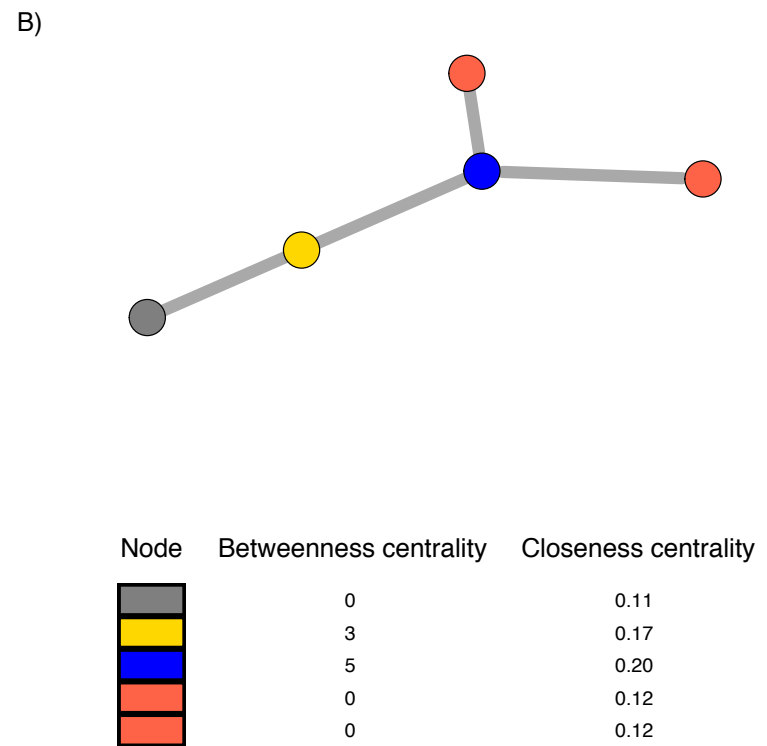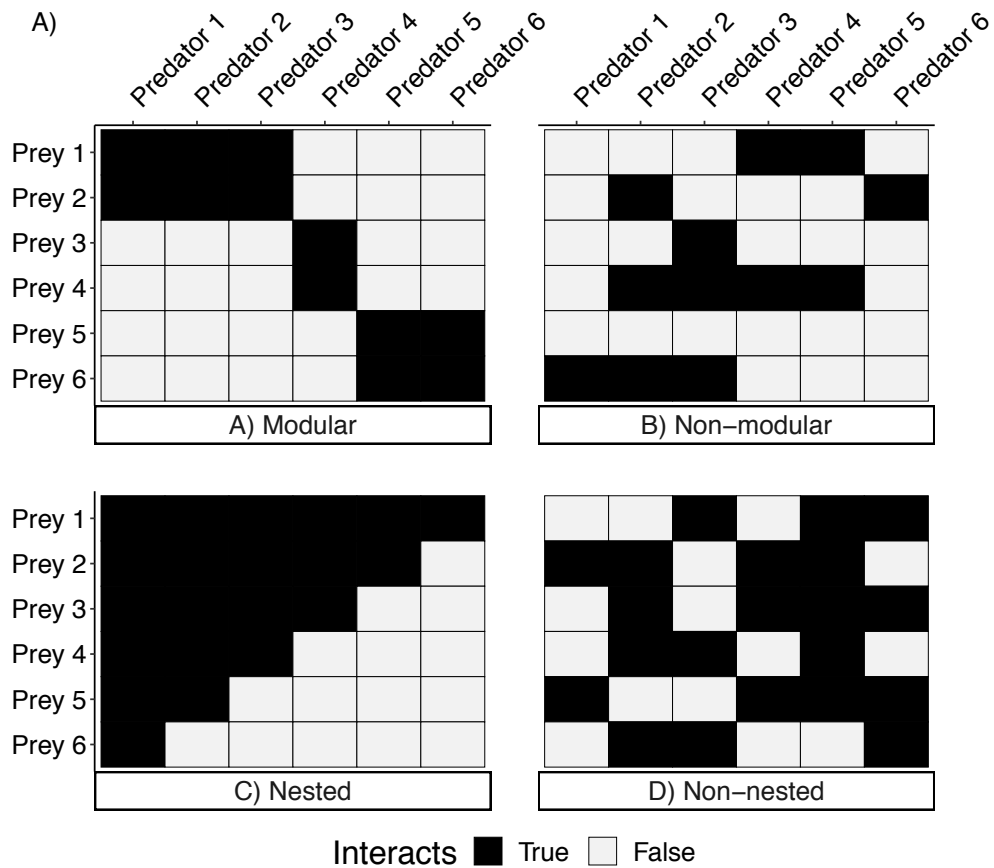
Figure 1). Panel 1 shows networks characterised by extreme a) modularity, b) non-modularity, c) nestedness structures and d) non-nestedness in bipartite networks. Panel 2 shows a simple network with values of betweenness centrality and closeness centrality for each node to 2 decimal places.

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).

17

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.

347

19

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
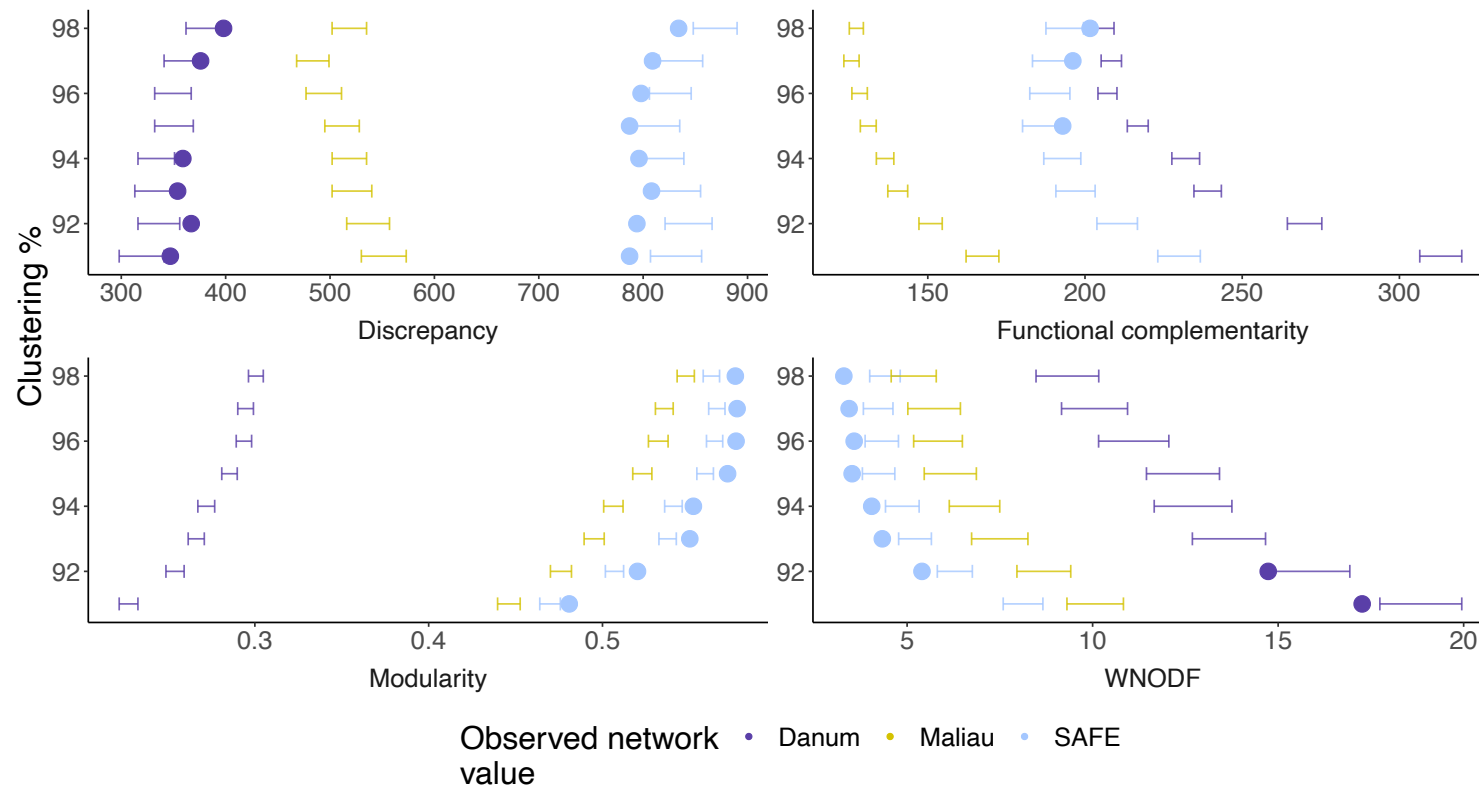
Figure 2. Summary plot showing the observed values (circles) and 95% confidence intervals (bars) given by the random values generated for each

metric studied at each MOTU clustering level, showing how conclusions drawn are altered by MOTU clustering level. The observed values for

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

most metrics studied, the 95% confidence intervals do not overlap at most clustering levels used, showing that the networks differ regardless of

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

22

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
Hipposideros diadema	-2.680	2.948	-0.909	0.364
Hipposideros dyacorum	-5.045	2.458	-2.053	0.040
Hipposideros ridleyi	2.407	2.820	0.854	0.394
Kerivoula hardwickii	-0.915	2.336	-0.392	0.695
Kerivoula intermedia	0.708	1.382	0.512	0.609
Kerivoula papillosa	-3.681	2.230	-1.651	0.099
Rhinolophus borneensis	4.198	1.928	2.178	0.030
Rhinolophus sedulus	0.617	2.201	0.281	0.779
Rhinolophus trifoliatus	2.491	1.552	1.605	0.109

389

23

390
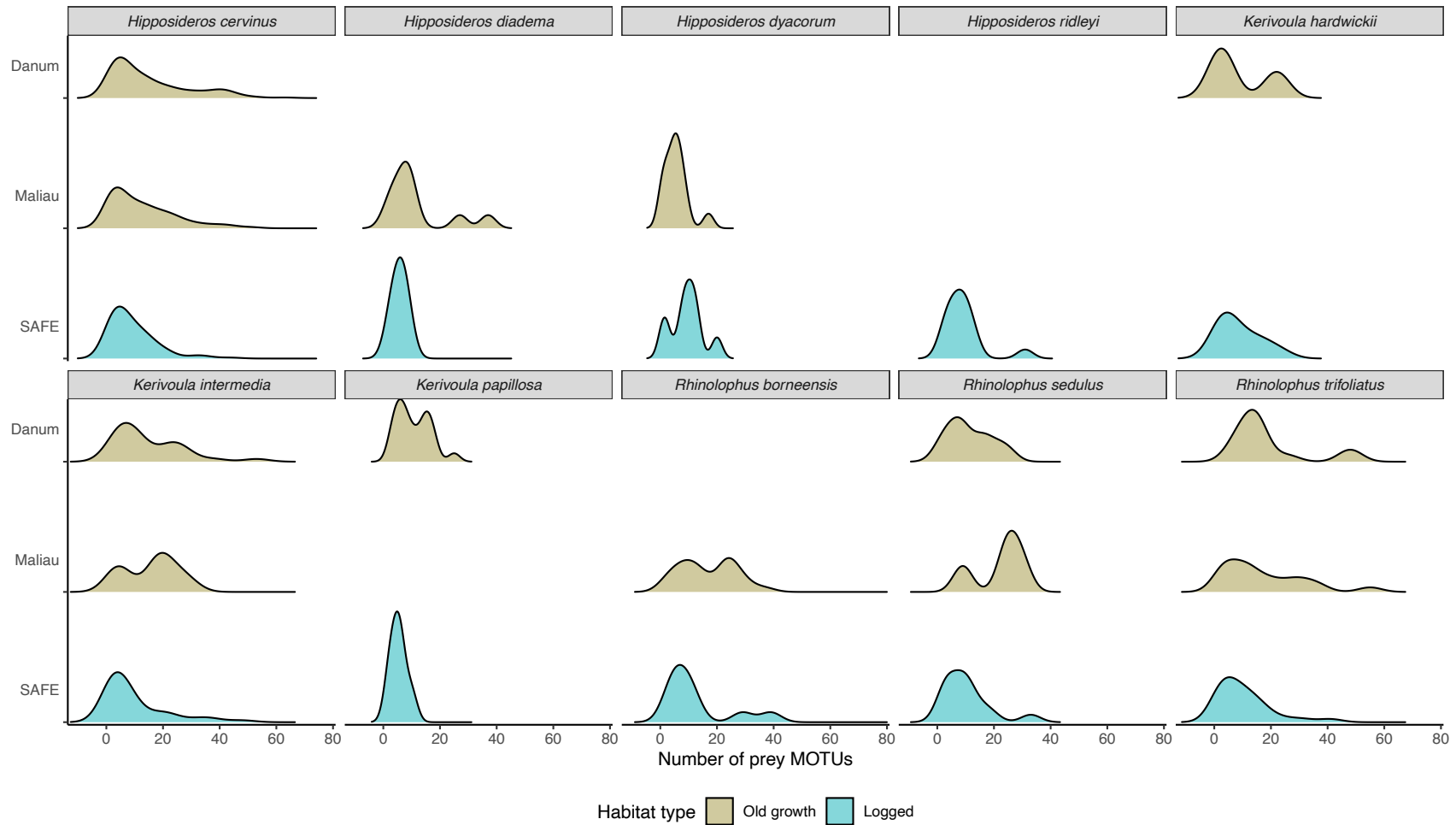
Figure 3. Smoothed histograms showing the number of MOTUs consumed by the individual bats for each focal bat species at each site. Species
on average consumed a greater number of MOTUs in old growth forest than in logged forest.
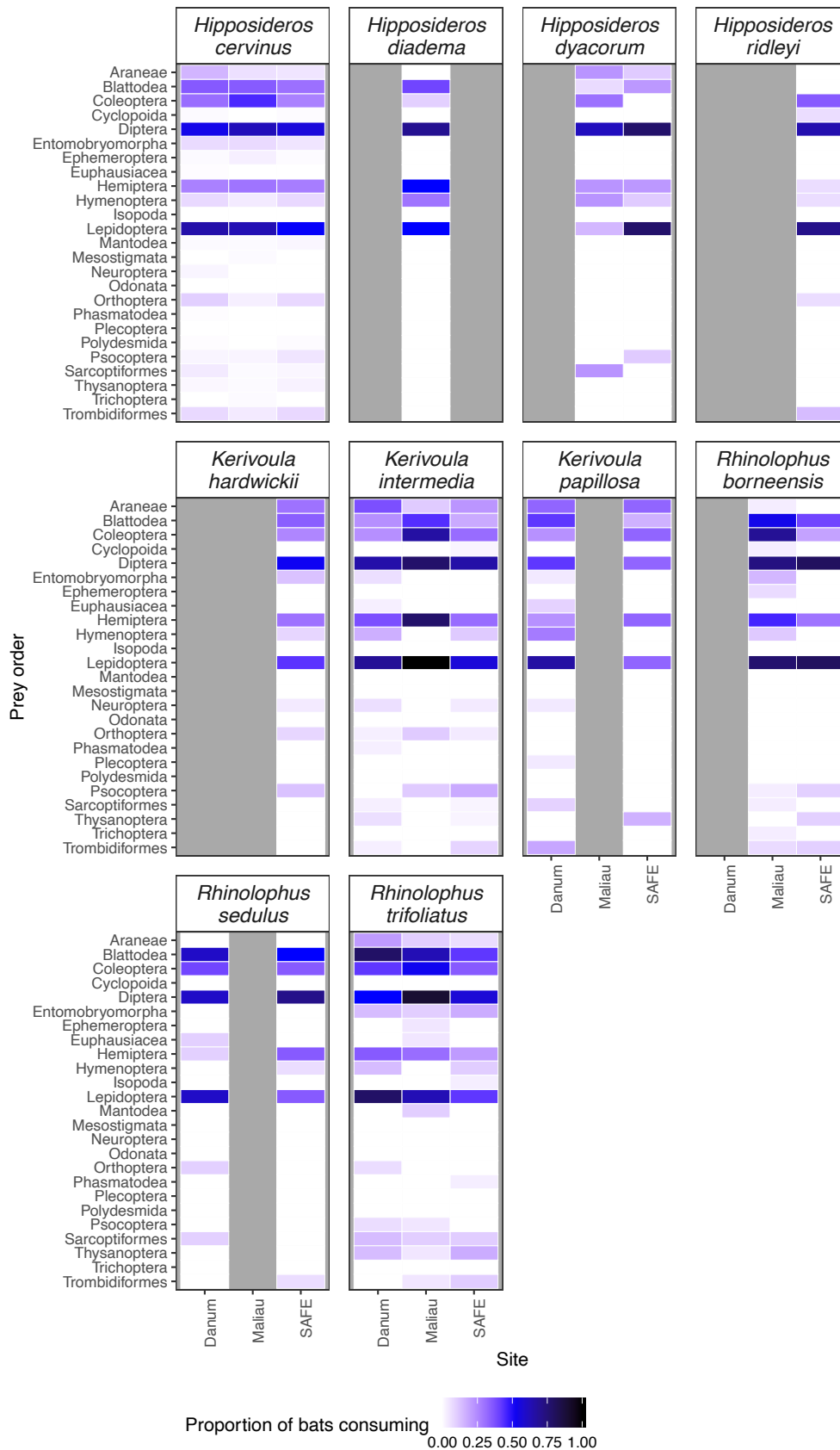
Figure 4. The proportion of individual bats of each species found to consume each taxonomic

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
P. balteata	*H. cervinus*	Danum	Old growth	3/184
P. balteata	*H. diadema*	Danum	Old growth	1/2
P. balteata	*R. trifoliatus*	Danum	Old growth	1/14
P. balteata	*H. cervinus*	Maliau	Old growth	2/90
P. balteata	*H. cervinus*	Maliau	Old growth	1/90
P. menephron	*H. cervinus*	SAFE	Logged	1/110
P. balteata	*H. cervinus*	SAFE	Logged	1/110
P. balteata	*K. intermedia*	SAFE	Logged	1/44
P. balteata	*R. sedulus*	SAFE	Logged	1/14
P. balteata	*R. trifoliatus*	SAFE	Logged	1/28

Discussion

403
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

27

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

Limitations

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

Conclusions

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

491 **References**

492 Aizpurua, O., Budinski, I., Georgiakakis, P., Gopalakrishnan, S., Ibañez, C., Mata, V., …

493   Alberdi, A. (2018). Agriculture shapes the trophic niche of a bat preying on multiple

494   pest arthropods across Europe: evidence from DNA metabarcoding. *Molecular*

495   *Ecology*, *27*(3), 815–825. doi: 10.1111/mec.14474

496 Almeida-Neto, M., Guimarães, P., Guimarães, P. R., Loyola, R. D., & Ulrich, W. (2008). A

497   consistent metric for nestedness analysis in ecological systems: reconciling concept

498   and measurement. *Oikos*, *117*(8), 1227–1239. doi: 10.1111/j.0030-1299.2008.16644.x

499 Andresen, E., Arroyo-Rodriguez, V., & Escobar, F. (2018). Tropical biodiversity: the

500   importance of biotic interactions for its origin, maintenance, function and

501   conservation. In *Ecological networks in the tropics. An integrative overview of*

502   *species interactions from some of the most species-rich habitats on earth*.

503   Gewerbestrasse, Switzerland: Springer Nature.

504 Baker, D. J., Garnett, S. T., O'Connor, J., Ehmke, G., Clarke, R. H., Woinarski, J. C. Z., &

505   McGeoch, M. A. (2018). The conservation of abundance in nonthreatened species.

506   *Conservation Biology*. doi: 10.1111/cobi.13197

507 Barlow, J., Lennox, G. D., Ferreira, J., Berenguer, E., Lees, A. C., Nally, R. M., … Gardner,

508   T. A. (2016). Anthropogenic disturbance in tropical forests can double biodiversity

509   loss from deforestation. *Nature*, *535*(7610), 144–147. doi: 10.1038/nature18326

510 Bascompte, J. (2009). Mutualistic networks. *Frontiers in Ecology and the Environment*, *7*(8),

511   429–436. doi: 10.1890/080026

512 Bastolla, U., Fortuna, M. A., Pascual-García, A., Ferrera, A., Luque, B., & Bascompte, J.

513   (2009). The architecture of mutualistic networks minimizes competition and increases

514   biodiversity. *Nature*, *458*(7241), 1018–1020. doi: 10.1038/nature07950

515   Beckett, S. J. (2016). Improved community detection in weighted bipartite networks. *Royal*

516   *Society Open Science*, *3*(1), 140536. doi: 10.1098/rsos.140536

517   Blüthgen, N. (2010). Why network analysis is often disconnected from community ecology:

518   A critique and an ecologist's guide. *Basic and Applied Ecology*, *11*(3), 185–195. doi:

519   10.1016/j.baae.2010.01.001

520   Blüthgen, N., & Klein, A.-M. (2011). Functional complementarity and specialisation: The

521   role of biodiversity in plant–pollinator interactions. *Basic and Applied Ecology*, *12*(4),

522   282–291. doi: 10.1016/j.baae.2010.11.001

523   Böhm, S. M., Wells, K., & Kalko, E. K. V. (2011). Top-Down Control of Herbivory by Birds

524   and Bats in the Canopy of Temperate Broad-Leaved Oaks (*Quercus robur*). *PLoS*

525   *ONE*, *6*(4), e17857. doi: 10.1371/journal.pone.0017857

526   Brualdi, R. A., & Sanderson, J. G. (1999). Nested species subsets, gaps, and discrepancy.

527   *Oecologia*, *119*(2), 256–264. doi: 10.1007/s004420050784

528   Camacho, C., Coulouris, G., Avagyan, V., Ma, N., Papadopoulos, J., Bealer, K., & Madden,

529   T. L. (2009). BLAST+: architecture and applications. *BMC Bioinformatics*, *10*, 421.

530   doi: 10.1186/1471-2105-10-421

531   Caporaso, J. G., Kuczynski, J., Stombaugh, J., Bittinger, K., & Bushman, F. D. (2010).

532   QIIME allows analysis of high-throughput community sequencing data. *Nature*

533   *Methods*, *7*, 335–336. doi: doi:10.1038/nmeth.f.303

534   Chamberlain, S. (2019). *bold: Interface to bold systems API*. Retrieved from

535   https://CRAN.R-project.org/package=bold

536   Cirtwill, A. R., Riva, G. V. D., Gaiarsa, M. P., Bimler, M. D., Cagua, E. F., Coux, C., &

537   Dehling, D. M. (2018). A review of species role concepts in food webs. *Food Webs*,

538   e00093. doi: 10.1016/j.fooweb.2018.e00093

32

539   Clare, E. L. (2014). Molecular detection of trophic interactions: emerging trends, distinct

540   advantages, significant considerations and conservation applications. *Evolutionary*

541   *Applications*, *7*(9), 1144–1157. doi: 10.1111/eva.12225

542   Clare, E. L., Chain, F. J. J., Littlefair, J. E., & Cristescu, M. E. (2016). The effects of

543   parameter choice on defining molecular operational taxonomic units and resulting

544   ecological analyses of metabarcoding data. *Genome*, *59*(11), 981–990. doi:

545   10.1139/gen-2015-0184

546   Clare, E. L., Fraser, E. E., Braid, H. E., Fenton, M. B., & Hebert, P. D. N. (2009). Species on

547   the menu of a generalist predator, the eastern red bat *Lasiurus borealis*: using a

548   molecular approach to detect arthropod prey. *Molecular Ecology*, *18*(11), 2532–2542.

549   doi: 10.1111/j.1365-294X.2009.04184.x

550   Creer, S., Deiner, K., Frey, S., Porazinska, D., Taberlet, P., Thomas, W. K., … Bik, H. M.

551   (2016). The ecologist's field guide to sequence-based identification of biodiversity.

552   *Methods in Ecology and Evolution*, *7*(9), 1008–1018. doi: 10.1111/2041-210X.12574

553   Czenze, Z. J., Tucker, J. L., Clare, E. L., Littlefair, J. E., Hemprich-Bennett, D. R., Oliveira,

554   H. F. M., … Parsons, S. (2018). Spatiotemporal and demographic variation in the diet

555   of New Zealand lesser short-tailed bats (*Mystacina tuberculata*). *Ecology and*

556   *Evolution*, *8*(15), 7599–7610. doi: 10.1002/ece3.4268

557   Deere, N. J., Guillera-Arroita, G., Baking, E. L., Bernard, H., Pfeifer, M., Reynolds, G., …

558   Struebig, M. J. (2017). High Carbon Stock forests provide co-benefits for tropical

559   biodiversity. *Journal of Applied Ecology*, *55*(2), 997–1008. doi: 10.1111/1365-

560   2664.13023

561   Deere, N. J., Guillera-Arroita, G., Platts, P. J., Mitchell, S. L., Baking, E. L., Bernard, H., …

562   Struebig, M. J. (2020). Implications of zero-deforestation commitments: Forest

563   quality and hunting pressure limit mammal persistence in fragmented tropical

564   landscapes. *Conservation Letters*, *n/a*(n/a), e12701. doi: 10.1111/conl.12701

565   Delmas, E., Besson, M., Brice, M.-H., Burkle, L. A., Riva, G. V. D., Fortin, M.-J., … Poisot,

566   T. (2019). Analysing ecological networks of species interactions. *Biological Reviews*,

567   *94*(1), 16–36. doi: 10.1111/brv.12433

568   Devoto, M., Bailey, S., Craze, P., & Memmott, J. (2012). Understanding and planning

569   ecological restoration of plant-pollinator networks: Understanding network

570   restoration. *Ecology Letters*, *15*(4), 319–328. doi: 10.1111/j.1461-0248.2012.01740.x

571   Dormann, C. F., Fründ, J., & Schaefer, H. M. (2017). Identifying Causes of Patterns in

572   Ecological Networks: Opportunities and Limitations. *Annual Review of Ecology,*

573   *Evolution, and Systematics*, *48*(1), 559–584. doi: 10.1146/annurev-ecolsys-110316-

574   022928

575   Dormann, C. F., Gruber, B., & Fründ, J. (2008). *Introducing the bipartite Package:*

576   *Analysing Ecological Networks*. *8*, 4.

577   Dormann, C. F., & Strauss, R. (2014). A method for detecting modules in quantitative

578   bipartite networks. *Methods in Ecology and Evolution*, *5*(1), 90–98. doi:

579   10.1111/2041-210X.12139

580   Edgar, R. C. (2010). Search and clustering orders of magnitude faster than BLAST.

581   *Bioinformatics*, *26*(19), 2460–2461. doi: 10.1093/bioinformatics/btq461

582   Edwards, D. P., Larsen, T. H., Docherty, T. D. S., Ansell, F. A., Hsu, W. W., Derhe, M. A.,

583   … Wilcove, D. S. (2010). Degraded lands worth protecting: the biological importance

584   of Southeast Asia's repeatedly logged forests. *Proceedings of the Royal Society B:*

585   *Biological Sciences*, *278*(1702), 82–90. doi: 10.1098/rspb.2010.1062

586   Evans, D. M., Kitson, J. J. N., Lunt, D. H., Straw, N. A., & Pocock, M. J. O. (2016). Merging

587   DNA metabarcoding and ecological network analysis to understand and build resilient

588   terrestrial ecosystems. *Functional Ecology*, *30*(12), 1904–1916. doi: 10.1111/1365-

589   2435.12659

590   Fortuna, M. A., Stouffer, D. B., Olesen, J. M., Jordano, P., Mouillot, D., Krasnov, B. R., …

591   Bascompte, J. (2010). Nestedness versus modularity in ecological networks: two sides

592   of the same coin? *Journal of Animal Ecology*, *79*(4), 811–817. doi: 10.1111/j.1365-

593   2656.2010.01688.x

594   Freeman, L. C. (1977). A Set of Measures of Centrality Based on Betweenness. *Sociometry*,

595   *40*(1), 35–41. doi: 10.2307/3033543

596   Freeman, L. C. (1978). Centrality in social networks conceptual clarification. *Social

597   Networks*, *1*(3), 215–239.

598   Frøslev, T. G., Kjøller, R., Bruun, H. H., Ejrnæs, R., Brunbjerg, A. K., Pietroni, C., &

599   Hansen, A. J. (2017). Algorithm for post-clustering curation of DNA amplicon data

600   yields reliable biodiversity estimates. *Nature Communications*, *8*(1), 1188. doi:

601   10.1038/s41467-017-01312-x

602   Fründ, J., McCann, K. S., & Williams, N. M. (2016). Sampling bias is a challenge for

603   quantifying specialization and network structure: lessons from a quantitative niche

604   model. *Oikos*, *125*(4), 502–513. doi: 10.1111/oik.02256

605   Gaveau, D. L. A., Sloan, S., Molidena, E., Yaen, H., Sheil, D., Abram, N. K., … Meijaard, E.

606   (2014). Four Decades of Forest Persistence, Clearance and Logging on Borneo. *PLOS

607   ONE*, *9*(7), e101654. doi: 10.1371/journal.pone.0101654

35

608   Ghazoul, J., Burivalova, Z., Garcia-Ulloa, J., & King, L. A. (2015). Conceptualizing Forest

609   Degradation. *Trends in Ecology & Evolution*, *30*(10), 622–632. doi:

610   10.1016/j.tree.2015.08.001

611   Gibson, L., Lee, T. M., Koh, L. P., Brook, B. W., Gardner, T. A., Barlow, J., … Sodhi, N. S.

612   (2011). Primary forests are irreplaceable for sustaining tropical biodiversity. *Nature*,

613   *478*(7369), 378–381. doi: 10.1038/nature10425

614   Hemprich-Bennett, D. R., Oliveira, H. F. M., Le Comber, S. C., Rossiter, S. J., & Clare, E. L.

615   (2018). Assessing the impact of taxon resolution on network structure, with

616   implication for comparative ecology. *BioRxiv*, 357376. doi: 10.1101/357376

617   Huson, D. H., Beier, S., Flade, I., Górska, A., El-Hadidi, M., Mitra, S., … Tappu, R. (2016).

618   MEGAN Community Edition - Interactive Exploration and Analysis of Large-Scale

619   Microbiome Sequencing Data. *PLOS Computational Biology*, *12*(6), e1004957. doi:

620   10.1371/journal.pcbi.1004957

621   Kalka, M., & Kalko, E. K. V. (2006). Gleaning Bats as Underestimated Predators of

622   Herbivorous Insects: Diet of Micronycteris microtis (Phyllostomidae) in Panama.

623   *Journal of Tropical Ecology*, *22*(1), 1–10. Retrieved from JSTOR.

624   Kalka, Smith, & Kalko. (2008). Bats Limit Arthropods and Herbivory in a Tropical Forest.

625   *Science*, *320*(5872), 71–71. doi: 10.1126/science.1153352

626   Kunz, T. H., Torrez, E. B. de, Bauer, D., Lobova, T., & Fleming, T. H. (2011). Ecosystem

627   services provided by bats. *Annals of the New York Academy of Sciences*, *1223*(1), 1–

628   38. doi: 10.1111/j.1749-6632.2011.06004.x

629   Lafferty, K. D., Dobson, A. P., & Kuris, A. M. (2006). Parasites dominate food web links.

630   *Proceedings of the National Academy of Sciences*, *103*(30), 11211–11216. doi:

631   10.1073/pnas.0604755103

632   Laurindo, R. S., Novaes, R. L. M., Vizentin-Bugoni, J., & Gregorin, R. (2019). The effects of

633   habitat loss on bat-fruit networks. *Biodiversity and Conservation*, *28*(3), 589–601.

634   doi: 10.1007/s10531-018-1676-x

635   Lewinsohn, T. M., Prado, P. I., Jordano, P., Bascompte, J., & Olesen, J. M. (2006). Structure

636   in plant–animal interaction assemblages. *Oikos*, *113*(1), 174–184. doi:

637   10.1111/j.0030-1299.2006.14583.x

638   Maas, B., Clough, Y., & Tscharntke, T. (2013). Bats and birds increase crop yield in tropical

639   agroforestry landscapes. *Ecology Letters*, *16*(12), 1480–1487. doi: 10.1111/ele.12194

640   Martín González, A. M., Dalsgaard, B., & Olesen, J. M. (2010). Centrality measures and the

641   importance of generalist species in pollination networks. *Ecological Complexity*, *7*(1),

642   36–43. doi: 10.1016/j.ecocom.2009.03.008

643   McCann, K. S. (2000). The diversity–stability debate. *Nature*, *405*, 228–233.

644   McCann, K. S., Rasmussen, J. B., & Umbanhowar, J. (2005). The dynamics of spatially

645   coupled food webs. *Ecology Letters*, *8*(5), 513–523. doi: 10.1111/j.1461-

646   0248.2005.00742.x

647   McCracken, G. F., Westbrook, J. K., Brown, V. A., Eldridge, M., Federico, P., & Kunz, T. H.

648   (2012). Bats Track and Exploit Changes in Insect Pest Populations. *PLoS ONE*, *7*(8),

649   e43839. doi: 10.1371/journal.pone.0043839

650   Meijaard, E., Garcia-Ulloa, J., Sheil, D., Wich, S. A., Carlson, K. M., Juffe-Bignoli, D., &

651   Brooks, T. M. (2018). *Oil palm and biodiversity*. Retrieved from

652   https://portals.iucn.org/library/node/47753

653   Meijaard, E., & Sheil, D. (2007). A logged forest in Borneo is better than none at all. *Nature*,

654   *446*. doi: 10.1038/446974a

655   Mello, M. A. R., Marquitti, F. M. D., Jr, P. R. G., Kalko, E. K. V., Jordano, P., & Aguiar, M.

656   A. M. de. (2011). The Missing Part of Seed Dispersal Networks: Structure and

657   Robustness of Bat-Fruit Interactions. *PLOS ONE*, *6*(2), e17395. doi:

658   10.1371/journal.pone.0017395

659   Mello, M. A. R., Rodrigues, F. A., Costa, L. da F., Kissling, W. D., Şekercioğlu, Ç. H.,

660   Marquitti, F. M. D., & Kalko, E. K. V. (2015). Keystone species in seed dispersal

661   networks are mainly determined by dietary specialization. *Oikos*, *124*(8), 1031–1039.

662   doi: 10.1111/oik.01613

663   Melo, F. P. L., Arroyo-Rodríguez, V., Fahrig, L., Martínez-Ramos, M., & Tabarelli, M.

664   (2013). On the hope for biodiversity-friendly tropical landscapes. *Trends in Ecology*

665   *& Evolution*, *28*(8), 462–468. doi: 10.1016/j.tree.2013.01.001

666   Memmott, J., Waser, N. M., & Price, M. V. (2004). Tolerance of pollination networks to

667   species extinctions. *Proceedings of the Royal Society of London. Series B: Biological*

668   *Sciences*, *271*(1557), 2605–2611. doi: 10.1098/rspb.2004.2909

669   Meyer, C. F. J., Struebig, M. J., & Willig, M. R. (2016). Chapter 4: Responses of Tropical

670   Bats to Habitat Fragmentation, Logging, and Deforestation. In *Bats in the*

671   *Anthropocene: Conservation of Bats in a Changing World* (pp. 63–105). Springer

672   Open.

673   Montoya, D., Rogers, L., & Memmott, J. (2012). Emerging perspectives in the restoration of

674   biodiversity-based ecosystem services. *Trends in Ecology & Evolution*, *27*(12), 666–

675   672. doi: 10.1016/j.tree.2012.07.004

676   Morrison, E. B., & Lindell, C. A. (2012). Birds and bats reduce insect biomass and leaf

677   damage in tropical forest restoration sites. *Ecological Applications*, *22*(5), 1526–1534.

678   doi: 10.1890/11-1118.1

679   Oliveira, H. F. M. (2018). *El Niño effects on the structure of mutualistic and antagonistic bat*

680   *food webs revealed by DNA barcoding* (PhD thesis). Queen Mary University of

681   London, London, UK.

682   Peralta, G., Frost, C. M., Rand, T. A., Didham, R. K., & Tylianakis, J. M. (2014).

683   Complementarity and redundancy of interactions enhance attack rates and spatial

684   stability in host–parasitoid food webs. *Ecology*, *95*(7), 1888–1896. doi: 10.1890/13-

685   1569.1

686   Peter, F., Berens, D. G., Grieve, G. R., & Farwig, N. (2015). Forest Fragmentation Drives the

687   Loss of Insectivorous Birds and an Associated Increase in Herbivory. *Biotropica*,

688   *47*(5), 626–635. doi: 10.1111/btp.12239

689   Peters, S. L., Malcolm, J. R., & Zimmerman, B. L. (2006). Effects of Selective Logging on

690   Bat Communities in the Southeastern Amazon. *Conservation Biology*, *20*(5), 1410–

691   1421. doi: 10.1111/j.1523-1739.2006.00526.x

692   R Core Team. (2017). *R: A Language and Environment for Statistical Computing*. Retrieved

693   from https://www.R-project.org/

694   Ratnasingham, S., & Hebert, P. D. (2007). BOLD: The Barcode of Life Data System

695   (http://www.barcodinglife.org). *Molecular Ecology Resources*, *7*(3), 355–364. doi:

696   10.1111/j.1471-8286.2007.01678.x

697   Razgour, O., Clare, E. L., Zeale, M. R. K., Hanmer, J., Schnell, I. B., Rasmussen, M., …

698   Jones, G. (2011). High-throughput sequencing offers insight into mechanisms of

699   resource partitioning in cryptic bat species. *Ecology and Evolution*, *1*(4), 556–570.

700   doi: 10.1002/ece3.49

39

701   Rezende, E. L., Albert, E. M., Fortuna, M. A., & Bascompte, J. (2009). Compartments in a

702   marine food web associated with phylogeny, body mass, and habitat structure.

703   *Ecology Letters*, *12*(8), 779–788. doi: 10.1111/j.1461-0248.2009.01327.x

704   Roslin, T., & Majaneva, S. (2016). The use of DNA barcodes in food web construction—

705   terrestrial and aquatic ecologists unite! *Genome*, *59*(9), 603–628. doi: 10.1139/gen-

706   2015-0229

707   Salinas-Ramos, V. B., Herrera Montalvo, L. G., León-Regagnon, V., Arrizabalaga-Escudero,

708   A., & Clare, E. L. (2015). Dietary overlap and seasonality in three species of

709   mormoopid bats from a tropical dry forest. *Molecular Ecology*, *24*(20), 5296–5307.

710   doi: 10.1111/mec.13386

711   Shannon, C. E. (1948). A Mathematical Theory of Communication. *Bell System Technical*

712   *Journal*, *27*(3), 379–423. doi: 10.1002/j.1538-7305.1948.tb01338.x

713   Slade, E. M., Mann, D. J., & Lewis, O. T. (2011). Biodiversity and ecosystem function of

714   tropical forest dung beetles under contrasting logging regimes. *Biological*

715   *Conservation*, *144*(1), 166–174. doi: 10.1016/j.biocon.2010.08.011

716   Soares, R. G. S., Ferreira, P. A., & Lopes, L. E. (2017). Can plant-pollinator network metrics

717   indicate environmental quality? *Ecological Indicators*, *78*, 361–370. doi:

718   10.1016/j.ecolind.2017.03.037

719   Song, X.-P., Hansen, M. C., Stehman, S. V., Potapov, P. V., Tyukavina, A., Vermote, E. F.,

720   & Townshend, J. R. (2018). Global land change from 1982 to 2016. *Nature*,

721   *560*(7720), 639. doi: 10.1038/s41586-018-0411-9

722   Struebig, M. J., Turner, A., Giles, E., Lasmana, F., Tollington, S., Bernard, H., & Bell, D.

723   (2013). Quantifying the Biodiversity Value of Repeatedly Logged Rainforests:

724   Gradient and Comparative Approaches from Borneo. *Advances in Ecological*

725   *Research*, *48*, 183–224. doi: 10.1016/B978-0-12-417199-2.00003-3

726   Struebig, M. J., Wilting, A., Gaveau, D. L. A., Meijaard, E., Smith, R. J., Abdullah, T., …

727   Kramer-Schadt, S. (2015). Targeted Conservation to Safeguard a Biodiversity

728   Hotspot from Climate and Land-Cover Change. *Current Biology*, *25*(3), 372–378.

729   doi: 10.1016/j.cub.2014.11.067

730   Thébault, E., & Fontaine, C. (2010). Stability of Ecological Communities and the

731   Architecture of Mutualistic and Trophic Networks. *Science*, *329*(5993), 853–856. doi:

732   10.1126/science.1188321

733   Tscharntke, T., Bommarco, R., Clough, Y., Crist, T. O., Kleijn, D., Rand, T. A., … Vidal, S.

734   (2007). Conservation biological control and enemy diversity on a landscape scale.

735   *Biological Control*, *43*(3), 294–309. doi: 10.1016/j.biocontrol.2007.08.006

736   Vun Khen, C. (1996). *Forest pest insects in Sabah*. Sandakan, Malaysia: Sabah Forest

737   Department.

738   Williams-Guillén, K., Perfecto, I., & Vandermeer, J. (2008). Bats Limit Insects in a

739   Neotropical Agroforestry System. *Science*, *320*(5872), 70–70. doi:

740   10.1126/science.1152944

741   Zeale, M. R. K., Butlin, R. K., Barker, G. L. A., Lees, D. C., & Jones, G. (2011). Taxon-

742   specific PCR for DNA barcoding arthropod prey in bat faeces. *Molecular Ecology*

743   *Resources*, *11*(2), 236–244. doi: 10.1111/j.1755-0998.2010.02920.x

744

41