

1 **Mammalian species abundance across a gradient of tropical land-use intensity: a**  
2 **hierarchical multi-species modelling approach**

3

4 Oliver R. Wearn<sup>1,2\*</sup>, J. Marcus Rowcliffe<sup>2</sup>, Chris Carbone<sup>2</sup>, Marion Pfeifer<sup>1</sup>, Henry Bernard<sup>3</sup>,  
5 Robert M. Ewers<sup>1</sup>

6 <sup>1</sup>Department of Life Sciences, Imperial College London, Silwood Park, Ascot SL5 7PY, UK

7 <sup>2</sup>Institute of Zoology, Zoological Society of London, Regent's Park, London NW1 4RY, UK

8 <sup>3</sup>Institute for Tropical Biology and Conservation, Universiti Malaysia Sabah, Jalan UMS,  
9 88400 Kota Kinabalu, Sabah, Malaysia

10 \*Corresponding author: Wearn, O. R. ([oliver.wearn@gmail.com](mailto:oliver.wearn@gmail.com))

11

12 **Abstract**

13 Recent work in the tropics has advanced our understanding of the local impacts of land-use  
14 change on species richness. However, we still have a limited ability to make predictions  
15 about species abundances, especially in heterogeneous landscapes. Species abundances  
16 directly affect the functioning of an ecosystem and its conservation value. We applied a  
17 hierarchical model to camera- and live-trapping data from a region in Borneo, and estimated  
18 the relative abundance (controlling for imperfect detection) of 57 terrestrial mammal species,  
19 as a function of either categorical or continuous metrics of land-use change. We found that  
20 mean relative abundance increased (by 28%) from old-growth to logged forest, but declined  
21 substantially (by 47%) in oil palm plantations compared to forest. Abundance responses to  
22 above-ground live tree biomass (a continuous measure of local logging intensity) were  
23 negative overall, whilst they were strongly positive for landscape forest cover. From old-  
24 growth to logged forest, small mammals increased in their relative abundance proportionately  
25 much more than large mammals (169% compared to 13%). Similarly, omnivores and

26 insectivores increased more than other trophic guilds (carnivores, herbivores and frugivores).  
27 From forest to oil palm, species of high conservation concern fared especially poorly  
28 (declining by 84%). Invasive species relative abundance consistently increased along the  
29 gradient of land-use intensity. Changes in relative abundance across nine functional effects  
30 groups based on diet were minimal from old-growth to logged forest, but in oil palm only the  
31 vertebrate predation function was maintained. Our results show that, in the absence of  
32 hunting, even the most intensively logged forests can conserve the abundance and functional  
33 effects of mammals. Recent pledges made by companies to support the protection of High  
34 Carbon Stock logged forest could therefore yield substantial conservation benefits. Within oil  
35 palm, our results support the view that “wildlife-friendly” practices offer a low potential for  
36 reducing biodiversity impacts.

37

38 **Key words:** land-use change, abundance responses, selective logging, oil palm agriculture,  
39 High Carbon Stock, hierarchical modelling, robust monitoring, multi-method sampling,  
40 mammals, Borneo.

41

## 42 **1. Introduction**

43 Land-use change is well-known as a major driver of ecological change, for example as a  
44 leading cause of species endangerment at global scales (Vié, Hilton-Taylor & Stuart 2009).  
45 However, there remains a limited capacity to make biodiversity predictions, in particular of  
46 species abundances, at scales which are relevant to local stakeholders and policy-makers  
47 responsible for making land-use decisions. There are at least three reasons for this: 1) a focus  
48 on species richness rather than species abundances, 2) a failure to disentangle the  
49 observational and ecological processes than generate datasets, and 3) the characterisation of  
50 heterogeneous landscapes using categorical descriptors.

51

52 Much of the previous research on the biodiversity impacts of land-use change has focussed  
53 on community-level parameters, and especially species richness (Gibson *et al.* 2011). In this  
54 case, there is a developing consensus about the impacts of land-use change on species  
55 richness, such as the relatively lower impacts of selective logging relative to plantation  
56 forestry, which in turn often retain more species than monoculture plantations (Scales &  
57 Marsden 2008; Gibson *et al.* 2011; Barnes *et al.* 2014; Edwards *et al.* 2014). The more subtle  
58 impacts of land-use change on species abundances have been quantified less frequently, and  
59 often only for single focal species (e.g. from capture-recapture studies) or a limited subset of  
60 species (e.g. Berry *et al.* 2010). This matters because abundance estimates give a finer  
61 resolution of information on species responses to environmental change than species richness  
62 measures, and may therefore facilitate better decisions surrounding trade-offs in land-use  
63 (Phalan *et al.* 2011). Importantly, species abundances may also be indicative of ecosystem  
64 functioning (Ewers *et al.* 2015), as well as the trophic structure and interaction strengths  
65 present in an ecosystem (Barnes *et al.* 2014).

66

67 Across the studies in which abundance in tropical landscapes have been quantified, consistent  
68 patterns across land-use types, and across taxonomic groups, have remained elusive (Sodhi *et al.*  
69 *al.* 2009; Gibson *et al.* 2011; Newbold *et al.* 2014). The majority of past studies have based  
70 their inferences about abundance on sparse data, often on a small subset of species in a  
71 community, and without controlling for the potentially confounding set of observational  
72 processes which, in combination with the ecological processes at work, create observed  
73 datasets (Royle & Dorazio 2008). Perhaps most importantly, changes in detection probability  
74 across treatment units, such as different land-uses, may confound any apparent changes in  
75 abundance and must be controlled for (Archaux *et al.* 2011), something which has rarely been

76 done (e.g. see Newbold *et al.* 2014). The widespread failure to disentangle the observational  
77 and ecological processes at work may, at least in part, explain the large variability in reported  
78 abundance responses and, in the worst cases, may be a source of systematic bias in  
79 inferences. As a result, there is still a limited capacity to make robust predictions about the  
80 impacts of land-use change on species abundances (e.g. Newbold *et al.* 2014).

81

82 Land-use change sometimes involves dramatic and rapid changes to a natural habitat, for  
83 example when a primary forest is converted to pasture. More often, land-use in the tropics  
84 manifests itself as a gradient of disturbance intensity, rather than distinct land-use categories  
85 (e.g. Asner *et al.* 2009). For example, the intensity of selective logging may vary  
86 considerably across a landscape, due to access constraints and natural variability in  
87 marketable timber volumes (Berry *et al.* 2008). Similarly, plantations may vary in their  
88 proximity to remaining forests and in their structural properties, such as height and canopy  
89 cover, as they mature (Luskin & Potts 2011). Continuous, as opposed to categorical, metrics  
90 of land-use change are rarely used (Cushman *et al.* 2010), but may offer an opportunity to  
91 increase the predictive power and practical relevance of forecasts for conservation and  
92 management, especially in highly heterogeneous landscapes.

93

94 Land-use change has been especially acute in Southeast Asia, with the vast majority of  
95 remaining forest now existing in a logged-over state (Margono *et al.* 2014; Gaveau *et al.*  
96 2014). Deforestation rates, in large part due to oil palm (*Elaeis guineensis*) plantation  
97 expansion, are also the highest among the major tropical forest regions (Asner *et al.* 2009).  
98 Palm oil producers, traders and buyers have increasingly recognised the reputational risk of  
99 being associated with deforestation, and dozens of the largest companies have recently made  
100 pledges to achieve “zero deforestation” within supply chains. In practice, the conservation of

101 High Carbon Stock (HCS) forest is likely to be the principal way these pledges will be  
102 implemented, with HCS forest delineated on the basis of gross structural properties (HCS  
103 Approach Steering Group 2015) or carbon-content (Raison *et al.* 2015). There is therefore an  
104 urgent need to consider the potential value of HCS forest for conserving biodiversity, and in  
105 particular the abundance of animal species.

106

107 Here we investigate species relative abundances for a community of terrestrial mammals  
108 across a land-use intensity gradient in Borneo. To do this, we use a hierarchical model of the  
109 mammal metacommunity in our study region which accounts for 1) changes in detection  
110 probability across space, 2) correlated detections in group-living species, 3) multiple  
111 sampling methods (camera traps and live traps), 4) a clustered sampling design, and 5) habitat  
112 filtering according to land-use and fine-scale habitat disturbance. We refer to “relative  
113 abundance”, since our measure can be used to make robust comparisons across space (e.g.  
114 across land-use types), but not across species. We used either categorical or continuous  
115 approaches to characterise the land-use gradient. In the former case, we used three categories  
116 which match the major land-use options for a forested concession in the region: old-growth  
117 forest, logged forest and oil palm plantation. In the latter case, we used satellite-derived  
118 measures of above-ground live tree biomass (AGB) and local landscape percent forest cover.  
119 AGB is directly proportional to carbon content (Martin & Thomas 2011) and is therefore  
120 relevant for assessing the value of HCS set-aside areas for mammal species. Landscape forest  
121 cover is relevant to management decisions concerning the quantity of forest set-aside within a  
122 concession, for example as High Conservation Value (HCV) areas or riparian reserves in oil  
123 palm plantations (Koh, Levang & Ghazoul 2009). We also partitioned the mammal  
124 community according to four ecological response traits – body size, conservation status,  
125 native status and trophic guild – as well as into functional effects groups based on diet, and

126 present relative abundance and biomass responses of these sub-groups. For the first time, this  
127 allowed us to robustly explore whether particular sub-groups of Southeast Asian mammal  
128 species show differential responses to land-use change.

129

## 130 **2. Materials and methods**

### 131 2. 1. Sampling design

132 We sampled mammals across the landscape encompassed by the Stability of Altered Forest  
133 Ecosystems (SAFE) Project in Sabah, Malaysian Borneo (Ewers *et al.* 2011). This  
134 heterogeneous landscape consists of old-growth forest within the Maliau Basin Conservation  
135 Area and Brantian-Tatulit Virgin Jungle Reserve (VJR), repeatedly-logged forest within the  
136 Kalabakan Forest Reserve and two adjacent oil palm plantations straddling the Kalabakan  
137 Forest Reserve boundary (see Appendix S1 in Supporting Information for further description  
138 of the study sites).

139

140 We employed a clustered hierarchical sampling design, with 48 sampling points (23 m apart)  
141 clustered together into each of 46 sampling plots (each covering 1.75 ha), in turn clustered  
142 into 11 sampling blocks distributed across the land-use gradient (Fig. 1). This included 13  
143 plots (in 4 blocks) in old-growth forest, 24 plots (in 4 blocks) in logged forest and 9 plots (in  
144 3 blocks) in oil palm plantations. Sampling plots overlapped the SAFE Project sampling  
145 design, and therefore benefitted from the deliberate control of potentially confounding factors  
146 (including latitude, slope and elevation) that was central to this project's design (Ewers *et al.*  
147 2011).

148

### 149 2. 2. Field methods

150 Of the 48 sampling points within each plot, a random subset of 13 points (range: 8 to 22) in  
151 each of the 46 plots were selected for camera-trapping, giving 590 points sampled in total.  
152 Camera-trapping methods followed Wearn *et al.* (2013), with cameras (Reconyx HC500,  
153 Holmen, Wisconsin, USA) deployed strictly within 5 m of each random point. Camera-  
154 trapping took place between May 2011 and April 2014, during which most plots (40 of 46)  
155 were sampled in multiple years (mean effort per plot = 635 trap nights). We excluded 18  
156 points which had been camera-trapped for less than seven days, giving a total sampling effort  
157 of 29,121 camera trap nights (after correcting for camera failures).

158

159 Of the 46 plots sampled using camera traps, 31 were also sampled using live traps. Two  
160 locally-made steel-mesh traps (18 x 10 - 13 x 28 cm), baited with oil palm fruit, were placed  
161 at or near ground level (0 - 1.5 m) within 10 m (mean = 4.8 m) of all 48 points in a plot. Each  
162 trapping session consisted of seven consecutive trapping days and some plots (14 of 31) were  
163 sampled for multiple sessions across the study period (mean effort per plot = 1099 trap  
164 nights). Traps were checked each morning and captured individuals were anaesthetised using  
165 diethyl ether (following Wells *et al.* 2007), measured, permanently marked using a  
166 subcutaneous passive inductive transponder tag (Francis Scientific Instruments, Cambridge,  
167 UK), identified to species using Payne *et al.* (2007) and released at the capture location.  
168 Trapping, totalling 34,058 trap nights, was carried out between May 2011 and July 2014,  
169 during which there were no major mast-fruiting events (O. R. Wearn, pers. obs.).

170

171 We scored the habitat disturbance in a 5 m radius around each sampling point on a 1-5 scale,  
172 representing a scale of low to high disturbance intensity. For example, a score of 1 was used  
173 in intact, high canopy forest, whilst a score of 5 was used in open areas, such as on roads or

174 log-landing areas (full definitions are provided in Appendix S1). This variable was used to  
175 model fine-scale variation in detection probability at the point scale.

176

### 177 2. 3. Modelling approach

178 To estimate species relative abundance, we used a form of multi-species occupancy model  
179 (Royle & Dorazio 2008). These models all require replicate samples in space and time, in  
180 order to separate the latent ecological processes of interest from the observational processes  
181 by which the data are generated. We therefore transformed our data to the required form of  
182 detections and non-detections within temporal replicates, or occasions, for each sampling  
183 point. Here we define an occasion, for live-trapping, as a single night's trapping at a point  
184 (i.e. two trap nights, given that two traps were deployed per point) or, for camera-trapping, as  
185 five consecutive calendar days (see Appendix S1 for further information on camera trap data  
186 pre-processing).

187

188 We here briefly describe the modelling approach we used (full details are provided in  
189 Appendix S1), highlighting where it differs from related models in the literature (Yamaura *et al.*  
190 *2011*; Tobler *et al.* 2015). The observational process was characterised using the binomial  
191 modelling approach of Royle & Nichols (2003), which uses the pattern of detections and non-  
192 detections across sampling occasions (i.e. the detection history) to provide information on the  
193 probability of detecting a species. Importantly, this model also exploits spatial heterogeneity  
194 in this species-level detection probability to obtain a measure of relative abundance (local  
195 abundance, as defined below), as well as the probability of detecting a single individual  
196 animal (Royle & Dorazio 2008; Yamaura *et al.* 2011). We extended this approach to  
197 incorporate multiple species and multiple sampling methods, by estimating individual-level  
198 detection probability for each species-by-sampling method combination. For group-living



199 species, we used a quasi-binomial model for the observational process (estimating an  
200 additional overdispersion parameter in the process), to allow us to relax an assumption of  
201 independent detections among individuals (Royle & Dorazio 2008). We considered two  
202 point-specific covariates – land-use type and fine-scale habitat disturbance – acting on  
203 individual-level detection probabilities. We also included a 2<sup>nd</sup>-degree polynomial term for  
204 habitat disturbance, to allow for unimodal responses.

205

206 Local abundance ( $\lambda$ ) – the latent ecological parameter in the model – was characterized by a  
207 zero-inflated Poisson mixed-effects model. Zero-inflation was incorporated at the land-use  
208 level, to allow species to be completely absent from certain land-use types, rather than just  
209 occurring at low abundance ( $\lambda$  cannot be zero in a Poisson distribution). The local abundance  
210 estimates provided by the Royle & Nichols (2003) model represent, for a given species, the  
211 number of individuals using a given sampling point. In this study, we refer to this abundance  
212 measure as “relative abundance” rather than “true abundance” or density (individuals per unit  
213 area) because, although we have controlled for imperfect detection, this measure is not  
214 directly comparable across species. Local abundance will be a function of the effective  
215 trapping area for each species, as is also true of occupancy estimates (Efford & Dawson  
216 2012). Specifically, we would expect a positive relationship between the home range of a  
217 species and its local abundance. However, local abundance likely serves as a robust measure  
218 of relative density changes across the land-use gradient, given that we controlled for  
219 detectability by land-use category and habitat disturbance. Our relative abundance measure is  
220 therefore spatially-comparable, and we restrict our inferences in this study to relative  
221 abundance comparisons across space, but not in absolute terms across species. Local  
222 abundance estimates are in units of individuals, irrespective of whether the species is group-  
223 living or not.

224

225 To account for our clustered sampling design, we used spatial random effects on local  
226 abundance, with sampling points nested within plots, in turn within blocks. In this study, we  
227 do not make inferences about the fine-scale variation in local abundance estimates. These  
228 estimates will be a function of both broad-scale population dynamics and local-scale use of  
229 habitat. We instead focus on the average local abundances (e.g. for a given land-use), having  
230 accounted for non-independence using the random effects. A temporal random effect of year  
231 enabled us to account for varying abundance across the multiple years of our study. Given  
232 this, we assume population and demographic closure over the time-scale of a year (i.e. that  
233 local populations do not go extinct or re-colonise, and that individuals are not dying,  
234 recruiting or migrating), but that changes can occur between years. However, by analogy with  
235 capture-recapture models, estimates may not be biased with a violation of closure, if changes  
236 in occupancy and local abundance are occurring at random (MacKenzie *et al.* 2006).

237

238 We characterised the land-use gradient in two different ways and present the relative  
239 abundance responses revealed by both approaches. The point-specific covariates on local  
240 abundance were either 1) categorical land-use types (abbreviated in the Results as LU) or 2)  
241 satellite-derived continuous metrics of AGB and percent forest cover (FCOV), both  
242 calculated within 500 m radius buffers around each sampling point (see Appendix S1 for  
243 further information). To allow for unimodal responses, we also included a 2<sup>nd</sup>-degree  
244 polynomial term for AGB. We did not include a polynomial term for percent forest cover  
245 because we had insufficient coverage of the covariate's full range within our sampled points,  
246 which meant that we did not have sufficient information to resolve any particular non-linear  
247 form of the response.

248

249 As in previous multi-species hierarchical models (Royle & Dorazio 2008; Tobler *et al.* 2015),  
250 species-level parameters in the observational and ecological components of the model were  
251 drawn from a common hyper-distribution for the metacommunity, rather than being modelled  
252 completely independently. This allows for inferences to be made about the most infrequently  
253 detected species by “borrowing strength” from the rest of the data, though this also involves  
254 making a trade-off for well-sampled species which could have been modelled independently  
255 (due to “shrinkage” of species-level parameter estimates towards the metacommunity mean).  
256 We made inferences from this model within a Bayesian framework, using JAGS (Just  
257 Another Gibbs Sampler) version 3.4.0 (Plummer 2013) to obtain samples of the joint  
258 posterior distribution (see Appendices S1-S2 for details of software implementation and  
259 model code). To test predictions about the overall effects (at the metacommunity level) of the  
260 categorical and continuous predictors on local abundance, we used the posterior distributions  
261 of the relevant hyperparameters to compute the probability that they were greater (or less)  
262 than zero.

263

264 To explore if particular mammal community sub-groups showed differential responses to  
265 land-use change, local abundance estimates for species were partitioned *post-hoc* according  
266 to ecological response traits: body size (large or small, using a 1 kg body mass threshold;  
267 63% and 27% of species, respectively), conservation status (threatened or non-threatened on  
268 the IUCN Red List; 44% and 56% of species, respectively), native status (native or invasive;  
269 95% and 5%, respectively) and trophic guild (carnivore, insectivore, frugivore, herbivore or  
270 omnivore; 21%, 21%, 28%, 9% and 21% of species, respectively). We also defined nine  
271 functional effects groups based on diet, i.e. all species implicated in each of: vertebrate  
272 predation, scavenging, invertebrate predation, fruit-eating, seed-eating, fungi-eating, leaf-  
273 eating, bark-eating and root-eating (see Appendix S1 for more information). Local biomasses

274 (the biomass of individuals using a given sampling point) were calculated by multiplying  
275 local abundance estimates by body mass estimates for each species. As for abundance, our  
276 measure of biomass is a spatially-comparable “relative biomass” measure, rather than  
277 biomass density (biomass per unit area).

278

### 279 **3. Results**

280 A total of 4,381 live trap captures and 15,148 camera trap captures were made, for 57  
281 mammal species. After reducing these data into detections or non-detections within sampling  
282 occasions (17,025 live trap occasions and 5,428 camera trap occasions), this translated into  
283 4,284 live trap detections of 23 species, and 7,772 camera trap detections of 53 species (19  
284 species were common to both sampling methods). We also had a limited number of captures  
285 (mostly  $\leq 2$  per species) for nine additional mammal species which we classified as obligate  
286 arboreal species (listed in Appendix S1) and which we did not include in our abundance  
287 models.

288

#### 289 3. 1. Relative abundance responses to land-use type

290 Mean local abundance across the mammal community was marginally higher (+28%, CI: -5  
291 to 66%) in logged forest compared to old-growth forest ( $\Pr(\beta_{Logged}^{\lambda,LU} > 0) = 0.76$ ), but much  
292 lower (-47%, CI: -67 to 8%) in oil palm compared to the two forest land-uses ( $\Pr$   
293  $(\beta_{OilPalm}^{\lambda,LU} < 0) = 1.00$ ). These overall trends, however, belie substantial differences among  
294 species groups (Fig. 2) and among individual species (Fig. 3; Appendix S3).

295

296 From old-growth to logged forest, large mammals exhibited a modest (+13%, CI: -18 to 51%)  
297 increase in mean local abundance, but small mammals increased substantially (+169%, CI: 67  
298 to 292%). The mean local abundance of high conservation concern species was similar in

299 logged forest compared to old-growth forest (Fig. 2), but dropped precipitously (-84%, CI: -  
300 93 to -59%) in oil palm compared to the two forest land-uses. In contrast, the local abundance  
301 of low conservation concern species was largely robust to the land-use gradient, whilst  
302 invasive species increased substantially along the gradient of land-use intensity (Fig. 2).  
303 There was a 27% chance of invasive species (one or more species) being present in old-  
304 growth forest (none were detected during sampling). From logged forest to oil palm, the local  
305 abundance of invasives increased by 598% (CI: -19 to 5644%). The mean local abundance of  
306 all trophic guilds except frugivores increased from old-growth to logged forest, whilst the  
307 local abundance of all guilds except carnivores declined in oil palm (Fig. 2).

308

309 The trends in summed local abundances and biomasses (i.e. summed across species) for each  
310 trait-defined group were largely similar to those for mean local abundance (Appendix S3).  
311 However, the relatively modest local abundance increases in herbivores (+14%, CI: -36 to  
312 112%) and threatened species (+29%, CI: -10 to 83%) from old-growth to logged forest were  
313 much more prominent in terms of summed local biomass (113% and 99%, respectively), due  
314 to increases in large-bodied species in these groups (e.g. sambar deer *Rusa unicolor*, banteng  
315 *Bos javanicus* and Asian elephant *Elephas maximus*). Similarly, large changes in mean local  
316 abundance in omnivores (97%, CI: 24 to 211%) were not as strong in terms of summed local  
317 biomass (49%, CI: -17 to 174%), because these abundance changes were partly driven by  
318 small-bodied murid rodent species.

319

320 The summed local biomasses of functional effects groups were maintained, or increased,  
321 from old-growth to logged forest, but from forest to oil palm substantial declines were  
322 evident in all cases except vertebrate predation (Fig. 4).

323

324 3. 2. Relative abundance responses to continuous metrics of land-use intensity  
325 Local abundance was negatively affected overall by AGB ( $\Pr(\beta^{\lambda,AGB} < 0) = 0.96$ ) and  
326 positively affected by forest cover ( $\Pr(\beta^{\lambda,FCOV} > 0) = 1.00$ ; Figs. 5-6). The effect of forest  
327 cover was stronger than the effect of AGB (standardised hyperparameter estimates:  $\beta^{\lambda,AGB} = -$   
328 0.18, CI: -0.35 to -0.01;  $\beta^{\lambda,AGB^2} = -0.10$ , CI: -0.22 to -0.003;  $\beta^{\lambda,FCOV} = 0.68$ , CI: 0.38 to 0.98),  
329 and this was also true at the species level in most cases (Appendix S3). There was evidence  
330 of overall unimodal responses to AGB ( $\Pr(\beta^{\lambda,AGB^2} < 0) = 0.96$ ), albeit with a weak effect (as  
331 confirmed visually), and this was also generally the case for individual species. Some species  
332 (e.g. long-tailed giant rat *Leopoldamys sabanus*, Low's squirrel *Sundasciurus lowii*, plain  
333 treeshrew *Tupaia longipes* and sambar deer) exhibited stronger threshold responses, in which  
334 increases in abundance with decreasing AGB were not maintained below  $\sim 90$  Mg/ha  
335 (Appendix S3).

336

337 All ecological response trait groups except frugivores showed a negative relationship  
338 between local abundance and AGB (Fig. 5A). The relationships were most strongly negative  
339 in omnivores, small mammals and invasives (Fig. 5A), all groups which are dominated by  
340 murid rodent species. All ecological response trait groups except carnivores and invasives  
341 showed a positive relationship between local abundance and forest cover (Fig. 6A). Mean  
342 carnivore local abundance exhibited a unimodal response curve, being lowest at  $\sim 70\%$  forest  
343 cover (Fig. 6A). This reflects a shift from native forest-dependent predators, including the  
344 yellow-throated marten (*Martes flavigula*) and Sunda clouded leopard (*Neofelis diardi*), to  
345 native and non-native carnivores tolerant of more open habitats, principally the leopard cat  
346 (*Prionailurus bengalensis*), Malay civet (*Viverra zibetha*) and domestic dog (*Canis*  
347 *familiaris*). For the continuous metrics, we also calculated the mean across species of the

348 percentage change in local abundance along the land-use gradient (effectively giving each  
349 species equal weight, irrespective of their absolute abundance). This measure exhibited  
350 similar trends to the mean local abundance of each species group (Figs. 5B and 6B), except  
351 there was stronger evidence in some groups of lower rates of abundance increases, or even  
352 decreases in abundance, at lower values of AGB ( $< 90$  Mg/ha), and there was no evidence of  
353 a recovery in carnivore local abundance at low forest cover. These slight differences arise  
354 because patterns in mean local abundance are determined primarily by abundance shifts in  
355 species with the highest local abundances.

356

357 The summed local biomasses of the dietary functional effects groups were mostly negatively  
358 affected by AGB and, except in the case of vertebrate predation, were positively affected by  
359 forest cover (Appendix S3).

360

#### 361 **4. Discussion**

362 Mammalian relative abundance (controlled for imperfect detection) was conserved, or  
363 increased, from old-growth to logged forest overall, whilst it declined substantially from  
364 forest to oil palm plantations. This was true of mean and summed local abundance, as well as  
365 local biomass. Mammalian relative abundance (mean and summed) and biomass responses to  
366 decreases in local landscape AGB due to logging were positive, albeit weakly unimodal, but  
367 were strongly negative for decreases in local landscape forest cover. It was primarily losses in  
368 forest cover, and not forest degradation, that negatively affected the conservation value of  
369 local landscapes in our study region.

370

371 Few previous studies in the region have investigated abundance responses to land-use  
372 change, but apparent trends across various taxonomic groups (based on uncorrected

373 abundance measures) have usually been similar to our results. Abundance in logged areas has  
374 usually been found to be maintained at a community level (Wells *et al.* 2007; Slade, Mann &  
375 Lewis 2011; Edwards *et al.* 2011), but substantially declines in oil palm plantations (e.g.  
376 Turner & Foster 2008; Edwards *et al.* 2010). However, our study is the first time, to our  
377 knowledge, that a robust assessment of animal relative abundance has been made along the  
378 principal land-use gradient in Southeast Asia.

379

#### 380 4. 1. The conservation value of heavily-degraded forests

381 The evidence overall, taken together with our findings for mammals, increasingly supports  
382 the view that large, contiguous areas of logged forest in Southeast Asia not only conserve  
383 similar levels of species richness to old-growth forest (e.g. Edwards *et al.*, 2014), but also  
384 conserve the community-level abundance of many groups. We note that this was true in our  
385 study even in the absence of any significant spill-over effect from large, continuous areas of  
386 old-growth forest (which were > 20 km away from our logged forest sites). This adds further  
387 emphasis to the calls for increasing recognition of logged forest as an essential part of the  
388 conservation estate (Edwards *et al.* 2011). These degraded forests have been the primary  
389 source of new land for expanding plantations in the region (Margono *et al.* 2014), but could  
390 represent a relatively low opportunity-cost option for conservation, given that much of their  
391 timber value has been extracted (Edwards *et al.* 2014). Our study is also one of the few that  
392 has been undertaken in repeatedly-logged forests (Edwards *et al.* 2011, 2014; Woodcock *et*  
393 *al.* 2011; Struebig *et al.* 2013), and the finding that terrestrial mammal community richness  
394 and abundance is maintained even in these heavily-degraded forests further strengthens the  
395 argument for low-cost conservation in such areas. There are signs that this argument is  
396 gaining traction in the Malaysian state of Sabah, at least, with the government recently  
397 setting-aside > 3,000 km<sup>2</sup> of logged forest for conservation (Reynolds 2012).



398

399 The biggest caveat on the conservation value of heavily-degraded forest is that hunting is  
400 strictly controlled. Bushmeat hunting is widely-practiced in logged-over forests (Bennett &  
401 Gumal 2001), and can lead to local population extirpations of high-value mammal species  
402 (Harrison *et al.* 2016). Brodie *et al.* (2015) found that the effect of hunting on large mammal  
403 occupancy was stronger than that of logging for most of the species investigated. Hunting  
404 pressure was very low across our study sites, due to inaccessibility and cultural factors  
405 (Appendix S1).

406

#### 407 4. 2. A trait-based view of mammal communities under land-use change

408 By assessing the whole terrestrial mammal community, we were also able to go further than  
409 previous studies in the region and assess the relative abundance responses of important sub-  
410 groups of mammals defined by their traits, as well as the potential functional effects of  
411 changes in relative abundance across the community. We found that, for almost all response  
412 trait groups, logged forests retained similar or higher local abundances (mean and summed  
413 across species) and biomasses compared to old-growth forest. This was also true for the local  
414 biomasses of functional effects groups we examined, a finding which is consistent with other  
415 evidence that the functional role of vertebrates increases in logged relative to old-growth  
416 forests (Ewers *et al.* 2015). Moreover, these group-level increases were largely maintained  
417 even at very low levels of AGB in a local landscape, indicative of high levels of logging  
418 disturbance. On the other hand, our results indicate that conversion to oil palm, and  
419 reductions in forest cover, cause declines in the local abundance (mean and summed) and  
420 biomass of almost all the trait-defined sub-groups we examined (not carnivores and  
421 invasives), as well as in the local biomasses of almost all the functional effects groups (not  
422 vertebrate predation).

423

424 Across the mammal sub-groups we assessed, small mammals exhibited the most dramatic  
425 change in relative abundance (in terms of both mean and summed local abundance),  
426 increasing substantially in logged forest, and also in response to declining AGB, similar to  
427 findings elsewhere in tropical forests (Isabirye-Basuta & Kasenene 1987; Lambert, Malcolm  
428 & Zimmerman 2006). This may have important implications for plant recruitment, since  
429 small mammals are significant seed predators in these forests (Wells & Bagchi 2005). For  
430 large mammals, the changes in relative abundance were not as dramatic as for small  
431 mammals, though we note that in this case the change in local biomass was much greater than  
432 the modest change in mean local abundance suggested. Much of this increase in local  
433 biomass was driven by a shift towards herbivore species with a larger body size. An increase  
434 in herbivore biomass will likely have as strong effects on ecosystem functioning as an  
435 increase in the abundance of small mammal seed predators, through changes in seedling  
436 recruitment rates (Harrison *et al.* 2013) and nutrient cycling (Wardle & Bardgett 2004).

437

438 Across the trophic guilds, we found that omnivores increased markedly in logged compared  
439 to old-growth forest, perhaps because wide dietary breadth confers dietary flexibility. This is  
440 likely the case for most of the omnivorous species in our dataset, including the murid rodents,  
441 bearded pig (*Sus barbatus*) and sun bear (*Helarctos malayanus*).

442

443 For insectivores, some studies on birds have shown a disproportionate sensitivity to  
444 disturbance for this guild (Gray *et al.* 2007). We found that mammalian insectivores  
445 increased in logged compared to old-growth forest. The abundance responses of insects, and  
446 invertebrates more generally, to logging is poorly known in Southeast Asia, but we note that,  
447 at our study sites, invertebrate biomass is apparently higher in logged forest compared to old-

448 growth forest (Ewers *et al.* 2015), potentially indicating that food resources for insectivorous  
449 mammals are higher.

450

451 For carnivores, the increase from old-growth to logged forest we observed would be expected  
452 based on a numerical response to the increased abundance of vertebrate prey. Most of the  
453 carnivores we studied, and in particular the felids, focus on mammal prey such as murid  
454 rodents (Grassman *et al.* 2005).

455

456 Frugivory is a trait which has often been associated with an increased susceptibility to  
457 disturbance (Gray *et al.* 2007), but it is not clear whether logging consistently causes a  
458 decline in fruit availability or not (e.g. Wong, 1986; Heydon & Bulloh, 1997; Munshi-South  
459 *et al.*, 2007). Certainly, some key fruiting resources such as hemi-epiphytic figs are often  
460 much reduced after logging (Lambert 1991), but the availability of small fruit on lianas and  
461 understorey shrubs might increase in gaps or along edges (Davies *et al.* 2001). Frugivores  
462 exhibited no change in relative abundance from old-growth to logged forest, but modelling  
463 using the continuous AGB metric revealed a modest decline in relative abundance with  
464 increasing logging disturbance. We note, however, that the summed local biomass of all  
465 species engaging in fruit-eating did not decline, suggesting frugivory as a function may be  
466 resilient to logging, even though specialist frugivores do not fare as well as other groups.

467

468 Finally, of crucial conservation relevance, we found that the relative abundance of high  
469 conservation concern species was retained in logged forests, and that this group was resilient  
470 even to high intensities of logging (low levels of AGB) in a given local landscape. We should  
471 emphasise, however, that this does not necessarily mean that high conservation concern  
472 species would persist in hypothetical landscapes consisting of homogeneously low AGB

473 areas; AGB values refer to an average over a local landscape, and will contain some patches  
474 of less intensively logged forest, as well as areas that are heavily-disturbed.

475

#### 476 4. 3. The promise of High Carbon Stock forest for conservation

477 Recent “zero deforestation” pledges within the palm oil industry represent an important  
478 positive step towards the increased conservation of heavily-disturbed forests. Removing  
479 deforestation from supply chains will, in practice, require a consistent definition of what  
480 constitutes a forest, and current dialogue has so far focussed on a carbon-based definition, in  
481 particular a threshold of  $\geq 35\text{-}50$  MgC/ha to define HCS forest (HCS Approach Steering  
482 Group 2015; Raison *et al.* 2015). This is equivalent to an AGB of  $\sim 75\text{-}100$  Mg/ha (assuming  
483 that carbon constitutes 47% of live tree biomass; Martin & Thomas, 2011), which could, if  
484 our findings apply more broadly in the region, yield major conservation benefits for  
485 mammals over the business-as-usual. Indeed, none of the mammal sub-groups we assessed,  
486 apart from frugivores, showed evidence of substantial relative abundance declines in forest  
487 with low AGB, suggesting that an even lower threshold for delimiting HCS could yield even  
488 larger conservation benefits. We emphasise, however, that the conservation potential of HCS  
489 forests for mammals will only be realized with additional investment to manage hunting  
490 pressure.

491

492 An important uncertainty remains surrounding the patch size at which HCS forest will be  
493 delimited in practice. We modelled relative abundance responses to AGB within 500 m  
494 buffers, but clearly this patch size is insufficient to maintain viable mammal populations. The  
495 conservation value of HCS forest set-aside will also lie in its spatial extent and connectivity,  
496 not just in the intensity of local logging disturbance.

497

498 4. 4. Mammal conservation in oil palm landscapes

499 Our conclusions concerning the conservation potential of oil palm are less optimistic.  
500 Although the plantations in which we sampled may represent something of a best-case  
501 scenario for oil palm, with relatively high levels of landscape forest cover and relatively low  
502 levels of hunting, our modelling of mammal relative abundance as a function of forest cover  
503 indicates only a very limited potential for conservation gains by attempting a land-sharing,  
504 ‘wildlife-friendly’ approach (e.g. Koh, Levang & Ghazoul 2009) to this land-use. Increases in  
505 local landscape forest cover from 0 to 30%, the likely range which could realistically be  
506 manipulated in oil palm landscapes, resulted in very limited relative abundance increases  
507 across species groups and across most individual species within the oil palm crop, suggesting  
508 only a limited degree of spill-over from remnant forest patches. Among trophic guilds, only  
509 carnivores showed some resilience to decreases in forest cover, but this was in large part  
510 driven by increases in free-ranging domestic dogs, which are considered a detrimental  
511 invasive species across Asian landscapes (Hughes & Macdonald 2013). We did not sample  
512 remnant forest fragments within the oil palm, but it is unlikely that the abundance and  
513 richness of mammals in these areas would approach that of contiguous forest (Bernard *et al.*  
514 2014), even if individuals present in the oil palm crop itself were also counted. Overall, this  
515 indicates that a land-sparing approach might better serve mammal conservation in the region,  
516 in which companies are encouraged to invest in the off-site conservation of large, contiguous  
517 forest areas (Edwards *et al.* 2010), rather than attempting to increase mammal populations  
518 within their plantations by retaining small forest patches. As a caveat to this, there may be the  
519 potential for ‘win-win’ solutions for both conservation and oil palm yield, such as in the bio-  
520 control of pest species, and in this case on-site conservation activities should be encouraged  
521 (Foster *et al.* 2011). In particular, the high relative abundance of leopard cats we found within

522 the oil palm crop, and the low relative abundance of invasive murid rodents, suggests a  
523 possible role for this species in bio-control.

524

#### 525 4. 5. Conclusions

526 Across a large assemblage of Southeast Asian mammal species, we have shed light on the  
527 contrasting relative abundance responses to logging and conversion to oil palm. We have also  
528 uncovered the relative abundance responses to the continuous metrics of logging intensity  
529 and forest cover loss. These results have direct relevance for conservation and management at  
530 local scales. Specifically, they suggest that conservation efforts should be directed at  
531 safeguarding all remaining forest in the region, both old-growth and logged forests alike, and  
532 that multiple-use landscapes (consisting of oil palm and small forest patches) will not be  
533 effective for conservation.

534

535 The hierarchical modelling approach that we used, which can integrate data from multiple  
536 sources, could be applied to other taxonomic groups and other land-use types. This could  
537 pave the way for more robust biodiversity forecasting and more effective decision-making in  
538 the face of biodiversity trade-offs across land-use.

539

#### 540 **Acknowledgements**

541 We are grateful to Yayasan Sabah, Benta Wawasan, Sabah Softwoods, the Sabah Forestry  
542 Department and the Maliau Basin Management Committee for allowing access to field sites,  
543 and to the Economic Planning Unit of Malaysia and Sabah Biodiversity Council for  
544 providing research permission. Fieldwork would not have been possible without the efforts of  
545 a great number of people and institutions, in particular the SAFE Project field staff, the Royal  
546 Society South East Asia Rainforest Research Programme, Glen Reynolds, Edgar Turner,

547 MinSheng Khoo, Leah Findlay, Jeremy Cusack, Matthew Holmes, Faye Thompson, Jack  
548 Thorley and Jessica Haysom. We also thank Luke Gibson and two anonymous reviewers for  
549 their constructive comments on the manuscript. This work made use of the Imperial College  
550 High Performance Computing facility. Full funding was provided by the Sime Darby  
551 Foundation.

552

### 553 **Supporting Information**

554 **Appendix S1.** Supplementary methods.

555 **Appendix S2.** Model code in BUGS (Bayesian inference Using Gibbs Sampling) language.

556 **Appendix S3.** Supplementary results.

557

### 558 **References**

559 Archaux, F., Henry, P.-Y. & Gimenez, O. (2012) When can we ignore the problem of  
560 imperfect detection in comparative studies? *Methods in Ecology and Evolution*, **3**, 188–  
561 194.

562 Asner, G.P., Rudel, T.K., Aide, T.M., Defries, R. & Emerson, R. (2009) A contemporary  
563 assessment of change in humid tropical forests. *Conservation Biology*, **23**, 1386–1395.

564 Barnes, A.D., Jochum, M., Mumme, S., Haneda, N.F., Farajallah, A., Widarto, T.H. & Brose,  
565 U. (2014) Consequences of tropical land use for multitrophic biodiversity and ecosystem  
566 functioning. *Nature Communications*, **5**, 5351.

567 Bennett, E. & Gumal, M. (2001) The inter-relationships of commercial logging, hunting and  
568 wildlife in Sarawak, and recommendations for forest management. *The cutting edge:  
569 conserving wildlife in logged tropical forest* (eds R. Fimbel), A. Grajal), & J.  
570 Robinson), pp. 359–374. Columbia University Press.

571 Bernard, H., Baking, E.L., Giordano, A.J., Wearn, O.R., Hamid, A. & Ahmad, A.H. (2014)

572 Terrestrial mammal species richness and composition in three small forest patches  
573 within an oil palm landscape in Sabah, Malaysian Borneo. *Mammal Study*, **39**, 141–154.

574 Berry, N.J., Phillips, O.L., Ong, R.C. & Hamer, K.C. (2008) Impacts of selective logging on  
575 tree diversity across a rainforest landscape: the importance of spatial scale. *Landscape*  
576 *Ecology*, **23**, 915–929.

577 Berry, N.J., Phillips, O.L., Ong, R.C. & Hamer, K.C. (2010) The high value of logged  
578 tropical forests: lessons from northern Borneo. *Biodiversity & Conservation*, **4**, 985–997.

579 Brodie, J.F., Giordano, A.J., Zipkin, E.F., Bernard, H., Mohd-Azlan, J. & Ambu, L. (2015)  
580 Correlation and persistence of hunting and logging impacts on tropical rainforest  
581 mammals. *Conservation Biology*, **29**, 110–121.

582 Cushman, S.A., Gutzweiler, K., Evans, J.S. & Mcgarigal, K. (2010) The gradient paradigm: a  
583 conceptual and analytical framework for landscape ecology. *Spatial Complexity,*  
584 *Informatics, and Wildlife Conservation* (eds S.A. Cushman), & F. Huettmann), pp. 83–  
585 108. Springer Japan, Tokyo.

586 Davies, G., Heydon, M., Leader-Williams, N., MacKinnon, J. & Newing, H. (2001) The  
587 effects of logging on tropical forest ungulates. *The cutting edge: conserving wildlife in*  
588 *logged tropical forest* (eds R.A. Fimbel, A. Grajal & J.G. Robinson), pp. 93–124.  
589 Columbia University Press, New York, USA.

590 Edwards, D.P., Hodgson, J.A., Hamer, K.C., Mitchell, S.L., Ahmad, A.H., Cornell, S.J. &  
591 Wilcove, D.S. (2010) Wildlife-friendly oil palm plantations fail to protect biodiversity  
592 effectively. *Conservation Letters*, **3**, 236–242.

593 Edwards, D.P., Larsen, T.H., Docherty, T.D.S., Ansell, F.A., Hsu, W.W., Derhé, M.A.,  
594 Hamer, K.C. & Wilcove, D.S. (2011) Degraded lands worth protecting: the biological  
595 importance of Southeast Asia’s repeatedly logged forests. *Proceedings of the Royal*  
596 *Society of London Series B: Biological Sciences*, **278**, 82–90.



597 Edwards, D.P., Magrath, A., Woodcock, P., Ji, Y., Lim, N.T.-L., Edwards, F.A., Larsen,  
598 T.H., Hsu, W.W., Benedick, S., Vun Khen, C., Chung, A.Y.C., Reynolds, G., Fisher, B.,  
599 Laurance, W.F., Wilcove, D.S., Hamer, K.C. & Yu, D.W. (2014) Selective-logging and  
600 oil palm: multitaxon impacts, biodiversity indicators, and trade-offs for conservation  
601 planning. *Ecological Applications*, **24**, 2029–2049.

602 Efford, M. & Dawson, D. (2012) Occupancy in continuous habitat. *Ecosphere*, **3**, 1–15.

603 Ewers, R.M., Boyle, M.J.W., Gleave, R.A., Plowman, N.S., Benedick, S., Bernard, H.,  
604 Bishop, T.R., Bakhtiar, E.Y., Chey, V.K., Chung, A.Y.C., Davies, R.G., Edwards, D.P.,  
605 Eggleton, P., Fayle, T.M., Hardwick, S.R., Homathevi, R., Kitching, R.L., Khoo, M.S.,  
606 Luke, S.H., March, J.J., Nilus, R., Pfeifer, M., Rao, S. V, Sharp, A.C., Snaddon, J.L.,  
607 Stork, N.E., Struebig, M.J., Wearn, O.R., Yusah, K.M. & Turner, E.C. (2015) Logging  
608 cuts the functional importance of invertebrates in tropical rainforest. *Nature*  
609 *Communications*, **6**, 6836.

610 Ewers, R.M., Didham, R.K., Fahrig, L., Ferraz, G., Hector, A., Holt, R.D., Kapos, V.,  
611 Reynolds, G., Sinun, W., Snaddon, J.L. & Turner, E.C. (2011) A large-scale forest  
612 fragmentation experiment: the Stability of Altered Forest Ecosystems Project.  
613 *Philosophical Transactions of the Royal Society of London. Series B, Biological*  
614 *Sciences*, **366**, 3292–3302.

615 Foster, W.A., Snaddon, J.L., Turner, E.C., Fayle, T.M., Cockerill, T.D., Ellwood, M.D.F.,  
616 Broad, G.R., Chung, A.Y.C., Eggleton, P., Khen, C.V. & Yusah, K.M. (2011)  
617 Establishing the evidence base for maintaining biodiversity and ecosystem function in  
618 the oil palm landscapes of South East Asia. *Philosophical transactions of the Royal*  
619 *Society of London. Series B, Biological sciences*, **366**, 3277–91.

620 Gaveau, D.L.A., Sloan, S., Molidena, E., Yaen, H., Sheil, D., Abram, N.K., Ancrenaz, M.,  
621 Nasi, R., Quinones, M., Wielaard, N. & Meijaard, E. (2014) Four decades of forest

622 persistence, clearance and logging on Borneo (ed K Bawa). *Plos One*, **9**, e101654.

623 Gibson, L., Lee, T.M., Koh, L.P., Brook, B.W., Gardner, T.A., Barlow, J., Peres, C.A.,  
624 Bradshaw, C.J.A., Laurance, W.F., Lovejoy, T.E. & Sodhi, N.S. (2011) Primary forests  
625 are irreplaceable for sustaining tropical biodiversity. *Nature*, **478**, 378–381.

626 Grassman, L.I., Tewes, M.E., Silvy, N.J. & Kreetiyutanont, K. (2005) Ecology of three  
627 sympatric felids in a mixed evergreen forest in north-central Thailand. *Journal of*  
628 *Mammalogy*, **86**, 29–38.

629 Gray, M.A., Baldauf, S.L., Mayhew, P.J. & Hill, J.K. (2007) The response of avian feeding  
630 guilds to tropical forest disturbance. *Conservation Biology*, **21**, 133–41.

631 Harrison, R.D., Tan, S., Plotkin, J.B., Slik, F., Detto, M., Brenes, T., Itoh, A. & Davies, S.J.  
632 (2013) Consequences of defaunation for a tropical tree community. *Ecology Letters*, **16**,  
633 687–94.

634 Harrison, R. D., Sreekar, R., Brodie, J. F., Brook, S., Luskin, M., O'Kelly, H., Rao, M.,  
635 Scheffers, B. & Velho, N. (2016) Impacts of hunting on tropical forests in Southeast  
636 Asia. *Conservation Biology*, **30**, 972-981.

637 HCS Approach Steering Group. (2015) *The High Carbon Stock Approach: No Deforestation*  
638 *in Practice. Version 1.0*.

639 Heydon, M. & Bulloh, P. (1997) Mousedeer densities in a tropical rainforest: the impact of  
640 selective logging. *Journal of Applied Ecology*, **34**, 484-496.

641 Hughes, J. & Macdonald, D.W. (2013) A review of the interactions between free-roaming  
642 domestic dogs and wildlife. *Biological Conservation*, **157**, 341–351.

643 Isabirye-Basuta, G. & Kasenene, J.M. (1987) Small rodent populations in selectively felled  
644 and mature tracts of Kibale Forest, Uganda. *Biotropica*, **19**, 260–266.

645 Koh, L.P., Levang, P. & Ghazoul, J. (2009) Designer landscapes for sustainable biofuels.  
646 *Trends in Ecology and Evolution*, **24**, 431–438.

647 Lambert, F. (1991) The conservation of fig-eating birds in Malaysia. *Biological*  
648 *Conservation*, **58**, 31–40.

649 Lambert, T.D., Malcolm, J.R. & Zimmerman, B.L. (2006) Amazonian small mammal  
650 abundances in relation to habitat structure and resource abundance. *Journal of*  
651 *Mammalogy*, **87**, 766–776.

652 Luskin, M.S. & Potts, M.D. (2011) Microclimate and habitat heterogeneity through the oil  
653 palm lifecycle. *Basic and Applied Ecology*, **12**, 540–551.

654 MacKenzie, D.I., Nichols, J.D., Royle, J.A., Pollock, K.P., Bailey, L.L. & Hines, J.E. (2006)  
655 *Occupancy Estimation and Modeling: Inferring Patterns and Dynamics of Species*  
656 *Occurrence*. Academic Press, New York.

657 Margono, B.A., Potapov, P. V., Turubanova, S., Stolle, F. & Hansen, M.C. (2014) Primary  
658 forest cover loss in Indonesia over 2000–2012. *Nature Climate Change*, **4**, 730–735.

659 Martin, A.R. & Thomas, S.C. (2011) A reassessment of carbon content in tropical trees. *PLoS*  
660 *ONE*, **6**, e23533.

661 Munshi-South J., Emmons, L. & Bernard, H. Behavioral monogamy and fruit availability in  
662 the large treeshrew (*Tupaia tana*) in Sabah, Malaysia. (2007) *Journal of Mammalogy*,  
663 **88**, 1427-1438.

664 Newbold, T., Hudson, L.N., Phillips, H.R.P., Hill, S.L.L., Contu, S., Lysenko, I., Blandon,  
665 A., Butchart, S.H.M., Booth, H.L., Day, J., Palma, A. De, Harrison, M.L.K.,  
666 Kirkpatrick, L., Pynegar, E., Robinson, A., Simpson, J., Mace, G.M., Scharlemann,  
667 J.P.W. & Purvis, A. (2014) A global model of the response of tropical and sub-tropical  
668 forest biodiversity to anthropogenic pressures. *Proceedings of the Royal Society of*  
669 *London Series B: Biological Sciences*, **281**, 20141371.

670 Payne, J., Francis, C.M. & Phillipps, K. (2007) *A Field Guide to the Mammals of Borneo*, 4th  
671 ed. The Sabah Society, Kota Kinabalu.

672 Phalan, B., Onial, M., Balmford, A. & Green, R.E. (2011) Reconciling food production and  
673 biodiversity conservation: land sharing and land sparing compared. *Science*, **333**, 1289–  
674 91.

675 Plummer, M. (2013) JAGS: Just Another Gibbs Sampler, version 3.4.0.

676 Raison, J., Atkinson, P., Chave, J., DeFries, R., Joo, G.K., Joosten, H., Navratil, P. & Siegert,  
677 F. (2015) *HCS Science Study: Draft Synthesis Report*.

678 Reynolds, G. (2012) Major expansion of Sabah’s fully protected forests announced. URL:  
679 <http://www.searrip.org/2012/06/directors-monthly-update-june-2012> (accessed July  
680 2015).

681 Royle, J.A. & Dorazio, R.M. (2008) *Hierarchical Modeling and Inference in Ecology: The*  
682 *Analysis of Data from Populations, Metapopulations and Communities*. Academic Press.

683 Royle, J. & Nichols, J. (2003) Estimating abundance from repeated presence-absence data or  
684 point counts. *Ecology*, **84**, 777–790.

685 Scales, B.R. & Marsden, S.J. (2008) Biodiversity in small-scale tropical agroforests: a review  
686 of species richness and abundance shifts and the factors influencing them.  
687 *Environmental Conservation*, **35**, 160–172.

688 Slade, E.M., Mann, D.J. & Lewis, O.T. (2011) Biodiversity and ecosystem function of  
689 tropical forest dung beetles under contrasting logging regimes. *Biological Conservation*,  
690 **144**, 166–174.

691 Sodhi, N.S., Lee, T.M., Koh, L.P. & Brook, B.W. (2009) A meta-analysis of the impact of  
692 anthropogenic forest disturbance on Southeast Asia’s biotas. *Biotropica*, **41**, 103–109.

693 Struebig, M.J., Turner, A., Giles, E., Lasmana, F., Tollington, S., Bernard, H. & Bell, D.  
694 (2013) Quantifying the biodiversity value of repeatedly logged rainforests: gradient and  
695 comparative approaches from Borneo. *Advances in Ecological Research*, **48**, 183–224.

696 Tobler, M.W., Hartley, A.Z., Carrillo-Percegué, S.E. & Powell, G.V.N. (2015)

697       Spatiotemporal hierarchical modelling of species richness and occupancy using camera  
698       trap data. *Journal of Applied Ecology*, **52**, 413–421.

699   Turner, E.C. & Foster, W.A. (2008) The impact of forest conversion to oil palm on arthropod  
700       abundance and biomass in Sabah, Malaysia. *Journal of Tropical Ecology*, **25**, 23–30.

701   Vié, J., Hilton-Taylor, C. & Stuart, S. (2009) *Wildlife in a Changing World - An Analysis of*  
702       *the 2008 IUCN Red List of Threatened Species*. IUCN, Gland, Switzerland.

703   Wardle, D.A. & Bardgett, R.D. (2004) Human-induced changes in large herbivorous  
704       mammal density: the consequences for decomposers. *Frontiers in Ecology and the*  
705       *Environment*, **2**, 145–153.

706   Wearn, O.R., Rowcliffe, J.M., Carbone, C., Bernard, H. & Ewers, R.M. (2013) Assessing the  
707       status of wild felids in a highly-disturbed commercial forest reserve in Borneo and the  
708       implications for camera trap survey design. *Plos One*, **8**, e77598.

709   Wells, K. & Bagchi, R. (2005) Eat in or take away - seed predation and removal by rats  
710       (Muridae) during a fruiting event in a dipterocarp rainforest. *Raffles Bulletin of Zoology*,  
711       **53**, 281–286.

712   Wells, K., Kalko, E.K.V., Lakim, M.B. & Pfeiffer, M. (2007) Effects of rain forest logging  
713       on species richness and assemblage composition of small mammals in Southeast Asia.  
714       *Journal of Biogeography*, **34**, 1087–1099.

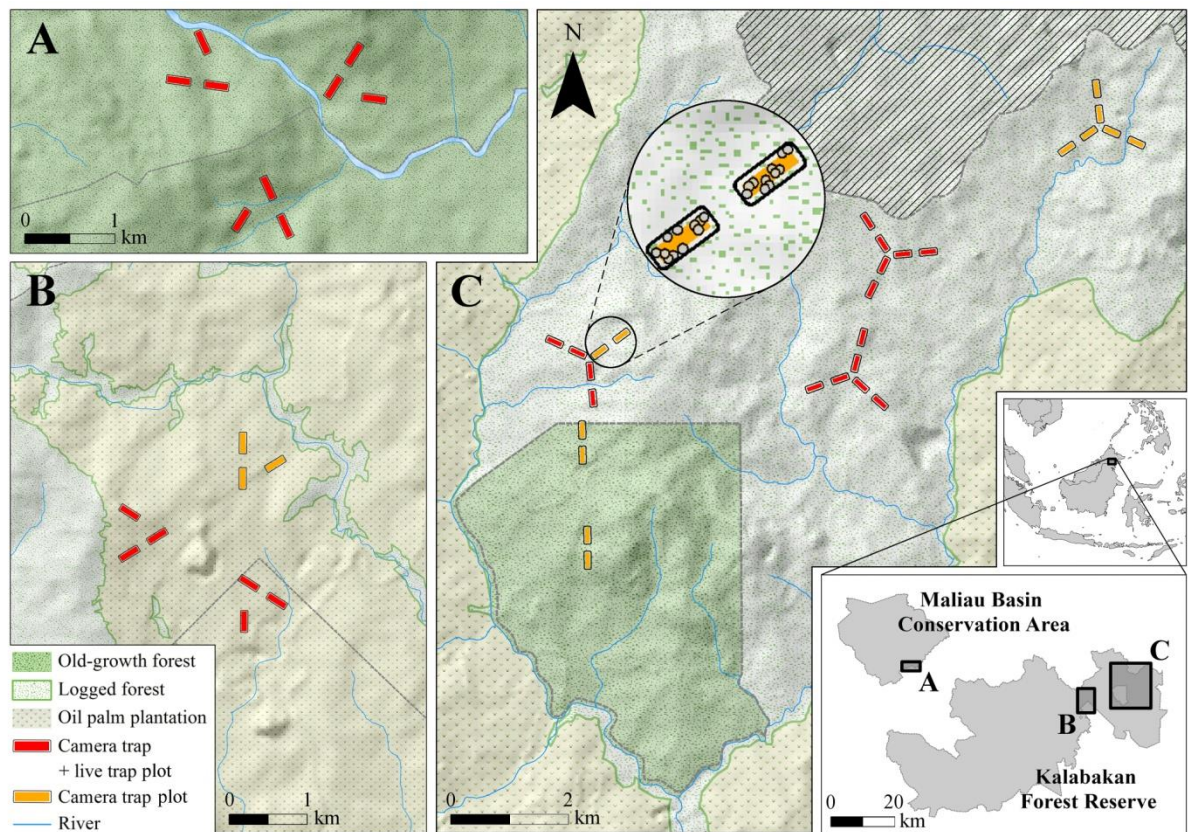
715   Wong, M. (1986) Trophic organization of understory birds in a Malaysian dipterocarp forest.  
716       *Auk*, **103**, 100–116.

717   Woodcock, P., Edwards, D.P., Fayle, T.M., Newton, R.J., Khen, C.V., Bottrell, S.H. &  
718       Hamer, K.C. (2011) The conservation value of South East Asia's highly degraded  
719       forests: evidence from leaf-litter ants. *Philosophical Transactions of the Royal Society of*  
720       *London. Series B, Biological sciences*, **366**, 3256–64.

721   Yamaura, Y., Andrew Royle, J., Kuboi, K., Tada, T., Ikeno, S. & Makino, S. (2011)

722 Modelling community dynamics based on species-level abundance models from  
723 detection/nondetection data. *Journal of Applied Ecology*, **48**, 67–75.  
724

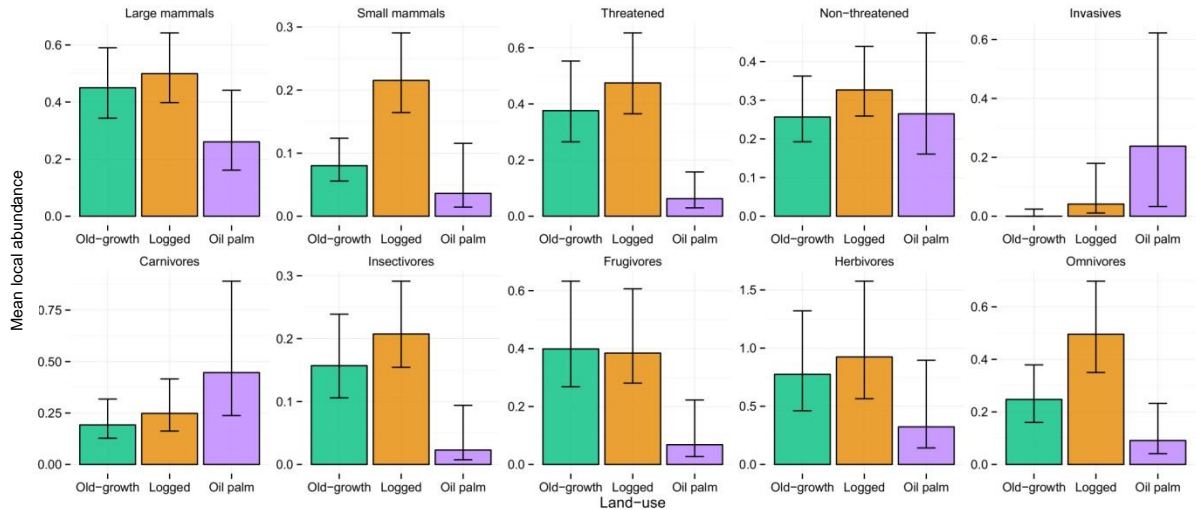
725 **Figures**



726

727 **Fig. 1.** Sampling design across a gradient of land-use intensities in Borneo, showing the plots  
728 sampled using both camera traps and live traps (in red) and plots sampled only with camera  
729 traps (in orange). The Kalabakan Forest Reserve connects to an extensive (>1 million ha)  
730 area of contiguous logged forest to the north (hatched area). Insets show: an example of how  
731 cameras were arranged within plots; the location of the study within insular Southeast Asia,  
732 and the spatial proximity of panels A to C within south-east Sabah, Malaysia. Land-cover  
733 surrounding the Maliau Basin and Kalabakan Forest Reserve (white areas in the inset map)  
734 was a mosaic of logged forest and plantations.

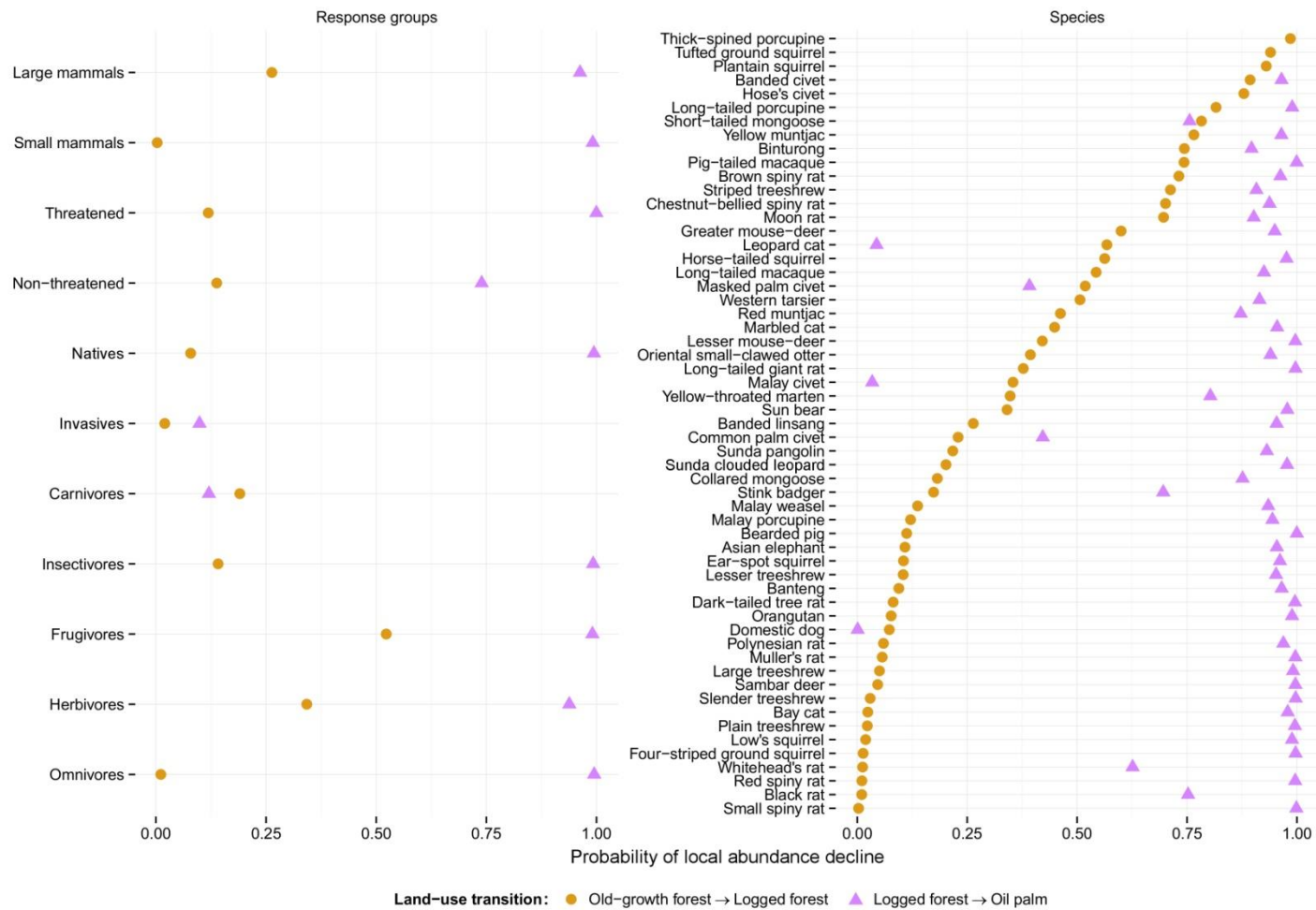
735



736

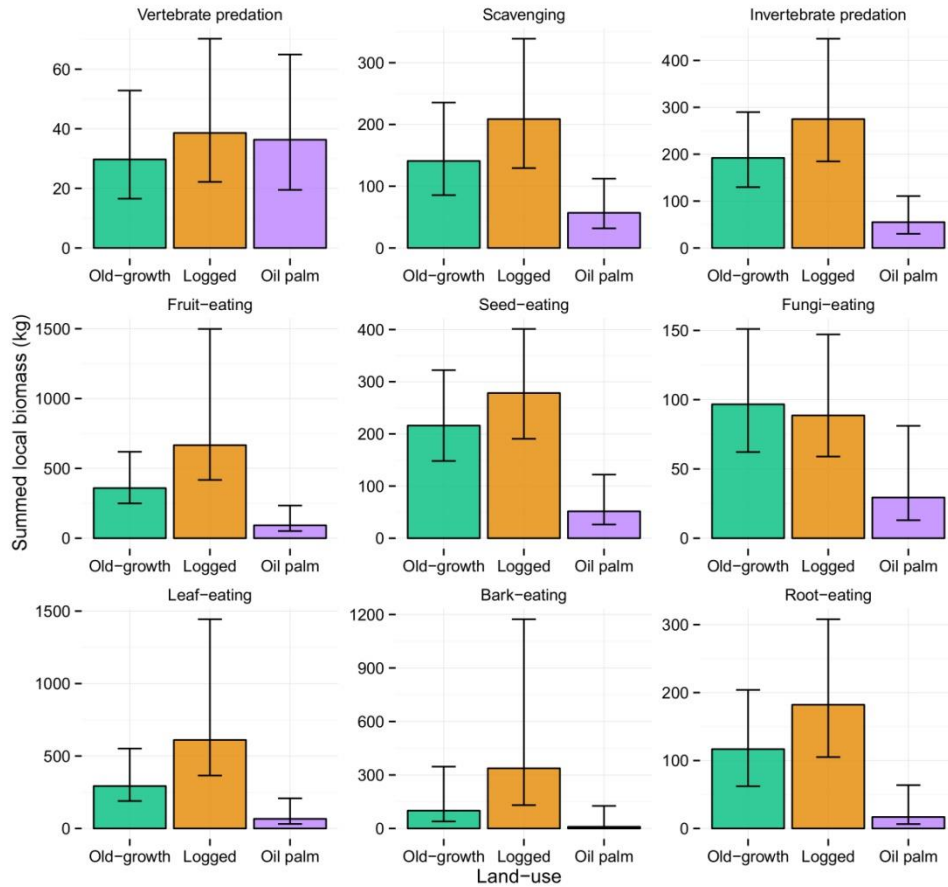
737 **Fig. 2.** Local abundance of mammals (average across species) across land-use categories,  
 738 partitioned by ecological response groups defined by body size (large and small mammals),  
 739 conservation status (threatened, non-threatened), native status (only invasives shown) and  
 740 trophic guild (five mutually-exclusive feeding guilds). Error bars indicate 90% credible  
 741 intervals.





742

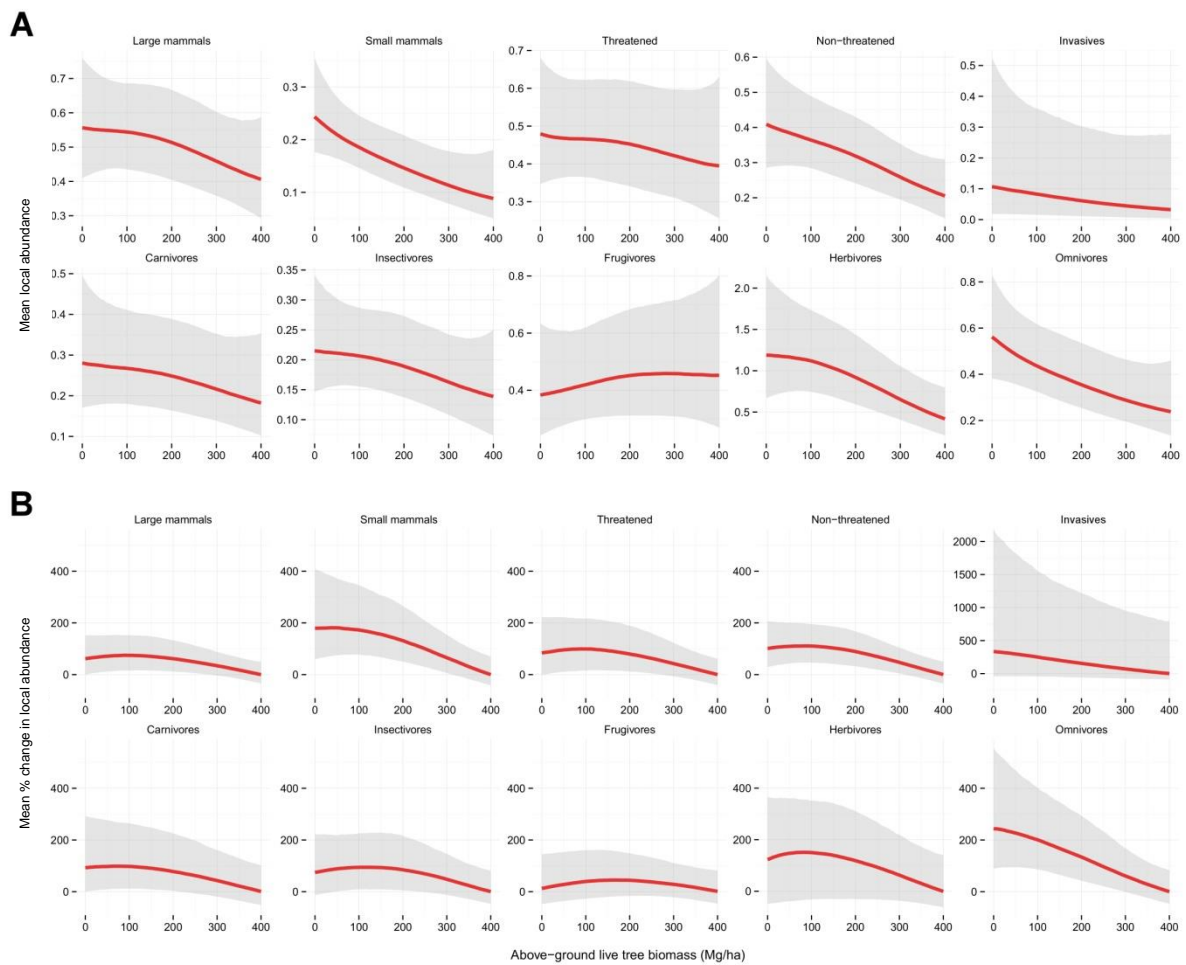
743 **Fig. 3.** Probabilities of a decline in local abundance from old-growth to logged forest (orange) and from logged forest to oil palm (purple), for  
 744 each ecological response group and each mammal species. We did not calculate the probability of decline from logged forest to oil palm for four  
 745 species which were not recorded in logged forest.



746

747 **Fig. 4.** Summed local biomass of mammals (a relative biomass measure) across land-use  
 748 categories, partitioned by functional effects groups based on diet. Error bars indicate 90%  
 749 credible intervals.

750



751

752

**Fig. 5.** Local abundance (A) and percentage change in local abundance (B) averaged across

753

mammal species, as a function of above-ground live tree biomass in a given local landscape.

754

Species are partitioned by ecological response groups defined by body size, conservation

755

status, native status (only invasives shown) and trophic guild. Percentage change refers to the

756

change relative to the abundance at AGB values typical of intact forest (400 Mg/ha). Forest

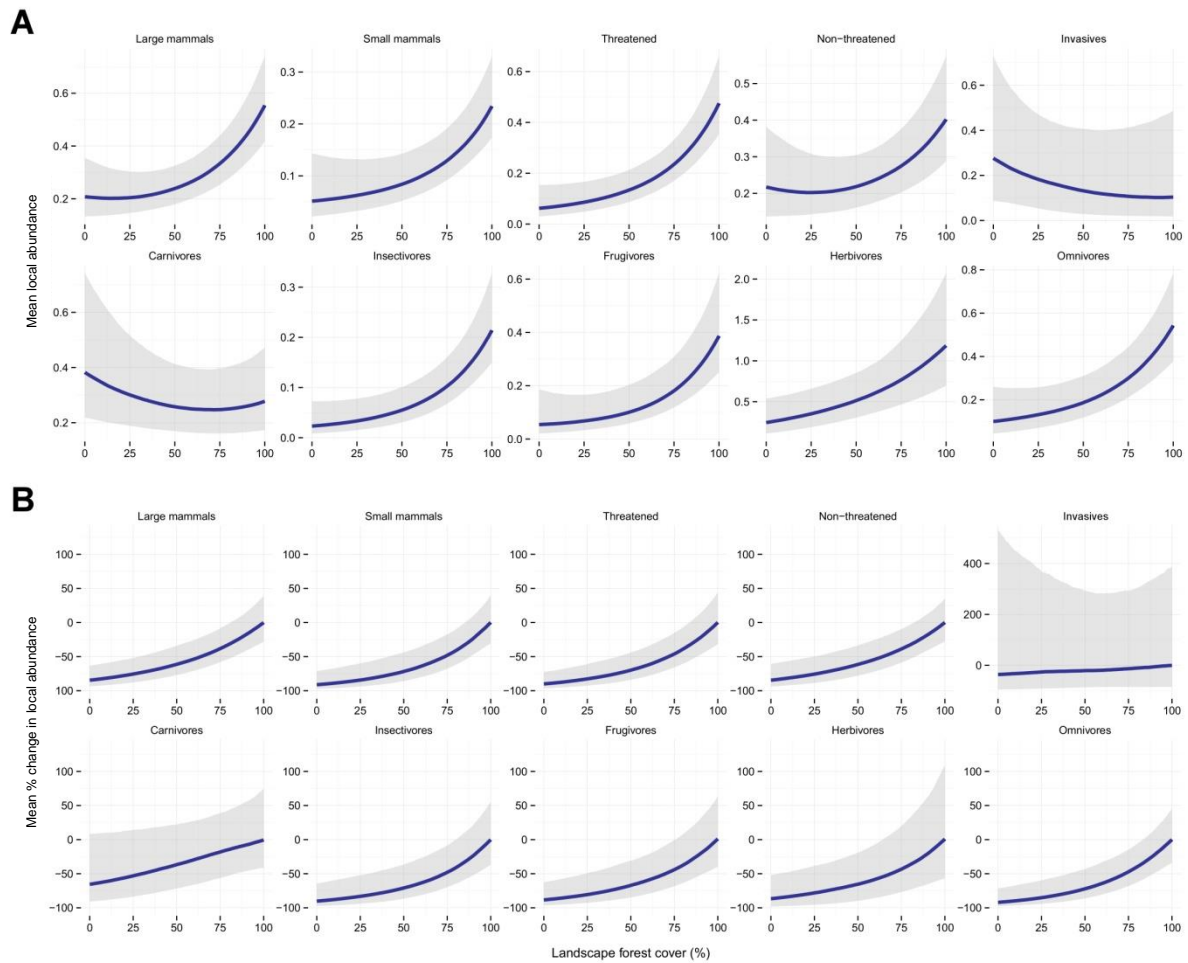
757

cover was fixed at 100%. 90% credible intervals (in grey) indicate uncertainty surrounding

758

median estimates (red line).

759



760

761

**Fig. 6.** Local abundance (A) and percentage change in local abundance (B) averaged across

762

mammal species, as a function of forest cover in a given local landscape. Species are

763

partitioned by ecological response groups defined by body size, conservation status, native

764

status (only invasives shown) and trophic guild. Percentage change refers to the change in

765

abundance as forest cover decreases from 100%. Above-ground live tree biomass was fixed

766

at the average across oil palm locations. 90% credible intervals (in grey) indicate uncertainty

767

surrounding median estimates (red line).

768

769