

1 **Logged tropical forests have amplified and diverse ecosystem energetics**

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16 **Old growth tropical forests are widely recognised as immensely important for their biodiversity and**

17 **high biomass¹. Conversely, selectively logged tropical forests are usually characterised as degraded**

18 **ecosystems². However, whether logging results in a degradation in ecosystem functions is less clear:**

19 **shifts in the strength and resilience of key ecosystem processes in large suites of species have rarely been**

20 **assessed in an ecologically integrated and quantitative framework. Here we adopt an ecosystem**

21 **energetics lens to gain new insight into the impacts of tropical forest disturbance on a key integrative**

22 **aspect of ecological function: food pathways and community structure of birds and mammals. We focus**

23 **on a gradient spanning old growth and logged forests and oil palm plantations in Borneo. In logged**

24 **forest there is a 2.5-fold increase in total resource consumption by both birds and mammals compared to**

25 **old growth forests, likely driven by greater resource accessibility and vegetation palatability. Most major**

26 **energetic pathways maintain high species diversity and redundancy, implying maintained resilience.**

27 **Conversion of logged forest into oil palm plantation results in the collapse of most energetic pathways.**
28 **Far from being degraded ecosystems, even heavily logged forests can be vibrant and diverse ecosystems**
29 **with enhanced levels of ecological function.**

30

31 Human-modified forests, such as selectively logged forests, are often characterised as degraded
32 ecosystems because of their altered structure and low biomass. The concept of ecosystem degradation
33 can be a double-edged sword. It rightly draws attention to the conservation value of old growth systems
34 and the importance of ecosystem restoration. However, it can also suggest that human-modified
35 ecosystems are of low ecological value and therefore, in some cases, suitable for conversion to
36 agriculture (such as oil palm plantations) and other land uses³⁻⁵.

37

38 Selectively logged and other forms of structurally altered forests are becoming the prevailing vegetation
39 cover in much of the tropical forest biome². Such disturbance leads to a frequent decline in old growth
40 specialist species¹, and also in non-specialist species in some contexts⁶⁻⁸. However, species-focused
41 biodiversity metrics are only one measure of ecosystem vitality and functionality, and rarely consider
42 the collective role that suites of species play in maintaining ecological functions⁹.

43

44 An alternative approach is to focus on the energetics of key taxonomic groups, and the number and
45 relative dominance of species contributing to each energetic pathway. Energetic approaches to
46 examining ecosystem structure and function have a long history in ecosystem ecology¹⁰. Virtually all
47 ecosystems are powered by a cascade of captured sunlight through an array of autotroph tissues and into
48 hierarchical assemblages of herbivores, carnivores and detritivores. Energetic approaches shine light on
49 the relative significance of energy flows among key taxa and provide insight into the processes that
50 shape biodiversity and ecosystem function. The common currency of energy enables diverse guilds and
51 taxa to be compared in a unified and physically meaningful manner: dominant energetic pathways can

52 be identified, and the resilience of each pathway to the loss of individual species can be assessed.
53 Quantitative links can then be made between animal communities and the plant-based ecosystem
54 productivity on which they depend. The magnitude of energetic pathways in particular animal groups
55 can often be indicators of key associated ecosystem processes, such as nutrient cycling, seed dispersal and
56 pollination, or trophic factors such as intensity of predation pressure or availability of resource supply,
57 all unified under the common metric of energy flux^{11,12}.

58
59 Energetics approaches have rarely been applied in biodiverse tropical ecosystems because of the range of
60 observations they require¹¹⁻¹³. Such analyses rely on: (i) population density estimates for a very large
61 number of species; (ii) understanding of the diet and feeding behaviour of the species; and (iii) reliable
62 estimation of net primary productivity, NPP. Here, we take advantage of uniquely rich datasets to apply
63 an energetics lens to examine and quantify aspects of the ecological function and vitality of habitats in
64 Sabah, Malaysia, which comprise old growth forests, logged forest and oil palm plantation (Figure 1;
65 ED1). Our approach is to calculate the short-term equilibrium production or consumption rates of food
66 energy by specific species, guilds or taxonomic groups. We focus on three taxonomic groups (plants,
67 birds and mammals) that are frequently used indicators of biodiversity and are relatively well-
68 understood ecologically.

69
70 We ask the following questions: (1) what fraction of primary productivity is consumed by birds and
71 mammals, and how does this vary along the disturbance gradient?; (2) how and why do various food
72 energetic pathways in mammals and birds, and the diversity of species contributing to those pathways,
73 vary along the disturbance gradient? To estimate the density of 104 mammal and 144 bird species in
74 each of the three habitat types, we aggregated data from 882 camera sampling locations (a total of 42,877
75 camera trap-nights), 508 bird point count locations, 1488 small terrestrial mammal trap locations (34058
76 live trap nights) and 336 bat trap locations (Figure 1; ED1). We then calculate Daily Energetic

77 Expenditure for each species based on their body mass, assign each species to a dietary group and
78 calculate total food consumption in energy units. For primary productivity, we relied on 34 plot-years
79 (summation of plots x number of years each plot is monitored) of measurements of the key components
80 of NPP (canopy litterfall, woody growth, fine root production) using the protocols of the Global
81 Ecosystem Monitoring Network ¹⁴⁻¹⁶ across old growth (n=4), logged (n=5) and oil palm (n=1) plots. This
82 dataset encompasses over 14,000 measurements of litterfall, 20,000 tree diameter measurements and
83 2700 fine root samples.

84
85 Overall bird species diversity is maintained across the disturbance gradient and peaks in the logged
86 forest; for mammals there is also a slight increase in the logged forest, followed by rapid decline in the
87 oil palm (Figure 2b, c). Strikingly, both bird and mammal biomass increases substantially (144% and
88 231% respectively) in the logged forest compared to the old growth forest, with mammals contributing
89 ~75% of total (bird plus mammal) biomass in both habitat types (Figure 2b, c).

90
91 The total flow of energy flux through consumption is amplified across all energetic pathways by a factor
92 of 2.5 (2.2-3.0; all ranges reported are 95% confidence intervals) in logged forest relative to old growth
93 forest. In all three habitat types, total energy intake by birds is much greater than by mammals (Figure
94 2d, e; Table ED1). Birds account for 67%, 68% and 90% of the total direct consumption by birds and
95 mammals combined in old growth forests, logged forests and oil palm respectively. Although mammal
96 biomass is higher than bird biomass in the old growth and logged forests, the metabolism per unit mass
97 is much higher in birds because of their small body size; hence in terms of the energetics and
98 consumption rates, the bird community dominates. The total energy intake by birds alone increases by a
99 factor of 2.6 (2.1-3.2) in the logged forest relative to old growth forest. This is mainly driven by a 2.5-
100 fold (1.7-2.8) increase in foliage-gleaning insectivory (the dominant energetic pathway), and most other
101 feeding guilds also show an even larger increase (Figure 2d, 3). However, total bird energy intake in the

102 oil palm drops back to levels similar to those in the old growth forest, with a collapse in multiple guilds.
103 For mammals, there is a similar 2.4-fold (1.9-3.2) increase in total consumption when going from old
104 growth to logged forest, but this declines sharply in oil palm plantation. Most notable is the 5.7-fold
105 (3.2-10.2) increase in the importance of terrestrial mammal herbivores in the logged forests relative to
106 old growth. All four individual old growth forest sites show consistently lower bird and mammal
107 energetics than the logged forests (Figure ED5).

108
109 The fraction of NPP flowing through the bird and mammal communities increases by a factor of 2.1
110 (1.5-3.0) in logged forest relative to old growth forest. There is a modest increase in net primary
111 productivity (NPP) in logged forest relative to old growth (Figure 2a) because increased NPP in patches
112 of relatively intact logged forest is offset by very low productivity in more structurally degraded areas
113 such as former logging platforms^{14,15}. In oil palm plantations, oil palm fruits account for a large
114 proportion of NPP, although a large fraction of these is harvested and removed from the ecosystem¹⁷. As
115 a proportion of NPP, 1.62% (1.35-2.13%) is directly consumed by birds and mammals in the old growth
116 forest; this rises to 3.36% (2.57-5.07%) in the logged forest but drops to 0.89% (0.57-1.44%) in oil palm
117 (Figure 1f, g; Table ED2).

118
119 If all invertebrates consumed are herbivores or detritivores (*i.e.* at a trophic level of 2.0), and trophic
120 efficiency is 10%¹⁰, the total amount of NPP supporting the combined bird and mammal food intake
121 would be 9%, 16% and 5% for old growth forest, logged forest and oil palm respectively. However, if
122 the mean trophic level of consumed invertebrates is 2.5 (*i.e.* a mix of herbivores and predators), the
123 corresponding proportions would be 27%, 51% and 17% (Figure 1f, g). As insectivory is the dominant
124 feeding mode for the avian community, these numbers are dominated by bird diets. For birds in the old
125 growth forests, 0.35% of NPP supports direct herbivory/frugivory, but around 22% of NPP (assumed
126 invertebrate trophic level 2.5) is indirectly required to support insectivory. The equivalent numbers for

127 birds in logged forest are 0.83% and 46%. Hence birds account for a much larger indirect consumption
128 of NPP. Bird diet studies in old growth and logged forest in the region suggest that consumed
129 invertebrates have a mean trophic level of 2.5¹⁸ (K. Sam, unpublished analysis), indicating that the
130 higher-end estimates of indirect NPP consumption (i.e. around 50% in logged forests) are plausible.

131

132 It is interesting to compare such high fractions of NPP to direct estimates of invertebrate herbivory.
133 Scans of tree leaf litter from these forests suggest that just 7.0% of tree canopy leaf area (1-3% of total
134 NPP) is removed by tree leaf herbivory^{14,16}, but such estimates do not include other pathways available
135 to invertebrates, including herbivory of the understory, above- and below-ground sap-sucking, leaf-
136 mining, fruit and wood-feeding, and canopy, litter and ground-layer detritivory. An increase in
137 invertebrate biomass and herbivory in logged forest compared to old growth forest has previously been
138 reported in fogging studies in this landscape¹⁹. Such high levels of consumption of NPP by invertebrates
139 could have implications on ecosystem vegetation biomass production, firstly, suggesting that
140 invertebrate herbivory has a major influence on recovery from logging, and, secondly, that insectivorous
141 bird densities may exert substantial indirect controls on ecosystem recovery.

142

143 The distributions of energy flows among feeding guilds are remarkably stable among habitat types
144 (Figure 3), indicating the amplified energy flows in the logged forests do not distort the overall trophic
145 structure of vertebrate communities. Overall bird diet energetics are dominated by insectivory, which
146 accounts for a strikingly invariant 66%, 63% and 66% of bird energetic consumption in old growth
147 forest, logged forest and oil palm respectively. Foliage-gleaning dominates as a mode of invertebrate
148 consumption in all three habitat types, with frugivory the second most energetically important feeding
149 mode (26%, 27% and 19% respectively). Mammal diet is more evenly distributed across feeding guilds
150 but frugivory (31%, 30%, 30%) and folivory (24%, 38%, 26%) dominate. Small mammal insectivores are
151 probably undersampled (see Methods) so the contribution of mammal insectivory may be slightly

152 greater than that estimated here. The apparent constancy of relative magnitude of feeding pathways
153 across the intact and disturbed ecosystems is noteworthy and not sensitive to plausible shifts in feeding
154 behaviour between habitat types (see supplementary discussion). There is no evidence of a substantial
155 shift in dominant feeding guild: the major feeding pathways present in the old growth forest are
156 maintained in the logged forest.

157

158 When examining change at species level in the logged forests, the largest absolute increases in bird food
159 consumption were in arboreal insectivores and omnivores (Figure 4a, ED2a). In particular, this change
160 was characterised by significant increases in the abundance of bulbul species (*Pycnonotus* spp.). No bird
161 species showed a significant or substantial reduction in overall energy consumption. In the oil palm
162 plantation, total food consumption by birds was less than in logged forests, but similar to old growth
163 forests. However, this was driven by very high abundance of a handful of species, notably a single
164 arboreal omnivore (yellow-vented bulbul *Pycnonotus goiavier*) and three arboreal insectivores
165 (*Mixornis bornensis*, *Rhipidura javanica*, *Copsychus saularis*), whilst energy flows through most bird
166 species were greatly reduced (Figure 4b, ED2b).

167

168 For mammals, the increase in consumption in logged forests is dominated by large terrestrial herbivores
169 increasing by a factor of 5.7 (3.2-10.2), particularly sambar deer (*Rusa unicolor*) and Asian elephant
170 (*Elephas maximus*; Figure 4a, ED2b, ED3), along with small omnivores, predominantly rodents (native
171 spiny rats, non-native black rat; Figure 4). A few rainforest species show a strong decline (e.g. greater
172 mouse deer *Tragulus napu* and brown spiny rat *Maxomys rajah*). In the oil palm, most mammal species
173 collapse (Figure 4b) and the limited consumption is dominated by a few disturbance-tolerant habitat
174 generalists (e.g. red muntjac *Muntiacus muntjak*, black rat *Rattus rattus*, civets), albeit at lower densities
175 than observed in old growth forest (Figure ED2).

176

177 With very few exceptions, the amplified energy flows in logged forest appear to retain the same level of
178 resilience as in old growth forest. The diversity and dominance of species within any pathway can be a
179 measure of the resilience of that pathway to loss of species. We assessed energetic dominance within
180 individual pathways by defining an Energetic Shannon-Wiener index (ESWI) to examine distribution of
181 energy flow across species; low ESWI indicates a pathway with high dependence on a few species and
182 hence potential vulnerability (Figure 3). The overall ESWI across guilds does not differ between the old
183 growth and logged forest ($t_{2,34} = -0.363$, $p=0.930$), but does decline substantially from old growth forest to
184 oil palm ($t_{2,34} = -3.826$, $p=0.0015$), and from logged forest to oil palm ($t_{2,34} = -3.639$, $p=0.0025$; linear mixed
185 effects models, with habitat type as fixed effect and guild as random effect; for model coefficients see
186 Table S3).

187

188 Hence for birds, the diversity of species contributing to dominant energetic pathways is maintained in
189 the transition from old growth to logged forests but declines substantially in oil palm. Mammals
190 generally show lower diversity and ESWI than birds, but 6 out of 10 feeding guilds maintain or increase
191 ESWI in logged forest relative to the old growth forests but collapse in oil palm (Figure 3). Terrestrial
192 herbivory is the largest mammal pathway in the logged forest but is dependent on only four species and
193 is probably the most vulnerable of the larger pathways: a few large mammals (especially sambar deer)
194 play a major role in the logged forest. In parallel, bearded pigs (*Sus barbatus*), the only wild suid in
195 Borneo, form a significant and functionally unique component of the terrestrial omnivory pathway.
196 These larger animals are particularly sensitive to anthropogenic pressures such as hunting, or associated
197 pathogenic pressures as evidenced by the recent precipitous decline of the bearded pig in Sabah due to
198 an outbreak of Asian swine fever (after our data were collected) ²⁰.

199

200 Vertebrate populations across the tropics are particularly sensitive to hunting pressure²¹. Our study site
201 has little hunting, but as a sensitivity analysis we explored the energetic consequences of 50% reduction

202 in population density of those species affected by targeted and/or indiscriminate hunting (Figure ED4).
203 Targeted hunted species include commercially valuable birds, and gun-hunted mammals (bearded pig,
204 ungulates, banteng and mammals with medicinal value). Indiscriminately hunted species include birds
205 and mammals likely to be trapped with nets and snares. Hunting in the logged forests lowers both bird
206 and mammal energy flows but still leaves them at levels higher than in faunally intact old growth
207 forests. Such hunting brings bird energetics levels close to (but still above) old growth forests. For
208 mammals, however, even intensively hunted logged forests seem to maintain higher energetic flows
209 than the old growth forests. Hence only very heavy hunting is likely to “offset” the amplified energetics
210 in the logged forest.

211

212 The amplified energetic pathways in our logged forest probably arise as a result of bottom-up trophic
213 factors including increased resource supply, palatability and accessibility. The more open forest structure
214 in logged forest results in more vegetation being near ground-level^{22,23} and hence more accessible to
215 large generalist mammal herbivores, which show the most striking increase of the mammal guilds. The
216 increased prioritisation by plants of light-competition and therefore rapid vegetation growth strategies
217 in logged forests results in higher leaf nutrient content and reduced leaf chemical defences against
218 herbivory^{24,25}, along with higher fruiting and flowering rates¹⁹ and greater clumping in resource supply⁹.
219 This increased resource availability and palatability likely supports high invertebrate and vertebrate
220 herbivore densities²⁵. Top-down trophic factors might also play a role in amplifying the energy flows,
221 through mechanisms such as increased protection of ground-dwelling or nesting mammals and birds
222 from aerial predators in the dense vegetation ground layer. This might partially explain the increased
223 abundance of rodents but there is little evidence of trophic release at this site because of the persisting
224 high density of mammal carnivores²⁶. Overall, the larger number of bottom-up mechanisms and surge in
225 invertebrate consumption suggests that increased resource supply and palatability largely explains the
226 amplification of consumption pathways in the logged forest. An alternative possibility is that the

227 amplified vertebrate energetics do not indicate amplified overall animal energetics but rather a large
228 diversion of energy from unmeasured invertebrate predation pathways (e.g. parasitoids); this seems
229 unlikely but warrants further exploration.

230

231 The proportion of NPP consumed by mammals and birds in oil palm shows a large decline relative to
232 logged forests¹². Mammal populations collapse because they are more vulnerable and avoid humans, and
233 there is no suite of mammal generalists that can step in^{27,28}. Birds show a more modest decline, to levels
234 similar to those observed in old growth forests, as there is a broad suite of generalist species that are able
235 to adapt to and exploit the habitat types across the disturbance gradient, and because their small size and
236 mobility renders them less sensitive to human activity²⁹. There is a consistent decline in the oil palm in
237 ESWI for birds and especially for mammals, indicating a substantial increase in ecosystem vulnerability
238 in many pathways.

239

240 In conclusion, our analysis demonstrates the tremendously dynamic and ecological vibrant nature of the
241 studied faunally intact logged forests, even heavily and repeatedly logged forests such as those found
242 across Borneo. It is likely that the patterns and basic ecological energetics we describe are general to
243 most tropical forests; amplification of multiple ecosystem processes after logging has also been reported
244 for logged forests in Kenya⁹, but detailed analyses are needed for a range of tropical forests to elucidate
245 the importance of biogeographic, climatic or other factors. We stress that our findings do not diminish
246 the importance of protecting structurally intact old growth forests, but rather questions the meaning of
247 degradation by shining a new light on the ecological value of logged and other structurally “degraded”
248 forests, reinforcing their significance to the conservation agenda³⁰. We have shown that a wide diversity
249 of species not only persist but thrive in the logged forest environment. Moreover, such ecological
250 vibrancy likely enhances the prospects for ecosystem structural recovery. In terms of faunal intactness,
251 our study landscape is close to a best-case scenario because hunting pressures were low. If logged forests

252 can be protected from heavy defaunation, our analysis demonstrates they can be vibrant ecosystems,
253 providing many key ecosystem functions at levels much higher than old growth forests.

254

255 **References**

256

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325

327 **Figure 1:** Map of the study sites in Sabah Borneo, showing locations of net primary productivity (NPP)
328 plots and biodiversity surveys in old growth forest, logged forest and oil palm plantations. The inset
329 shows the location of the four sites within Sabah Shade of green indicates old growth (dark green), twice
330 logged (intermediate green) or heavily logged (light green) forests. The camera and trap grid includes
331 cameras and small mammal traps. White areas indicate oil palm plantations.

332
333 **Figure 2** Variation of energy production and consumption along the disturbance gradient from old
334 growth forest (OG) through logged forest to oil palm (OP): total net primary productivity (NPP) along
335 the gradient (mean of intensive 1 ha-plots; n=4 for OG, n=5 for Logged and n=1 for OP, error bars are
336 95% confidence intervals derived from propagated uncertainty in the individually measured NPP
337 components), with individual data points overlaid (a); total body mass (left axis) and number of species
338 counted (right axis) of birds (b); and mammals (c); total direct energetic food intake by birds (d) and
339 mammals (e); and percentage of NPP directly consumed by birds (f) and mammals (g); in (b-e), body
340 mass and energetics were estimated for individual bird and mammal species, with the bars showing the
341 sum. Error bars denote 95% confidence intervals derived from 10,000 Monte Carlo simulation estimates
342 incorporating uncertainty in body mass, population density, the daily energy expenditure equation,
343 assimilation efficiency of the different food types, composition of the diet of each species, and NPP. In
344 (f) and (g), the white bars denote the % of NPP supporting bird and mammal food intake when the mean
345 trophic level is assumed to be 2.5, with the error bars denoting mean trophic levels of 2.4 and 2.6. Note
346 the log scale of the y axis in (f) and (g).

347
348 **Figure 3:** Magnitude of consumption energetic pathways in old growth forest, logged forest and oil palm.
349 Size of circles indicates magnitude of energy flow, and colour indicates birds or mammals. S = number of
350 species, E = Energetic Shannon-Wiener index, an index of species redundancy and, therefore, resilience

351 (high values indicate high redundancy; see main text). For clarity, guilds with small energetic flows are
352 not shown, but are listed in Supplementary Table 4 Figure art: Jacob Bentley

353

354 **Figure 4:** Changes in energy consumption by species in logged forest relative to old growth forest (a);
355 and oil palm relative to old growth forest (b). The twenty species experiencing the largest increase (red)
356 and decrease (blue) in both habitat types are shown. Bird species are shown in lighter tone and mammal
357 species in darker tone. Error bars denote 95% confidence intervals, derived from 10,000 Monte Carlo
358 simulation estimates incorporating uncertainty in body mass, population density, the daily energy
359 expenditure equation, assimilation efficiency of the different food types and composition of the diet of
360 each species.

361

362 **Methods**

363 *Field sites*

364 Data from logged forests were collected across the Stability of Altered Forest Ecosystems (SAFE) Project
365 Landscape (4° 43' N, 117° 35' E) in Sabah, Malaysia ³¹, a lowland mosaic landscape of logged forest and oil
366 palm plantation (Figure 1). The logged forest had been through one round of selective logging (removing
367 113 m³ ha⁻¹) in the 1970s and an additional cumulative volume of 37–66 m³ ha⁻¹ during the subsequent
368 rotations up until the early 2000s, which is similar to the mean extracted volume of 152 m³ ha⁻¹ within a
369 larger, 220,000 ha area in Sabah ^{32,33}. The most heavily logged plots have been logged over four times,
370 while the less logged plots only twice, hence logging intensity was high throughout the landscape. Data
371 for oil palm plantations were collected from adjoining oil palm estates. Data for the old growth forests
372 (Figure 1) were collected from the Braintian-Tantulit Virgin Jungle Reserve (VJR, a large fragment
373 adjoining the logged forest landscape), and also in three other old growth forest reserves in Sabah, the
374 Maliau Basin Conservation Area (vegetation, birds and mammals), the Danum Valley Conservation Area
375 (vegetation and birds) and Sepilok Forest Reserve (birds only). Data collection took place between 2010

376 and 2017. The sample sites spanned the gradient of logging intensity and biomass observed across the
377 landscape (Figure ED1). The study sites have experienced very low hunting pressure compared to other
378 areas of Borneo due to difficult access from nearby towns and cultural factors, including the relatively
379 limited forest use among local populations ²⁷. Data on every species surveyed or estimated are given in
380 Supplementary Data 1.

381

382 *Vegetation and NPP surveys*

383 Net primary productivity was measured in five logged 1 ha plots in the SAFE Project area with varying
384 intensity of logging (five years of data), in four old growth forest 1 ha plots in the Maliau Basin (two
385 plots, four years of data) and Danum Valley Conservation Areas (two plots, two years of data) ^{14,16}, and
386 one 0.36 ha mature oil palm plot (two years of data), following the standardised protocols of the Global
387 Ecosystems Monitoring (GEM) network ¹⁵ (Figure 1, ED1). We quantified the following NPP
388 components: woody NPP (stems, coarse roots and branches), canopy NPP (leaves, twigs and
389 reproductive parts) and fine root NPP ¹⁰. All plots had at least two tree censuses for quantifying stem and
390 coarse root NPP. Canopy NPP (litter traps) and fine root NPP (root ingrowth cores) were monitored
391 monthly and quarterly, respectively. Oil palm plantation NPP estimates were based on palm censuses
392 and allometry with height, monthly counts of flower bunches, fruit bunches and attached and pruned
393 fronds combined with a one-off survey of their mass, and quarterly harvest of the root ingrowth cores.

394

395 *Mammal surveys*

396 To characterise the terrestrial medium/large non-volant mammal community, we obtained detection/non-
397 detection data from remotely operated digital camera traps (Reconyx HC500, Wisconsin, USA) between
398 May 2011 and December 2017 ^{27,34}. Camera traps were deployed at 882 locations, stratified across old
399 growth forest (N=236), logged forest (N=539) and oil palm (N=107). Two survey designs were adopted: (i)
400 a hierarchical, clustered design whereby cameras were placed 23-232 m apart in grids (42,877 camera trap

401 nights (CTN), with cameras deployed 49 consecutive nights on average ³⁵), and (ii) a systematic design
402 with pairs of cameras spaced more broadly over the landscape at stations >1 km apart (11,403 CTN, with
403 cameras deployed 47 consecutive nights on average³⁴). In both cases, cameras were deployed 20–50 cm off
404 the ground, disturbance to vegetation was kept to a minimum, and no baits or lures were used.

405

406 Terrestrial small mammals were surveyed between May 2011 and July 2014 using locally-made steel-
407 mesh traps, deployed at 1,488 locations stratified across the habitat types (432, 768 and 288 in old
408 growth forest, logged forest and oil palm, respectively³⁵). Trap locations were clustered into 1.75 ha
409 trapping grids of 12 x 4 locations with 23 m spacing. Each location was sampled using two traps (spaced
410 5-20 m apart) placed at or near ground level (0-1.5 m) and baited with oil palm fruit. Traps were
411 checked for seven consecutive mornings and captured individuals were marked using a subcutaneous
412 passive inductive transponder tag before being released at the capture location^{27,35}. Some trapping grids
413 were sampled more than once (14 of 31 grids) and the total sampling effort was 34,058 trap nights.

414

415 For volant mammals we used bat capture data from harp traps set in forests between April 2011 and June
416 2012 ³³. Bats were captured at 42 sampling points in each of 12 sites (3 old growth forest, 9 logged forest),
417 in traps set 50-150 m apart. Up to seven traps were set across forest trails and logging skids each night
418 and then moved to a new position the following day. Bats were marked with unique forearm bands or
419 wing biopsies before release so that recaptured individuals could be identified and removed from
420 analyses. No comparable data were available for oil palm as harp traps are ineffective in open habitats.

421

422 *Bird surveys*

423 Avian point counts were conducted across 356 locations spanning forests and surrounding oil palm estates,
424 with sites separated by 180-220 m ³⁶. Each count involved a single experienced observer (SLM) recording
425 all species seen and heard within an unlimited distance over a 15-minute period, including birds flying

426 over. Four counts were conducted at each site between 05:00 and 11:00 on mornings without rain between
427 2014 and 2016. Sites were sampled at mean intervals of 72 days between first and last visits. Three species
428 of swift (*Aerodramus maximus*, *A. salangana* and *A. fuciphagus*) that cannot be reliably separated in most
429 field conditions were collectively considered as *Aerodramus* spp.

430

431 *Density estimation*

432 For the terrestrial medium/large mammals, we estimated density at each camera trap point using the
433 Random Encounter Model (REM) ³⁷. This approach uses information about the size of the camera trap
434 detection zone, and the movement speeds of animals, in order to correct the trapping rate data (number
435 of animal passes per unit time) and estimate density. Specifically, the parameters required for REM
436 include, for each species: (i) the activity level (i.e., proportion of 24 hr diel cycle spent active and available
437 for detection); (ii) movement speed when active; (iii) effective detection angle of camera traps; (iv)
438 effective detection distance of camera traps; and (v) the trapping rate. Activity levels were estimated based
439 on the timestamps of the camera trap detections³⁸, whilst movement speeds and the detection zone
440 parameters were estimated based on animal location data recovered from the camera trap image sequences.
441 This was possible because we ‘calibrated’ both camera trap locations (using an object of known size, *i.e.*, a
442 1 m pole) and the specific camera trap model that we used (by taking pictures of objects of known size at
443 known distances from the camera). This allowed us to recover the distance and angle of animals in image
444 sequences and thereby estimate animal speed when active³⁹. The effective detection angle and distance
445 were estimated using an adapted distance sampling approach ³⁸. We implemented the REM using multi-
446 species Bayesian approaches, in which species are treated as random effects and estimates for rare species,
447 with only sparse data available, become possible by ‘borrowing’ information from the more common
448 species ⁴⁰. Separate multi-species models (with land-use type included as a covariate) for activity levels,
449 speeds and the detection zone parameters were used to estimate the posterior distributions for each species
450 in each land use. These posterior distributions were then combined with the trapping rate data in order

451 to estimate density, with bootstrapping of the data providing the uncertainty estimates. The final density
452 estimates are broadly comparable with published estimates for other sites in the region.

453

454 To estimate terrestrial small mammal densities⁴¹, we used spatially explicit capture-recapture modelling
455 (SECR ⁴²). This modelling framework explicitly accounts for the fact that some individuals with home
456 ranges at the edge of a trapping grid may not always be available for capture. The SECR approach therefore
457 controls for variation in the effective sampling area of a trapping grid that might occur (e.g. across the
458 disturbance gradient). Separate models for each land-use type were fit in the R package 'secr' ⁴³ using
459 default parameters (i.e., a Poisson-distribution of animal home-range centres and a half-normal detection
460 function) and no covariates. A buffer of 100 m around the trap locations defined the region of model
461 integration. Sufficient data were available to estimate density for 14 species of small mammal in old growth
462 and logged forest. There were too few captures in oil palm to allow for model fitting.

463

464 Unlike the terrestrial mammals, bat data were not acquired via a repeated survey design. Therefore,
465 densities were derived based on a 20m detection radius (i.e., 0.126 ha) around each trap, and estimates
466 calculated as the total counts of each species per cumulative detection area in each habitat type.

467

468 We estimated mean local abundance of birds as a function of per capita detection using the Royle-Nichols
469 model ⁴⁴. Prior to analysis, species-specific detection histories were constructed by pooling detection/non-
470 detection data into discrete sampling occasions according to site visit. Our modelling framework described
471 abundance and detection using categorical habitat-specific intercepts (old growth forest, logged forest and
472 oil palm), incorporating species-specific slopes and intercepts, drawn as random effects from a common
473 community-level distribution. Model specification and checking procedures followed established
474 protocols ³⁴. We scaled modelled bird abundance (number of individuals within the effective sampling

475 area: 7,854 m² buffer around each point count) to density per km² post-hoc using a conversion factor of
476 0.785.

477

478 *Expert judgement and independent estimates*

479 For some other mammal species that could not be reliably sampled by camera traps or small animal traps,
480 for example due to obligately arboreal habitat use (e.g. some primate and squirrel species) or migratory
481 behaviour (e.g. Asian elephant *Elephas maximus*), we relied on estimates based on encounter rates with
482 these species during the course of fieldwork, or on independent studies in the same study area
483 (Supplementary Data 1), e.g. for Bornean orangutan (*Pongo pygmaeus*)⁴⁵. Asian elephant densities in
484 logged forest and oil palm were estimated based on the observed behaviour of the single 15-elephant herd
485 in the SAFE landscape, and for old growth forest as an average of the low densities reported in Maliau
486 and the higher values densities in other Sabah old growth forests⁴⁶. Due to bias introduced by highly
487 mobile bird life-histories, modelled densities of five species of hornbill (*Anthracoseros malayanus*,
488 *Anorrhinus galeritus*, *Buceros rhinoceros*, *Rhinoplax vigil*, *Rhyticeros undulatus*) as well as great argus
489 (*Argusianus argus*) and crested serpent-eagle (*Spilornis cheela*) were corrected using available information
490 from the literature. Home-range estimates of each hornbill species in each habitat type were centred
491 around the mean value and scaled to one-unit standard deviation. This was multiplied by a conversion
492 factor of 465.3 ha based on the mean home-range reported across the seven species (radio telemetry
493 studies; Supplementary Data 1) to calculate scaled home range estimates for each species. Per hectare
494 density estimates were inferred as the inverse of scaled home-range. These large bird species contributed
495 a very small part to total ecosystem energetics.

496

497 *Aggregation to habitat type*

498 Since we combined data across taxa for which we needed the largest sampling effort and 'best'

499 description of the community possible, we aggregated species abundance estimates to a single value per

500 habitat type. For the REM modelling, data for a given habitat were used in the model to estimate a single
501 value of each of the required REM parameters (e.g. speed, detection angle/distance, activity level, trap
502 rate and density) in each habitat. Hence our unit of replication is guild, which has no spatial component
503 within habitat type and hence no spatial autocorrelation variable that can be explored.

504

505 *Daily Energetic Expenditure and Food Uptake*

506 Daily energetic expenditure for each individual species was calculated from body mass using published
507 multi-species allometric equations for field metabolic rates for mammals and birds ⁴⁷ (see Table S1 for the
508 equations and parameter values). The fractions of diet deriving from each food type were assigned to
509 each species based on specialist expert judgement by three coauthors (OW, NJD, SM), and food uptake
510 rates were calculated based on assimilation efficiency for each feeding guild and food type ^{48,49}
511 (summarised in Table S2).

512

513 *Energetic Shannon-Wiener Index (ESWI)*

514 We define and employ ESWI to examine the partition of energy flow across species by analogy to the
515 diversity Shannon-Wiener Index which is a measure of how population abundance is spread across
516 species.

517
$$ESWI = - \sum_{i=1}^N e_i \ln(e_i)$$

518

519 where e_i is the proportion energy flow through species i in a total community of N species, relative to
520 total energy flow through the community.

521

522 *Comparison across guilds and habitat types*

523 To test for significant difference in ESWI across habitat types, we applied linear mixed-effects models
524 with ESWI as a response variable, habitat type (old-growth forest, logged forest, oil palm) as a fixed

525 effect and guild (n=18, see Supplementary Data 1) as a random effect (random intercept), with variance
526 structure to allow for unequal variances among habitat types ('*varIdent*' function, which implements a
527 different variance for each habitat; model with variance structure is better than without, AIC of 120.5
528 vs. 128.3, respectively), using the '*nlme*' package⁵⁰. Pairwise post hoc comparison of the habitats, with
529 Tukey adjustment, was carried out using the '*emmeans*' package⁵¹.

530

531 *Uncertainty calculation*

532 We assumed there was uncertainty in the following variables: body mass of species, population density,
533 daily energy expenditure (DEE) equation, assimilation efficiency of the different food types, composition
534 of the diet of each species, and NPP. For body mass, we drew from a truncated normal distribution
535 (lower bound = 1 g), where mean was the observed body mass and standard deviation was 15 %. We
536 based this standard deviation for birds on a study of tropical birds⁵² and applied the same 15% for
537 mammals for consistency, in the absence of other data⁵². For population density, we used the 10,000
538 bootstrapped estimates of the population density models. In addition, for birds and bats (the population
539 density estimates of which were based on a detection radius around the sampling point) we incorporated
540 the uncertainty in the radius by drawing from a truncated normal distribution with standard deviation
541 of 20%, and lower and upper bounds of 50% and 150% of the estimated radius. We assigned 30%
542 uncertainty for each of the few 'expert guess' species, which had a very minor influence in the final
543 results. For DEE, we estimated the 95% confidence intervals for the predictions as described in⁴⁷. For
544 assimilation efficiency, we drew from a random beta distribution, using the mean and standard
545 deviation by food type and guild from the literature (Table S2). For fractional diet composition, we
546 generated a symmetrical beta distribution, with the peak uncertainty of 20% when the food group made
547 up 50% of a species' diet and no uncertainty when the food group made up 0% or 100% of the diet. It is
548 possible that logging and conversion to oil palm results in systematic shifts in diet composition towards
549 arthropods. Therefore, we also carried out two additional analyses where the fractional consumption of

550 (i) arthropods and (ii) leaves was increased by 30% for species that had a mixed diet. Uncertainty in NPP
551 was drawn from a truncated normal distribution with the mean and standard deviation derived from the
552 field data^{14,16} and lower and upper bounds of the distribution set at mean \pm 2 standard deviations.

553

554 To quantify the uncertainty in our estimates for energetic intake and proportion of NPP consumed, we
555 ran 10,000 simulations, replacing the values in our original calculations with values drawn from the
556 random distributions. Firstly, we estimated the total uncertainty by assuming uncertainty in all
557 components simultaneously and calculated the 2.5% and 97.5% percentiles of the simulations to derive
558 95% confidence intervals for our estimates. Secondly, to quantify how much each variable contributed
559 to the total uncertainty, we ran sets of 10,000 simulations where only one variable at the time had
560 uncertainty while others were kept constant. We calculated the 5% to 95% percentile range for the
561 ‘uncertainty-in-one-variable-at-the-time’ estimates and the ‘uncertainty-in-all-variables’ estimates, and
562 the contribution of each variable to the total uncertainty considered to be the ratio of the two⁵³.

563

564 Uncertainty estimates of absolute consumption are dominated by uncertainty in the population density
565 and DEE allometry of the dominant consumers (Figure ED6). Uncertainties in diet fraction allocation,
566 assimilation efficiency or the consumption allometric equation make relatively modest contributions.
567 Hence further reduction in uncertainty is best targeted in improving estimates of the abundance and
568 producing better DEE allometries specific to the few dominant consumers (Figure ED7), as well as better
569 assessing key undersampled groups such as small forest-floor and arboreal mammals. When calculating
570 the fraction of NPP consumed, the uncertainty in NPP estimates dominates over the uncertainty in
571 consumption estimates, and particularly so in logged forest and oil palm.

572

573 *Caveats*

574 There are a number of caveats in our analysis. Some taxa are probably under sampled. These include
575 several small ground-layer insectivorous mammals (in particular, shrews) that cannot be reliably
576 detected using either camera traps or fruit-baited live traps (pitfall traps with drift fence would be
577 required) and 16 frugivorous or nectivorous bat species that are difficult to capture in the tropical forest
578 understorey ⁵⁴ and are likely to utilise the study area to some degree. Fully arboreal mammal species
579 such as primates and flying squirrels were estimated from other studies in the same region
580 (Supplementary Data 1). We did not measure NPP in old-growth forests within same landscaped as the
581 logged forests. However, the variation of measured NPP across old growth sites in NE Borneo with very
582 strongly varying soil is fairly small (range 12.03 – 15.53 Mg C ha⁻¹ year⁻¹ (i.e. ±9%)¹⁴, so we fully expect
583 that NPP in old-growth forests in the SAFE landscape to be within this range. Our analysis also assumes
584 no dietary shifts within species across the disturbance gradients, e.g. invertebrates make up the same
585 fraction of diet of particular species whether in old growth or logged forest, but a sensitivity test shows
586 possible dietary shifts have negligible effect (Supplementary Discussion). Finally, we assume a
587 correlation between animal presence and consumption of resources that may not hold in all cases. As
588 noted above, the animals observed in the oil palm plantation may be passing between fragments of
589 logged and/or riparian forest, and hence our estimate of consumption within oil palm is likely to be an
590 overestimate. There are, nonetheless, a small number of animals such as bearded pig, macaques and
591 small carnivores that favour the oil palm as a feeding area, with its abundance of palm fruit and rodents
592 ^{27,55}. Our logged forest landscape is adjacent to a larger area of more moderately logged forests to the
593 north (Figure 1). More isolated and fragmented logged forests might be more defaunated than those
594 studied here, even in the absence of hunting, and would there show a smaller increase in energetics.

595

596 **Methods References**

597

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721

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735 NJD, ZD, RME and MS. ORW developed the REM modelling, ORW, NJD, SM and MS collected and
736 analysed the animal data, TR collected and analysed the vegetation data and worked on energetic data
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739 **Competing Interests:** The authors declare no competing interests.

740 **Data Availability:** The per-species energetics data, and REM model parameters (mammals) are available
741 in Supplementary Data Tables 1 and 2.

742 **Code Availability:** The data processing statistical analysis code is available as Supplementary Methods.
743 The REM analysis code will be available and described in detail in a forthcoming publication led by OW.

744 **Extended Data Legends**

745 **Table ED1:** Energetic food intake ($\text{kJ m}^{-2} \text{year}^{-1}$) of different food types by birds and mammals and 95%
746 confidence intervals of the estimates across the disturbance gradient from old growth forest through
747 logged forest to oil palm. Numbers with an asterisk include estimates for some bats, values without the
748 bat estimates are $47.7 \text{ kJ m}^{-2} \text{year}^{-1}$ in old growth and $99.3 \text{ kJ m}^{-2} \text{year}^{-1}$ in logged forest. The confidence
749 intervals are derived from 10,000 Monte Carlo simulation estimates incorporating uncertainty in body
750 mass, population density, the daily energy expenditure equation, assimilation efficiency of the different
751 food types, and composition of the diet of each species.

752

753 **Table ED2:** Proportion of NPP (%), and 95% confidence intervals of the estimates, consumed by food
754 type across the disturbance gradient from old growth forest (OG) through logged forest to oil palm.
755 Numbers with an asterisk include estimates for some bats, values without the bat estimates are 0.081% in
756 old growth and 0.138% in logged forest. The confidence intervals are derived from 10,000 Monte Carlo
757 simulation estimates incorporating uncertainty in body mass, population density, the daily energy
758 expenditure equation, assimilation efficiency of the different food types, composition of the diet of each
759 species, and NPP.

760

761 **Figure ED1:** Distribution of sampling locations across a gradient of logging intensity, characterised using
762 aboveground biomass (t/ha). We estimate biomass from a spatially-explicit surface of carbon density (30
763 m resolution) derived from airborne Light Detection and Ranging (LiDAR) data (see ⁵⁶ for full sampling
764 details) and convert carbon to biomass using a conversion factor of 0.47 (⁵⁷). To provide a representative
765 sample of local habitat conditions, biomass was extracted as mean values from 100 m radii buffers around
766 each sampling point. At this resolution there are a broad range of biomass values in both old growth and
767 logged forests, but the mean values are clearly distinguished. The sampling points for vegetation primary
768 productivity, bats, birds and terrestrial mammals span this gradient well.

769

770 **Figure ED2:** Species-level resource consumption in birds (a-c) and mammals (d-f) (top 20 consumers in
771 each forest type). Error bars denote 95% confidence intervals, derived from 10,000 Monte Carlo
772 simulation estimates incorporating uncertainty in body mass, population density, the daily energy
773 expenditure equation, assimilation efficiency of the different food types and composition of the diet of
774 each species.

775

776 **Figure ED3:** Direct energetic intake of birds (a) and mammals (b) by body mass class (logarithmic scale)
777 in old growth forest (OG), logged forest and oil palm plantation (OP). The numbers next to the bars
778 indicate the number of species in each class. Error bars denote 95% confidence intervals, derived from
779 10,000 Monte Carlo simulation estimates incorporating uncertainty in body mass, population density,
780 the daily energy expenditure equation, assimilation efficiency of the different food types and
781 composition of the diet of each species.

782

783 **Figure ED4:** Body mass of birds (a) and mammals (b) and energetic food intake of birds (c) and mammals
784 (d) in old growth forest (OG, dark grey, no hunting) and in logged forest (light grey) under four different
785 hunting scenarios: observed low hunting pressure (baseline) and simulated 50% reduction in population
786 density of targeted hunted species, indiscriminately hunted species and both targeted and
787 indiscriminately hunted species. Targeted hunted species include commercially valuable birds, and gun-
788 hunted mammals (bearded pig, ungulates, banteng and mammals with medicinal value).
789 Indiscriminately hunted species include birds and mammals likely to be trapped with nets and snares.
790 For the list of species in each category see Supplementary Data 1. Note that this is not an exhaustive
791 analysis of the hunting pressure in the study area but an illustrative estimate of the potential impact of
792 hunting on trophic energetics.

793 Targeted hunted bird species potentially include 13% of bird species, which account for 17% of bird
794 body mass and 14% of bird energy consumption under the observed low hunting pressure. Targeted
795 hunted mammal species potentially include 10% of mammal species, which account for 46% of body
796 mass, 42% of mammal energy consumption under the observed low hunting pressure. Indiscriminately
797 hunted bird species potentially include 72% of bird species, which account for 78% of bird body mass
798 and 82% of bird energy consumption under the observed low hunting pressure. Indiscriminately hunted
799 mammal species potentially include 22% of mammal species, which account for 2% of mammal body
800 mass and 2% of mammal energy consumption.

801 With both hunting pressures applied simultaneously, hunted bird species potentially include 86% of
802 species, 95% of bird body mass and 96% of bird energy consumption under the observed low hunting
803 pressure, and hunted mammal species potentially include 32% of mammal species, 48% of mammal body
804 mass and 44% of mammal energy consumption under the observed low hunting pressure.

805

806 **Figure ED5:** Body mass and species richness of birds (a) and mammals (b) and energetic food intake of
807 birds (c) and mammals (d) across old growth forests (OG), logged forests and oil palm plantations (OP).
808 OG forest data were analysed separately by four OG sites for birds and two sites for mammals (see Fig 1
809 for map), and the logged forest data were split into twice logged and heavily logged areas. For mammals,
810 only species studied using camera traps and harp traps were included (63%, 63% and 77% of mammal
811 species, and 53%, 45% and 63% of total energetic food intake in OG, logged forest and OP, respectively).
812 Error bars are 95% confidence intervals derived from 10,000 Monte Carlo simulation estimates
813 incorporating uncertainty in body mass, population density, the daily energy expenditure equation,
814 assimilation efficiency of the different food types and composition of the diet of each species.

815

816 **Figure ED6:** Sources of contribution to uncertainty in energetic intake (a) and proportion of net primary
817 productivity (NPP) consumed (b) for birds and mammals across the habitat types of old growth forest
818 (OG), logged forest and oil palm plantation (OP). We assumed there was uncertainty in the following
819 variables: body mass of species, population density, the daily energy expenditure (DEE) equation,
820 assimilation efficiency of the different food types, fractional composition of the diet of each species, and
821 NPP. Uncertainty estimates were derived from 10,000 Monte Carlo simulations, and the contribution of
822 each variable to the total uncertainty was assessed by running the simulations assuming uncertainty in
823 all variables simultaneously and in one variable at a time.

824

825 **Figure ED7:** The proportion of total uncertainty contributed by each species ranked by energy
826 consumption for birds (a) and mammals (b).

827