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Main Manuscript for

Maximizing the value of forest restoration for tropical mammals by detecting three-dimensional habitat associations

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Ecological thresholds | LiDAR | occupancy | prioritization | forest degradation

Author Contributions

N.J.D, M.J.S and Z.G.D. conceived and designed the study; N.J.D led the collection of mammal data with field support from H.B. and G.R.; D.A.C., D.T.M. and T.S. collected and processed LiDAR data; N.J.D. analysed the data with assistance from G.G.A.; all authors contributed to the discussion of results and revision of the manuscript.

The authors declare no competing interest.

1 **Abstract**

2 Tropical forest ecosystems are facing unprecedented levels of degradation, severely
3 compromising habitat suitability for wildlife. Despite the fundamental role biodiversity
4 plays in forest regeneration, identifying and prioritising degraded forests for restoration
5 or conservation, based on their wildlife value, remains a significant challenge. Efforts to
6 characterize habitat selection are also weakened by simple classifications of human-
7 modified tropical forests as intact versus degraded, which ignore the influence that three-
8 dimensional forest structure may have on species distributions. Here, we develop a
9 framework to identify conservation and restoration opportunities across logged forests in
10 Borneo. We couple high-resolution airborne Light Detection and Ranging (LiDAR) and
11 camera trap data to characterize the response of a tropical mammal community to
12 changes in three-dimensional forest structure across a degradation gradient. Mammals
13 were most responsive to covariates that accounted explicitly for the vertical and
14 horizontal characteristics of the forest, and actively selected structurally-complex
15 environments comprising tall canopies, increased plant area index throughout the vertical
16 column, and the availability of a greater diversity of niches. We show that mammals are
17 sensitive to structural simplification through disturbance, emphasising the importance of
18 maintaining and enhancing structurally-intact forests. By calculating occurrence
19 thresholds of species in response to forest structural change, we identify areas of
20 degraded forest that would provide maximum benefit for multiple high conservation
21 value species if restored. The study demonstrates the advantages of using LiDAR to map

22 forest structure, rather than relying on overly simplistic classifications of human-modified
23 tropical forests, for prioritising regions for restoration.

24

25 **Significance statement**

26 Forest restoration has become a global conservation priority, particularly in the tropics
27 where a significant proportion of remaining forest ecosystems are degraded. To achieve
28 ambitious restoration targets via limited conservation funds, areas that will deliver the
29 greatest biodiversity value must be prioritized. Here, we combine airborne laser scanning
30 with an extensive camera trap dataset to target conservation and restoration across a
31 degraded logged forest gradient. We demonstrate the importance of accounting for three-
32 dimensional habitat structure when defining forest suitability and restoration potential for
33 mammals. Consequently, we provide a robust quantitative framework to prioritize
34 degraded forest restoration based on biodiversity considerations.

35 **Introduction**

36 Habitat degradation is pervasive in forest ecosystems, affecting ~4 billion ha worldwide
37 (1), with profound impacts on habitat suitability for wildlife and the delivery of
38 ecosystem functions and services. The restoration of degraded forests has emerged as a
39 global conservation priority, underwritten by the Bonn Challenge and New York
40 Declaration on Forests, which seek to restore 350 million ha of forest by 2030 (2). Given
41 limited conservation funding, it is imperative to maximize return on investment by
42 targeting areas where interventions will have the greatest impact (i.e. optimize ecological
43 benefits relative to opportunity and implementation costs). However, sophisticated
44 frameworks to prioritize degraded forests for conservation and restoration are lacking,
45 hindering the realization of ambitious policy targets (3).

46 Biodiversity underpins the ecological processes that facilitate forest regeneration
47 (4), meaning that wildlife persistence and restoration are inextricably linked. For
48 example, it is estimated that 90% of tropical tree species depend on interactions with
49 vertebrates to complete their life cycle (5). Given the importance of biodiversity for
50 maintaining forest quality and ecosystem stability, policy and management interventions
51 that prioritize restoration based on wildlife retention are fundamental to achieving long-
52 term restoration goals. This is paramount in the tropics where a significant proportion of
53 the remaining forest extent is degraded, placing vertebrate taxa that use these regions at
54 greater risk of extinction (6). Here, we introduce a framework based on high-resolution
55 remote sensing and wildlife monitoring data to integrate biodiversity considerations into
56 conservation and restoration planning for degraded forests in vulnerable tropical regions.

57 Selective logging is the principle driver of forest degradation across the tropics
58 (7). Over a fifth of remaining forests have been logged, while an area of up to 600 million
59 ha is currently designated as production forest (7, 8). Logged forests afford refuge to
60 species of conservation concern (9) and play a pivotal role protecting wildlife against the
61 impacts of environmental change (10). Despite this, the conversion of degraded forests to
62 agricultural land of limited ecological value is a common land-use trajectory across the
63 tropics (9). Selecting which areas of degraded logged forest to protect or restore is
64 hampered by the coarse classification of forest into logged versus pristine categories (11).
65 Such simplistic assessments overlook substantial spatial heterogeneity in levels of
66 logging-induced degradation (12), and are often unable to provide specific
67 recommendations to inform management and policy. To most effectively retain and
68 enhance logged forests for biodiversity, we need to understand what habitat features
69 species actively utilize.

70 Habitat selection is a nested hierarchical process describing home range
71 establishment and episodic use of the home range to meet ecological demands (13). It is
72 an adaptive process through which species balance reward (resource acquisition, mating
73 opportunities) relative to risk (energy expenditure, predation) (14). It is generally
74 assumed, therefore, that areas of habitat used preferentially by species convey the highest
75 levels of ecological benefits to them (15). Forest structure is a key determinant of species
76 diversity (16, 17). Logging results in the structural simplification of forest habitats (18),
77 however, the extent to which structural alterations associated with logging influence
78 habitat selection by wildlife remain poorly understood, particularly in a spatial context.

79 This information is essential to delineate areas of forest that promote biodiversity
80 retention and therefore optimize the success of restoration initiatives.

81 Habitat selection models for species predominantly focus on a single spatial
82 extent (13), potentially obscuring scale-dependent associations and hierarchical
83 environmental interactions (14). These issues are exacerbated for rare and cryptic species
84 that are observed too infrequently to quantify their habitat associations, but are often most
85 sensitive to forest degradation (19). Modern advances in statistical methods afford an
86 analytical platform to overcome these challenges. Multi-species occupancy models
87 provide robust parameter estimates for species infrequently encountered during
88 biodiversity surveys while correcting for sampling bias (20). Moreover, the advent of
89 multi-scale occupancy models account for the complexity of habitat selection (21), but, to
90 date applications have been limited to single-species approaches (e.g. 22, 23). Thus, the
91 formal integration of multi-species methods within a multi-scale framework provides a
92 powerful statistical tool to capture hierarchical habitat selection for vulnerable and rare
93 species.

94 Efforts to characterize habitat selection to inform conservation are further
95 hindered by multi-dimensionality in forest ecosystems. Tropical forests are three-
96 dimensional environments comprised of horizontal and vertical structural components. It
97 is estimated that 75% of forest-dwelling vertebrates demonstrate some degree of
98 arboreality, indicating that multi-dimensional interactions with vegetation structure are an
99 important aspect of habitat selection (16, 17, 24). Nonetheless, structural complexity is
100 rarely accounted for in conservation assessments due to challenges in measuring

101 structural elements at scales appropriate to management. Airborne Light Detection and
102 Ranging (LiDAR) has emerged as a possible solution to these challenges, and has the
103 potential to significantly advance our understanding of the structural signature of logging
104 on biodiversity. However, applications in degraded tropical regions are yet to catch up
105 with these technological advances (16, 17). While LiDAR has been widely implemented
106 in tropical forest carbon assessments (25), it has received much less attention for its
107 potential to quantify three-dimensional habitat associations, particularly for mammals
108 (16), which occupy key trophic positions in tropical forest ecosystems and are a focus of
109 global conservation efforts (4).

110 Here, we couple high resolution airborne LiDAR with bespoke multi-species
111 multi-scale Bayesian occupancy models to provide unprecedented insights into the
112 conservation value of logged forests and demonstrate how species-habitat associations
113 can be aligned with efforts to prioritize degraded forests for conservation and restoration.
114 We examine the complexity of habitat selection in logged forests and assess degradation
115 impacts on forest structure and biodiversity. We develop structural metrics from three-
116 dimensional plant area distributions to capture the horizontal and vertical components of
117 forest architecture. Our appraisal was conducted in a region characterized by high levels
118 of forest degradation in Borneo, where 46% of the remaining forest area is degraded, a
119 figure which could increase to 88% based on land-use allocations to the timber estate
120 (26).

121 We assess forest structure deterioration across a logging-induced degradation
122 gradient, comprising Old Growth Forest ($N=10$), Managed Forest (twice-logged; $N=15$),

123 Heavily-degraded Forest (repeatedly-logged; $N=28$) and Remnant Forest embedded
124 within an oil palm matrix ($N=21$; Fig. 1). Integrating an extensive camera trap dataset (74
125 sampling locations, comprising two camera trap stations, $N=148$; 5,472 camera trap
126 nights) within a multi-scale modelling framework, we explore how structural features
127 influence hierarchical habitat selection by tropical biodiversity at the species and
128 community level. Throughout, we define occupancy as the probability that a sampling
129 location is situated within the home-range of at least one individual of a given species,
130 and specify probability-of-use as preferential habitat selection at the scale of the camera
131 trap station, conditional on the home range being represented by the sampling location.
132 By linking LiDAR-derived structural characteristics operating at different spatial extents
133 to species detection data, we elucidate the forest architectural properties that characterize
134 a home-range and habitat preferences.

135 Our appraisal focuses on medium to large mammals, which have lost 70% of their
136 original habitat across Southeast Asia (27). The development of effective conservation
137 measures for threatened mammals has proved challenging due to a weak evidence base.
138 Despite substantial value as conservation flagship species, basic ecological information is
139 still lacking for many Southeast Asian vertebrates, 32% of which are considered data-
140 deficient (28). Given the scale of regional forest modification, interventions that
141 recognize the potential value of degraded habitat are essential to safeguard Southeast
142 Asia's imperiled biodiversity.

143

144 **Results and Discussion**

145 *The structural signature of forest degradation*

146 We quantified eight forest metrics from LiDAR point-cloud data, reflecting horizontal
147 and vertical structure, vertical heterogeneity and landscape context (Table 1; SI Appendix
148 S1.1; 16). Consistent patterns of habitat simplification relative to logging intensity were
149 identified between the Managed, Heavily-degraded and Remnant Forest classes,
150 demonstrated by a lack of overlap between Bayesian 95% credible intervals (BCI; Fig. 2;
151 SI Appendix, Table S1). Simplification was characterized by a lower height profile and
152 reduced vegetation density, resulting in fewer environmental niches, fewer canopy
153 pathways and an increase in canopy gaps. This structural simplification is driven by the
154 removal of large trees and damage to surrounding vegetation. In addition, intensive
155 forestry causes soil compaction and eradication of the seedling community (29), which
156 restricts the successional capacity of forests (30). Furthermore, forest remnants are
157 susceptible to wind damage and altered microclimatic conditions which lead to additional
158 mortality of large trees in fragmented landscapes (31). While structural simplification
159 associated with logging is well documented (32), we provide the first empirical evidence
160 of progressive multi-dimensional architectural deterioration due to repeated logging and
161 habitat fragmentation.

162

163 *Multi-scale habitat selection in degraded forest ecosystems*

164 Landscape context covariates, indicative of forest availability (forest cover) and quality
165 (canopy height variability), were important drivers of occupancy for nine of 28 mammal

166 species, representing 32% of the sampled community (SI Appendix, Figs. S1-S3). Habitat
167 availability has been shown to be an important factor defining species persistence (33).
168 However, our results indicate divergent species-specific responses, driven by differences
169 between forest specialists (e.g. banded civet, *Hemilagus derbyanus*, mean of posterior
170 distribution=0.83, BCI=0.01-2.02; Bornean yellow muntjac, *Muntiacus atherodes*, 1.14,
171 0.36-2.26) and taxa adapted to take advantage of resources in degraded or non-forest
172 habitats (e.g. greater mouse-deer, *Tragulid napu*, -0.99, -1.78 to -0.28; leopard cat,
173 *Prionailurus bengalensis*, -1.27, -2.49 to -0.38). Species demonstrated a greater number
174 of positive responses to forest quality (SI Appendix, Fig. S1), likely reflecting a greater
175 abundance of resources typical of structurally complex habitats, such as fruit and browse
176 availability for ungulates (34), and small mammal prey for carnivores (35). The
177 contrasting influences of forest cover and quality may be indicative of the degree of
178 habitat degradation across the study site, with old growth forests accounting for ~8% of
179 the landscape. Given the limited spatial extent of preferential habitat, species appear to be
180 actively selecting areas that retained adequate structural quality to meet their ecological
181 requirements. Our findings emphasize the importance of maintaining forest quality, as
182 well as extent, in a region characterized by high levels of forest degradation. This concurs
183 with evidence from elsewhere in the tropics (33).

184 Patterns in probability-of-use revealed the structural properties that constitute
185 quality habitat and help maintain ecological processes. Looking at the mammal
186 community as a whole, forest structure was a key determinant of probability-of-use,

187 highlighting the importance of mature, connected forest habitat, containing a breadth of
188 environmental niches for mammal persistence (Fig. 2).

189 At the species level, species-habitat structure associations were evident for 16 of
190 the 28 mammals assessed (57% of the sampled community; Fig. 2; SI Appendix, Figs.
191 S4-S9). In general, species were most responsive to structural measures that captured the
192 inherent multi-dimensionality of the forest environment, emphasizing the importance of
193 recognizing the three-dimensional signature of habitat degradation in management and
194 policy. Plant area index throughout the vertical column was the strongest predictor of
195 probability-of-use (Fig. 2; SI Appendix, Table S2). For arboreal ambush predators, such
196 as the Sunda clouded leopard, *Neofelis diardi*, dense vegetation provides cover that
197 increases hunting efficiency through visual or locomotive obstruction, as shown
198 previously for lions (36). Conversely, vegetation density and distribution may provide
199 refuges for prey species such as ungulates, particularly when engaged in vulnerable
200 behaviors such as resting or rumination (37). Mammals actively selected forest areas with
201 taller canopies and a greater breadth of environmental niches (Fig. 2), which are
202 characteristic properties of late-successional stands (38). Mature, diverse forests
203 demonstrate higher primary productivity (39), affording greater resources to primary
204 consumers such as the Bornean yellow muntjac. Moreover, tall trees are fruiting oases for
205 frugivorous species like the binturong, *Arctictis binturong*, as has been demonstrated for
206 species with similar dietary preferences (40). Forests with late-successional
207 characteristics also accumulate leaf litter at a faster rate, attracting a diverse, abundant

208 invertebrate community (41) that may encourage the persistence of insectivorous
209 mammals such as the banded civet.

210 To date, a limited understanding of the structural features of logged forests that
211 promote species persistence has restricted our capacity to capitalize on conservation
212 opportunities within the vast global timber estate. Here, we identify consistent active
213 selection of structurally complex environments by mammals at fine spatial scales
214 indicative of episodic habitat use to meet ecological demands, revealing a causal
215 mechanism for the negative effects of forest degradation on mammal persistence. This
216 emphasizes the importance of maintaining and/or restoring structurally intact forests for
217 biodiversity conservation. Taken as a whole, our results confirm that species will track
218 resources at successively lower hierarchical levels of habitat selection in degraded forests
219 to overcome limitations at the preceding level (14). Here, the mammal community was
220 more responsive to changes in the structural environment at the scale of probability-of-
221 use, presumably because resources were limited throughout the home range to the extent
222 that species tracked relevant structural variations at progressively finer scales. Moreover,
223 these findings suggest the potential for negative feedback loops in degraded systems.
224 Mammals occupy key ecological roles in tropical forests, thus active avoidance of
225 heavily-degraded areas could potentially affect the resilience of these systems, preventing
226 natural post-disturbance recovery and leaving ecosystems in a state of arrested succession
227 and, ultimately, defaunation (4).

228

229 *Prioritizing degraded forests for restoration and conservation*

230 The capacity to identify and prioritize areas of degraded forests for improved
231 management is imperative to inform biodiversity conservation and restoration objectives.
232 To achieve this, we employed Bayesian change point analysis to detect thresholds in
233 forest structural properties, based on records of active habitat selection by tropical
234 mammals. Thresholds were applied to partition species response curves into three distinct
235 occurrence states: (1) zones of tolerance – high probability-of-use and low rate of
236 change, representing optimal conservation areas; (2) zones of transition – variable
237 probability-of-use and high rate of change, ideal for restoration as they offer substantial
238 gains in species persistence per unit management effort, and; (3) zones of stress – low
239 probability-of-use and low rate of change, thus low priority for any habitat intervention
240 (Fig. 3a).

241 By linking the species-habitat relationships to extensive LiDAR habitat maps,
242 covering 40,150 ha, we were able to estimate occurrence states for multiple species from
243 the structural covariates (SI Appendix, Table S3). At the species level, consensus across
244 covariates reveals priority areas for conservation (i.e. tolerance zones) and restoration
245 (i.e. transition zones). Moreover, spatial agreement between areas prioritized for multiple
246 species indicates where interventions will be most optimal (i.e. of benefit to the most
247 species). For example, adopting a conservative approach whereby only areas of high
248 consensus (i.e. full agreement between all structural measures) qualified for management,
249 the highly-threatened Sunda clouded leopard would benefit from 6,767 ha (16.7%) of the
250 landscape prioritized for conservation and 4,415 ha (10.7%) for restoration (Fig. 3b).
251 Combining this information with findings from six other high conservation value species

252 (either endemic or IUCN threatened (Vulnerable/Endangered/Critically Endangered):
253 banded civet, binturong, Bornean yellow muntjac, marbled cat, sambar deer *Rusa*
254 *unicolor* and tufted ground squirrel *Rheithrosciurus macrotis*; Fig. 3c; SI Appendix, Figs.
255 S14-S20), conservation activities would be best targeted to 11,300 ha (27.4%), and
256 restoration 16,410 ha (39.7%) of the landscape (Fig. 3d; SI Appendix, Table S4).

257 Logged forests have been proposed as a cost-effective strategy to expand the
258 existing protected area network to connect pristine habitats (10). The most extensive
259 areas to prioritize for conservation were in Old Growth (1,680 ha, 14.9%) and Managed
260 Forests (7,899 ha, 69.8%). However, within these classes, optimal habitat for all seven
261 target species covered only 443 ha and 1,747 ha (26.3% and 22.1%) respectively (SI
262 Appendix, Table S5). These findings illustrate the challenge of identifying conservation
263 areas that maximize species representation, even when only a fraction of the mammal
264 community is considered. Collectively, our results provide further evidence of declining
265 conservation value with increasing logging intensity (42). We therefore advocate
266 reduced-impact logging as a preventative measure to maintain forest structural integrity
267 and reconcile production and conservation (43).

268 There is a growing concern that many tropical countries lack the capacity to fulfil
269 their international restoration commitments (44). Our framework provides a methodology
270 to direct restoration activities to optimize biodiversity conservation outcomes and support
271 restoration initiatives such as the Bonn Challenge and New York Declaration on Forests.
272 Restoration opportunities were predominantly identified in Managed (5,612 ha; 34.2%)
273 and Heavily-degraded Forests (7,046 ha; 42.9%). However, areas that would universally

274 benefit all target species were again rare (Managed Forest: 1,747 ha; 6.8%; Heavily-
275 degraded Forest: 1,988 ha, 28.2%; SI Appendix, Table S5). This demonstrates the
276 potential for ecological trade-offs during the implementation of restoration initiatives,
277 reinforcing the need for restoration planning to avoid perverse management outcomes.
278 Based on economic data available elsewhere in Borneo (45), combined restoration and
279 opportunity costs for the study landscape would be financially prohibitive (average net
280 present value: US\$943 ha⁻¹, equating to >US\$5 million for the entire landscape). It is
281 therefore essential that any forest restoration efforts are deployed in such a way that they
282 optimize conservation value for associated biodiversity, including mammals. Based on
283 our findings, we believe that buffering pristine conservation areas and enhancing
284 connectivity between them is most likely to maximize species representation and returns
285 on investment within our study system. Applying these principles over much larger
286 spatial scales also serves as an effective climate-change mitigation measure for wildlife
287 conservation (10).

288 Here we demonstrate the use of a robust prioritization framework that can identify
289 priority areas for habitat restoration and conservation, ensuring biodiversity is better
290 integrated into land management decision-making. Moreover, our methodology has the
291 potential to deliver important co-benefits due to documented spatial concordance between
292 areas of high biodiversity and those offering climate change mitigation and water security
293 (46). However, we recognize that restoration is a holistic process containing a significant
294 socio-economic dimension (47) that is not captured by our framework. Our approach
295 maximizes benefits for highly threatened species prioritized by conservation, but like all

296 approaches, may lead to trade-offs between addressing various goals (45). While our
297 approach focused on species of conservation concern to guide restoration planning, the
298 study system could be restricted to taxonomic groups/species that underpin ecological
299 processes if the recovery of ecosystem functions is the ultimate goal of restoration.
300 Although we have shown the value of our approach at the landscape scale, it could
301 equally be applied to direct conservation policy at regional and global scales. Recent
302 proposals by the Sabah government to increase protected area coverage by 5%, coupled
303 with the state-wide availability of LiDAR data (25), provides an unparalleled opportunity
304 to mobilize a collaborative network of species occurrence data and fully integrate
305 biodiversity considerations into the conservation agenda. Moreover, the launch of
306 NASA's Global Ecosystem Dynamics Investigation promises to increase the scope of
307 LiDAR coverage to global scales (48). Capitalizing on these developments could greatly
308 enhance the limited ecological understanding of biodiversity across a pantropical gradient
309 of forest degradation.

310

311 **Methods**

312 *Study landscape*

313 Fieldwork was undertaken at the Stability of Altered Forest Ecosystems Project (SAFE;
314 www.SAFEproject.net) and neighboring oil palm estates in Sabah, Malaysian Borneo.
315 The SAFE Project area is nested within the Kalabakan Forest Reserve (KFR; 4°33'N,
316 117°16'E), comprising lowland and hill dipterocarp forest. A legacy of commercial

317 logging has resulted in a heterogeneous forest stand (Fig. 1). Between 1978 and 2008
318 KFR experienced multiple logging rotations (cumulative extraction rate = $179 \text{ m}^3 \text{ ha}^{-1}$)
319 (11). Similarly, the neighboring Ulu Segama Forest Reserve underwent two logging
320 rounds (cumulative extraction rate = $150 \text{ m}^3 \text{ ha}^{-1}$) with more stringent size quotas. In
321 contrast, Brantian-Tantulit Virgin Jungle Reserve (VJR) retains near-pristine, old growth
322 forest, with some past encroachment on the western and southern borders. The
323 disturbance gradient is representative of transitional degradation states seen elsewhere on
324 Borneo and much of tropical Southeast Asia.

325

326 *Mammal surveys and sampling design*

327 To characterize the mammal community, we collected detection/non-detection data using
328 camera traps deployed between June 2015 and August 2017, following protocols
329 described in Deere *et al.* (49). Remotely-operated digital cameras (Reconyx HC500,
330 Wisconsin, USA) were deployed across 74 sampling locations, separated by a mean
331 distance of 1.6 km, and randomly stratified to capture the degradation gradient relative to
332 logging intensity using the Putz and Redford (50) classification scheme: Old Growth
333 Forest (VJR), Managed Forest (Ulu Segama Forest Reserve; $N=15$) and Heavily-
334 degraded Forest (KFR). We also sampled Remnant Forest embedded within an oil palm
335 matrix, differentiated from Heavily-degraded Forest due to isolation and increased
336 exposure to anthropogenic stressors.

337 Sampling locations comprised two camera trap stations, positioned up to 250 m
338 apart depending on the terrain and availability of forest cover (mean=185 m), resulting in
339 a total of 148 deployments. Cameras were unbaited, positioned at a standardized height
340 (ca. 30 cm) and preferentially placed above flat surfaces, targeting low resistance travel
341 routes and randomized locations simultaneously to maximize detections. Accounting for
342 theft, vandalism, malfunction and animal damage, data were obtained from 125 stations
343 distributed across 74 sampling locations. Cameras were deployed for a minimum of 42
344 consecutive nights per camera station, yielding a total survey effort of 5,427 camera trap
345 nights.

346

347 *LiDAR methods and structural covariates*

348 To characterize the structural properties of the landscape, LiDAR surveys were
349 conducted in November 2014 by NERC's Airborne Research Facility. LiDAR is an
350 active remote sensor that emits a laser pulse from an aircraft towards a target object and
351 quantifies distance based on the time elapsed between emission and reflection (16).
352 Surveys employed a Leica ALS50-II sensor attached to a Dornier 228-201 light aircraft,
353 flown at an elevation of 1400-2400 masl and a velocity of 120-240 knots. The sensor
354 produced pulses at a frequency of 120 kHz, encompassing a scan angle of 12° and a
355 footprint of 40 cm, resulting in a point-cloud density of 25-50 points m⁻². Concurrent
356 ground surveys using a Leica base station facilitated accurate geo-referencing of the
357 point-cloud.

358 To quantify structural metrics, point-cloud data were subjected to two processing
359 procedures. Initially, ground and non-ground returns were partitioned from the point-
360 cloud, using the former to generate a 1 m resolution digital elevation model (DEM). We
361 constructed a canopy height model (CHM) of similar resolution by normalizing non-
362 ground returns and subtracting ground observations derived from the DEM. To develop a
363 three-dimensional insight into canopy structure, plant area density (PAD) distributions
364 were generated from point-cloud data using a one-dimensional Beer-Lambert
365 approximation for the propagation of LiDAR pulses through the canopy (51). We provide
366 a detailed description of LiDAR processing methods in SI Appendix, S1.1.

367 We employed Bayesian linear models to determine differences in forest structural
368 properties across a degradation gradient (see SI Appendix, S1.2 for model specification
369 details). Structural covariates were extracted as mean values across buffer radii
370 corresponding to optimal scales of habitat use (SI Appendix, Table S1).

371

372 *Modelling framework*

373 We developed a multi-species extension to Bayesian multi-scale occupancy models to
374 explore occupancy and probability-of-use by medium-large terrestrial mammals relative
375 to LiDAR-derived structural covariates. We specified models of the form:

$$376 \quad \text{logit}(\psi_{i,j}) = \alpha_{0i} + \alpha_{1i}\text{Forest Cover}_j + \alpha_{2i}\text{Canopy Height Variability}_j + \varepsilon(\text{Year}_j)_i$$

$$377 \quad \text{logit}(\vartheta_{i,j,l}) = \beta_{0i} + \beta_{1i}\text{Structure}_{j,l} + \beta_{2i}\text{Structure}^2_{j,l} + \varepsilon(\text{Year}_{j,l})_i$$

378
$$\text{logit}(p_{i,j,l,k}) = \delta_{0i} + \delta_{1i}\text{Trap Effort}_{j,l} + \delta_{2i}\text{PAD Herb}_{j,l} + \delta_{3i}\text{Nlay}_{j,l}$$

379 Occupancy (ψ), probability-of-use (ϑ) and detection probabilities (p) were
380 modelled on the logit scale with random intercepts ($\alpha_0, \beta_0, \delta_0$) and slopes ($\alpha_{1-2}, \beta_{1-2}, \delta_{1-3}$)
381 for each species (i). We modelled occupancy of species i , at sampling location j ($\psi_{i,j}$), as a
382 function of Forest Cover and Canopy Height Variability, at coarse spatial-scales (buffer
383 radii: 1, 1.5, 2 km). We assessed probability-of-use of species i , within sampling location
384 j , at camera trap station l ($\vartheta_{i,j,l}$), at finer spatial scales (radii: 10, 25, 50, 100, 150, 250, 500
385 m) relative to covariates associated with our three structural axes (“Structure”; Table 1),
386 and incorporated second-order polynomial terms (“Structure²”) to account for non-linear
387 responses. Due to analytically prohibitive levels of multicollinearity ($|r| > 0.7$; Generalized
388 Variance Inflation Factor, GVIF > 5), independent models were constructed for each
389 structural predictor (Table 1; $N=6$). We implemented temporal random effects (ε) for
390 both the occurrence and probability-of-use models, addressing unmeasured inter-annual
391 variation due to sampling across multiple years (“Year”). We modelled detection
392 probability of species i , at sampling location j , camera trap station l , across temporal
393 replicates k ($p_{i,j,l,k}$), as a function of structural and sampling covariates presumed to
394 influence the observation process, including: sampling intensity (“Trap Effort”),
395 obstructing vegetation features in the camera trap detection zone (“PAI Herb”; plant area
396 index values extracted from 2-5 m within the vertical column, broadly corresponding to
397 the herbaceous layer) and alternative pathways in the vertical column (i.e. number of
398 layers: “Nlay”; Table 1). Detection covariates were extracted across a fixed buffer of 25
399 m, corresponding to the detection zone of our camera trap models. Prior to analysis, all

400 continuous covariates were centered and standardized to place them on a comparable
401 scale and improve model convergence. We outline a formal model description, including
402 specification details and predictive performance checks in SI Appendix, S2.1 and S2.2.

403 We constructed 126 models to identify the most influential structural covariates
404 and inform scale optimization methods (see SI Appendix, S2.1). We ranked competing
405 models using WAIC (Watanabe Akaike-Information-Criterion; SI Appendix, Table S2), a
406 within-sample model selection criteria analogous to AIC and robust to latent parameters
407 (52). We report findings for occupancy and detection parameters corresponding to the
408 overall best fitting model, presenting the results according to the highest ranked spatial-
409 scale associated with that structural covariate. Throughout, we consider parameters
410 influential if their 95% Bayesian credible interval did not overlap zero.

411

412 *Delineating restoration and conservation priority areas*

413 Focusing on seven high conservation value species, we implemented change point
414 analysis to link abrupt shifts in the occurrence state to specific forest structural attributes.
415 Using the “bcp” package in R, we employed a Bayesian algorithm (10,000 iterations,
416 2,000 burn-in) to identify upper and lower transition zone thresholds (53), characterized
417 by high rates of change in probability-of-use relative to spatial variation in structural
418 covariates. Thresholds were used to partition species response curves into three distinct
419 occurrence states (zone of stress: below the lower threshold; zone transition: between the
420 lower and upper threshold; zone of tolerance: above the upper threshold), each associated

421 with a specific management intervention (low priority, restoration priority and
422 conservation priority respectively; Fig. 3a). This protocol was embedded within a
423 spatially-explicit framework to prioritize degraded forests for conservation and
424 restoration. For each species, thresholds were implemented to reclassify LiDAR-derived
425 maps of significant structural covariates, which were averaged to generate single-species
426 consensus maps delineating priority conservation and restoration areas based on levels of
427 agreement between structural covariates (Fig. 3b-c). The species-specific prioritization
428 maps were reclassified according to areas of high consensus (i.e. full agreement between
429 all structural predictors) and averaged across focal taxa to produce a multi-species
430 zonation illustrating the proportion of target species that would benefit from management
431 action (Fig. 3d).

432

433 **Data Deposition**

434 Species detection data for 28 medium-large mammals and spatial delineations of LiDAR-
435 derived structural covariates are available for download from the Zenodo online
436 repository: *DOI TBC*

437

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602

603 **Table/Figure Legends**

604

605

606 **Table 1:** Structural covariates quantified from LiDAR-derived point-cloud data (25-50
607 pulses m⁻²; aggregated at 20 m resolution), capturing three distinct axes of forest structure
608 (horizontal structure, vertical structure, vertical heterogeneity). The covariates were
609 derived from either canopy height models (CHM) or plant area density (PAD)
610 distributions, estimated based on a one-dimensional Beer-Lambert-type model of light
611 propagation through the canopy (51). We calculated landscape context covariates to
612 describe forest extent and quality across broader spatial scales. Covariates were
613 aggregated across spatial extents informed by scale optimization methods to characterize
614 optimal scales of selection for predictors and determine sensitivity to spatial scale (SI
615 Appendix, Table S2).

616 **Figure 1:** Map of the study site and sampling design showing the broader geographic
617 context of the study site in Malaysia (inset), the classification of forest across the
618 disturbance gradient within the Stability of Altered Forest Ecosystems project area,
619 LiDAR flight path (black outline) and camera trap sampling locations ($N=74$).

620 **Figure 2:** Habitat use by tropical forest mammals in response to the degradation of three
621 structural axes: horizontal structure, vertical structure and vertical heterogeneity (see
622 Table 1 for a formal description of structural covariates). The top row represents
623 structural modification across a tropical disturbance gradient. Violin plots depict the
624 kernel density distribution of the data (colored shapes), wider sections indicate greater
625 probability that structural characteristics within a disturbance class will take a given
626 value. Boxplots contained therein describe the median (central vertical line), interquartile

627 range (outer vertical lines of the box) and 95% Bayesian Credible Interval (thin
628 horizontal lines). The middle row demonstrates probability-of-use of the mammal
629 community relative to structural alterations. Community trends are presented as predicted
630 responses derived from posterior means and 95% Bayesian Credible Intervals (BCI). The
631 bottom row denotes effect sizes for species-specific responses to structural modification.
632 We present effect sizes for species parameters as posterior means (points) and BCI
633 (horizontal lines). Grey points and horizontal lines represent non-responsive species, blue
634 suggests influential unimodal effects and red indicates influential non-linear associations
635 described by second-order polynomial terms. Effects for species-specific associations are
636 considered substantial if the BCI does not overlap zero (vertical dashed black line).

637 **Figure 3:** A spatial delineation of conservation and restoration priority areas for high
638 conservation value mammals, defined as endemic or classified as threatened
639 (Vulnerable/Endangered/Critically Endangered) by the IUCN (banded civet, binturong,
640 Bornean yellow muntjac, marbled cat, sambar deer, Sunda clouded leopard and tufted
641 ground squirrel), based on records of active habitat selection. Using the Sunda clouded
642 leopard as an example, response curves for each structural covariate (blue lines) were
643 partitioned into occurrence states (dashed vertical black lines), corresponding to priority
644 conservation and restoration areas using Bayesian change point analysis. Areas of the
645 curve exhibiting the highest rate of change in occupancy (peaks in the probability of
646 change red line graphs) were deemed optimal restoration (yellow-brown gradient), while
647 areas characterized with high stable occurrence were deemed optimal conservation areas
648 (green gradient) (a). Agreement between structural covariates was visualized in a

649 consensus map (b). This process was replicated for the remaining six other species (c).
650 Single-species consensus maps were combined to produce a multi-species zonation
651 indicating taxonomic agreement between proposed conservation/restoration areas. Forest
652 areas only qualified for intervention in areas of highest consensus for each species (d).