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1 **Determinants of sun bear *Helarctos malayanus* habitat use in Sabah, Malaysian Borneo and**  
2 **its predicted distribution under future forest degradation and loss**

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39 **Abstract**

40 Habitat loss, habitat degradation and poaching threaten the survival of large mammals in Southeast  
41 Asia. Studies on these threats tend to focus on small spatial scales (i.e. a protected area), precluding  
42 region-wide species assessments that can inform conservation management. Using existing camera  
43 trap data, we constructed occupancy models to understand patterns of habitat use as well as predict  
44 the distribution of sun bears *Helarctos malayanus* across Sabah, Malaysian Borneo. We found that  
45 bear distribution was related to above-ground carbon density and human settlement density,  
46 characteristics that describe the quality of bear habitat and a potential threat of poaching,  
47 respectively. Only half of sun bear distribution in Sabah falls within protected areas. Outside of  
48 protected areas, we predicted the reduction of sun bear distribution under simulated future  
49 conventional selective logging (forest degradation) and industrial tree plantation expansion (forest  
50 loss) scenarios. In the scenario involving forest degradation, sun bear distribution across Sabah  
51 only decreased by ~4%, supporting existing evidence that sun bears are resilient to selective  
52 logging impacts. Forest loss, however, had a larger impact, reducing sun bear distribution by ~11%  
53 in the scenario involving high forest loss. We recommend a focus on long term monitoring of sun  
54 bear habitat suitability trends, especially outside protected areas, along with strong anti-poaching  
55 efforts. Our study demonstrates the utility of pooling existing camera trap data to understand  
56 region-wide species distributions that could assist in setting conservation priorities.

57 **Keywords** sun bear, *Helarctos malayanus*, selective logging, industrial tree plantation, Sabah,  
58 Malaysian Borneo

59  
60 **Introduction**

61 Southeast Asian biodiversity is in decline due to overexploitation (Gray et al., 2017, 2018, Tilker  
62 et al., 2018, Tilker & Abrams et al. 2019) as well as forest loss and degradation (Curtis et al.,  
63 2018). In particular, the island of Borneo has seen drastic forest loss (Gaveau et al., 2014, 2016,  
64 2019), while the state of Sabah (Malaysian Borneo) has recorded some of the highest deforestation  
65 rates in Borneo (39% over four decades; Gaveau et al., 2014). A large portion of remaining forests  
66 (60%) have been degraded by selective logging (Gaveau et al., 2014). Despite this, many large  
67 mammal species persist in Borneo's human-modified landscapes, including the Sunda clouded  
68 leopard *Neofelis diardi*, Bornean orangutan *Pongo pygmaeus* and sun bear *Helarctos malayanus*  
69 ((Brodie et al., 2015; Sollmann et al., 2017; Deere et al., 2018).

70 The sun bear ranges from eastern India and southern China to Sumatra and Borneo (Scotson,  
71 Fredriksson, Augeri, et al., 2017). Although the species has been negatively impacted by  
72 deforestation (W-M. Wong, Leader-Williams, & Linkie, 2012; Scotson, Fredriksson, Ngoprasert,  
73 et al., 2017), it persists in selectively logged forests (Brodie et al., 2015; Lindsell et al., 2015; Adila  
74 et al., 2017; Jati et al., 2018), including those undergoing active timber extraction (Sollmann et al.,  
75 2017). Sun bears are able to survive in oil palm (Yue et al., 2015; Deere et al., 2018; Guharajan et  
76 al., 2018) and industrial tree plantations (McShea et al., 2009; Yaap et al., 2016; Wong et al.,

77 unpublished data), as long as forested areas are present. While sun bears are tolerant of certain  
78 levels of habitat degradation and modification, they show a general avoidance of humans (Augeri,  
79 2005; Brodie et al., 2015; Guharajan et al., 2018). Even when depredated human-grown crops,  
80 sun bears minimise their activity during hours when people are active (Fredriksson, 2005; Cheah,  
81 2013; Guharajan et al., 2017; Ross, Hearn, & Macdonald, 2017).

82 Apart from habitat degradation, poaching is another threat to sun bears. The ongoing wildlife  
83 snaring crisis in Southeast Asia (Gray et al., 2017, 2018; Tilker & Abrams et al., 2019) has likely  
84 contributed to the reduction of sun bear populations on mainland Southeast Asia. In Sabah,  
85 incidents of sun bear poaching have been reported (L. Liman, WWF-Malaysia, pers. comm.; J.  
86 Kissing, Sabah Forestry Department, pers. comm.) and bears with snare injuries have been  
87 documented through camera trap photographs (Hearn et al., unpublished data; Mohamed &  
88 Wilting, unpublished data). While it is unclear if these animals were targeted or represented  
89 incidental offtakes, these observations indicate that sun bears are falling prey to poaching across  
90 Sabah.

91 From the studies focusing on sun bears in Sabah (Normua et al., 2004; S. T. Wong, Servheen, &  
92 Ambu, 2004; S. T. Wong et al., 2005; Guharajan et al., 2018), only limited information can be  
93 gleaned on their habitat use trends and distribution at a state-wide scale. With this study, our aims  
94 were to: 1) understand drivers of sun bear habitat use at a Sabah-wide scale, 2) predict the  
95 distribution of sun bears across forested areas in Sabah, and 3) examine the impacts of simulated  
96 future forest degradation and loss on sun bear distribution. To accomplish this, we collated and  
97 used an extensive dataset of camera trap records of sun bears across Sabah.

## 98 **Materials and Methods**

### 99 *Study area*

100 Surveyed areas in Sabah included selectively logged (the logging of selected trees to allow for  
101 regeneration) and primary (not impacted by industrial activities, e.g. Danum Valley) forests  
102 (Brodie et al., 2015; Granados et al., 2017; Deere et al., 2018; Guharajan et al., 2018; Hearn et al.,  
103 2018; Mohamed et al., 2019). The majority of forested areas in Sabah have been logged (Gaveau  
104 et al., 2014), and the surveyed logged forests encompassed those actively/recently logged to those  
105 logged more than 10 years ago (Brodie et al., 2015; Mohamed et al., 2019). Selective logging  
106 practices in the past were not uniform, with some forests logged just once and others multiple  
107 times with slightly different techniques. This has resulted in present day forests with variable  
108 structure and canopy conditions. In terms of elevation, surveys were conducted in forests up to  
109 1,595 m a.s.l.

### 110 *Data collection*

111 We examined multiple camera trap surveys across Sabah that were conducted during 2007 – 2018  
112 (Table 1; Figure 1). Surveyed areas were mostly in eastern and central Sabah, with minimal effort  
113 in western Sabah especially and no surveys in coastal areas (i.e. mangroves). Despite this spatial

114 bias in the data, our surveyed areas were somewhat representative of conditions across Sabah  
115 (Figure S1), with surveys generally in forests of lower above-ground carbon density (logged) and  
116 further from anthropogenic features. This was expected as surveys were targeted in large, more  
117 remote forested areas (most of which have been logged) that corresponded with important natural  
118 habitats of sun bears in Sabah. The surveys were led by different researchers, but cameras were  
119 generally set up in locations that maximised detections of large mammals, such as wildlife trails,  
120 logging roads, skid trails and ridgelines. Camera traps were set perpendicular to the ground, at a  
121 height between 20 and 80 cm. Each station comprised 1- 5 camera traps, with a range of models  
122 used, including Reconyx RM45, HC500, PC800 and PC850; Bushnell TrophyCam; Cuddeback  
123 Expert and Capture; PantheraCam V3 and Snapshot Sniper P41. For stations with more than one  
124 camera trap, we pooled detections from all cameras and treated them as one sampling unit. We did  
125 not include camera trap stations that were placed in oil palm plantations ( $n = 26$ ), because none of  
126 these had detections of sun bears and the overall low sampling effort precluded us from making  
127 reasonable predictions.

128 To minimise the spatial autocorrelation resulting from a wide-ranging species (S. T. Wong,  
129 Servheen, & Ambu, 2004; Cheah, 2013), we only considered data from camera trap stations  
130 separated by a minimum distance of 1 km. We used R software (R Core Team, 2020) to randomly  
131 select a starting station, removed all stations that fell within 1 km of it and then moved to the next  
132 closest station to repeat the process. This was repeated one million times in a for-loop to find the  
133 optimal combination that retained the most stations. Our aim was to keep the maximum number  
134 of stations, regardless of whether or not they had sun bear detections.

### 135 *Preparation of occupancy covariates*

136 We selected all covariates based on an a priori approach. We considered covariates relating to sun  
137 bear habitat (above-ground carbon density) and poaching pressure (distance to roads and  
138 settlement density). We used above-ground carbon density as a measure of forest quality and level  
139 of degradation. We were unable to directly measure poaching pressure but surmised that roads  
140 (Clements et al., 2014; Brodie et al., 2015) and settlements (Tilker & Abrams et al., 2019) would  
141 be useful proxies for this threat. We also included covariates that encompassed both habitat  
142 preferences and poaching pressure (elevation, distance to oil palm plantation and distance to  
143 industrial tree plantation).

144 Due to the highly variable nature of past selective logging in Sabah, there are no readily available  
145 accurate logging records that could be used to separate survey areas by management history.  
146 Instead, we relied on another metric as a measure of forest quality: above-ground carbon density.  
147 We obtained a raster for forested areas in Sabah from 2016 (see Asner et al., 2018). This was  
148 derived using high resolution LiDAR flight data and field calibration plots from across Sabah.  
149 Above-ground carbon density provides information on carbon stored in living plant tissue located  
150 above the soil. The spatial coverage and quality of this data made it possible to better distinguish  
151 fine scale differences in various post-logged regenerating forest (as a result of different logging

152 intensity and years post-logging), something that indices such as Normalised Difference Moisture  
153 Index are unable to effectively do (Niedballa and Wilting, unpublished data).

154 We developed the elevation covariate from a 10 m interval contour vector file that was converted  
155 to a raster grid using ArcGIS 10.4 (Esri, Redlands, California, USA). For the other covariates, we  
156 digitised high-resolution true colour imagery (SPOT 5, 1.5 m resolution) from years 2014 and  
157 2015 to demarcate asphalt roads, oil palm estates, smallholding agriculture and identifiable areas  
158 of industrial tree plantations (i.e. acacia and eucalyptus). We decided to group smallholding  
159 agriculture and oil palm estates together as a single category (as oil palm plantation) as the former  
160 mostly contained oil palm. We then used the Euclidian distance tool in ArcGIS 10.4 to create  
161 continuous rasters of distance in meters from asphalt roads, oil palm and industrial tree plantation.

162 We obtained the locations of settlements from the Sabah Land and Surveys Department  
163 (<http://www.jtuwma.net/>, accessed 27<sup>th</sup> December 2017). We verified the accuracy of these data  
164 with high resolution SPOT 5, 1.5 m resolution imagery (from years 2014 and 2015); where  
165 necessary, removing, adding or moving points to the nearest identified settlement, assuming that  
166 the point was associated with the nearest settlement seen on the satellite images. We then used the  
167 R package *spatialEco* (Evans, 2018) to calculate kernel density estimate rasters within circular  
168 spatial areas with radii 10, 15 and 20 km. These radii were selected subjectively by referencing  
169 forest patrol data and reflected spatial extents that a poaching gang would be active in (R.  
170 Guharajan, unpublished data). Kernel densities were expressed as the number of settlements per  
171 unit area in 314.2 km<sup>2</sup> (10 km radius), 706.9 km<sup>2</sup> (15 km radius) and 1256.6 km<sup>2</sup> (20 km radius).  
172 All covariate rasters had a resolution of 91.7 x 91.7 m.

173 We extracted the values of distance to oil palm plantation, distance to industrial tree plantation,  
174 distance to road, settlement density, and elevation at each camera trap station. As above-ground  
175 carbon density values were not available for the location of four camera trap stations, we extracted  
176 the mean density value of this covariate within a buffer of 200 m centred around each station,  
177 thereby allowing every station to have a covariate value. With multiple researchers working in  
178 different landscapes, we found that covariate values at camera trap stations were fairly  
179 representative of forest conditions across Sabah (Figure S1). We tested for correlations among  
180 covariates using Pearson's correlation coefficient. Two covariates were considered to be correlated  
181 if the absolute value of the coefficient was > 0.7, and we avoided using correlated covariates in  
182 the same model. We centred and scaled each covariate to improve model convergence and  
183 facilitate comparison among fitted model coefficients.

#### 184 *Preparation of future forest degradation rasters*

185 We simulated forest degradation through conventional selective logging in: (1) production forest  
186 reserves and (2) state and alienated land forests. Production forest reserves are managed either for  
187 selective logging or for some form of commodity plantation. State and alienated land forests are  
188 largely unprotected forest areas, with the only difference being that alienated lands have a title  
189 issued. State and alienated land forests are generally small and isolated, while production forest

190 reserves are often large and form contiguous forest blocks with protected areas. In reality,  
191 conventional selective logging is extremely limited in its use today and is being phased out, with  
192 many forests logged using reduced-impact techniques. However, we are unable to accurately  
193 measure the real impact of reduced impact logging, as many forests logged using this technique  
194 were earlier logged conventionally. With these constrains, we use a simplified general approach  
195 and simulated how conventional selective logging effects might further degrade forests. We further  
196 assumed that this degradation would happen simultaneously, as we did not have any way to specify  
197 a time period.

198 We used the mean and standard deviation of above-ground carbon density from one forest reserve  
199 (Northern Kuamut Forest Reserve) that had been undergone conventional selective logging during  
200 2004-2012 as a reference to simulate the degradation caused by conventional selective logging.  
201 We selected Northern Kuamut Forest Reserve as it was among the most recent conventional  
202 selectively logged forests for which we had some information on when harvesting operations  
203 ceased. Furthermore, this reserve was one of the areas where LiDAR flights and calibration plots  
204 were focused, giving us more precise estimates of above-ground carbon density after selective  
205 logging. We did not use information from other forest reserves as we did not have information on  
206 past logging operations. For every individual production forest reserve (excluding Northern  
207 Kuamut), we reduced the value of each above-ground carbon density raster cell that was higher  
208 than the mean above-ground carbon density value for Northern Kuamut Forest Reserve. We did  
209 this to simulate a somewhat realistic harvesting situation where only those forests with higher  
210 above-ground carbon density than the mean of Northern Kuamut would be logged, and those with  
211 lower above-ground carbon density (i.e. those already degraded) would not. We used the R  
212 package *msm* (Jackson, 2011) to draw the reduced values from a truncated normal distribution (to  
213 ensure they were not higher than their original raster cell value) with the mean ( $76.7 \text{ Mg C ha}^{-1}$ )  
214 and standard deviation ( $31.8 \text{ Mg C ha}^{-1}$ ) from Northern Kuamut Forest Reserve. These new  
215 reduced values were then merged with the original above-ground carbon density raster using the  
216 R package *raster* (Hijmans, 2019) to create a raster for this scenario. We repeated the process with  
217 the same mean and standard deviation for the entire area of state and alienated land forests.

#### 218 *Preparation of future forest loss rasters*

219 We simulated potential forest loss in production forest reserves and in state and alienated land  
220 forests. Future forest loss in Sabah is likely to be driven by the conversion of forest to industrial  
221 tree plantations, as the state government has imposed restrictions on the expansion of oil palm  
222 plantations. In general, planters will establish new industrial tree plantations in degraded areas  
223 within each production forest reserve, although factors such as access to roads will also influence  
224 planting area choice. As we did not have information on where exactly these plantations would be  
225 established, we therefore relied on above-ground carbon density to identify these potential areas.  
226 For each individual production forest reserve, we selected the lowest 15% (low forest loss  
227 scenario) and 30% (high forest loss scenario) of above-ground carbon density raster values  
228 (representing the most degraded forests within each production forest reserve) and reduced them

229 to “0”. We reduced the values to “0” as the expansion of tree plantations required a clear cut,  
230 resulting in complete forest loss. As we did not have camera trap stations located within established  
231 industrial tree plantations, we were not able to assess future sun bear distribution in these areas  
232 and limited our inference only to the impact of future clear cutting on sun bear distribution. We  
233 then merged the new “0” values with the original above-ground carbon density raster using the R  
234 package *raster* (Hijmans, 2019) to create unique rasters for low forest loss and high forest loss  
235 scenarios in production forest reserves. We repeated the process for the whole area of state and  
236 alienated land forests, creating rasters for a low forest loss and high forest loss scenario  
237 respectively. Our scenarios created a matrix of forested areas and deforested areas in each  
238 production forest reserve and across state and alienated land. Similar to the forest degradation  
239 rasters, we were not able to specify a timeline of forest loss due to a lack of information on when  
240 tree plantations would be established across Sabah. Instead, we assumed that plantation expansion  
241 would happen simultaneously.

#### 242 *Occupancy analysis*

243 We interpret sun bear occupancy as habitat use, as the spacing between camera trap stations  
244 allowed for multiple stations to overlap a single bear’s home range (Normua et al., 2004; S. T.  
245 Wong, Servheen, & Ambu, 2004; Fredriksson, 2012; Cheah, 2013). We conducted all analyses in  
246 R version 3.5.3 (R Core Team, 2020). We used the package *camtrapR* (Niedballa et al., 2016) to  
247 create sun bear detection histories and effort matrices from camera trap data. We used 15-day  
248 occasion lengths, as this allowed us to obtain sufficient detections per occasion for model  
249 convergence (Brozovic et al., 2018). We truncated data from each camera trap station at a  
250 maximum of 120 days, if camera stations were active beyond that time. We did this in order to  
251 meet the closure assumption (MacKenzie et al., 2006), as a long survey period might have resulted  
252 in detections in previously unused sites which would result in inflated occupancy estimates. We  
253 felt that 120 days would allow us to include more detections of a large-bodied, long-lived and  
254 uncommonly detected mammal while not overestimating occupancy. To account for different  
255 methods of camera placement and number of cameras per station by each survey researcher, we  
256 included “researcher” as a covariate on detection. One researcher had different camera placements  
257 in 2008 (mostly on logging roads) and 2014 (mixture of logging roads, ridges and wildlife trails).  
258 Another researcher had repeated surveys in 2015 and 2016; however, in 2016 the number of  
259 cameras per station increased. To account for this, in both cases, we treated this as two separate  
260 researchers. We also included an effect of survey effort (number of days a station was active in an  
261 occasion) on detection.

262 We ran single-season occupancy models (MacKenzie et al., 2006) to investigate sun bear habitat  
263 use across Sabah using the R package *unmarked* (Fiske, Chandler, & others, 2011). We kept two  
264 covariates permanently on the detection component of the model (researcher and survey effort).  
265 We then ran two sets of occupancy models. The first set was to choose an appropriate circular  
266 spatial area radius for settlement density (10 km, 15 km and 20 km) to then use in the second set  
267 of models. For the first set, we ran three models where each had a different settlement density



268 circular spatial area radius as a covariate. We compared model Akaike's Information Criterion  
269 (AIC), and selected the 15 km bandwidth as it was ranked highest.

270 For the second set of models, we first ran the following single-covariate models, including  
271 quadratic terms: elevation, above-ground carbon density, settlement density (15 km), distance to  
272 asphalt road, distance to oil palm plantation and distance to industrial tree plantation. For each  
273 covariate, we compared if the linear or quadratic-term response had a better fit ( $p < 0.05$ ) and used  
274 these as the covariates for the next step. We then compared and ranked all single-covariate models  
275 using AIC. We further tested all possible combinations of covariates that performed better than  
276 the null model. We ranked and chose the best-ranked models using the difference in AIC ( $\Delta AIC$   
277  $\leq 2$ ). If a competing model only constituted a single-covariate extension of the better-ranked  
278 model, we ignored that competing model as it had very little additional explanatory power (Arnold,  
279 2010).

### 280 *Predictions of sun bear distribution*

281 To predict current sun bear distribution, we used the rasters of covariates (resolution at 91.7 x 91.7  
282 m) contained in the best-ranked occupancy model. We then used coefficient estimates from the  
283 best-ranked occupancy model together with the covariate rasters to predict sun bear distribution  
284 across Sabah. We only predicted sun bear distribution to areas of natural forest (primary and logged  
285 dipterocarp forest). As we had little or no camera stations in commodity plantations (oil palm and  
286 industrial tree), smallholding agriculture, mangrove forests and forests over 1,600 m in elevation,  
287 we masked these areas of predicted sun bear distribution. In addition, we wanted to avoid  
288 predicting sun bear distribution in small, isolated forest fragments. As there is no information on  
289 the minimum size of fragments considered too small to sustain sun bears, we conservatively  
290 considered 1 km<sup>2</sup> as the minimum size in which sun bears would be able to persist in. While it is  
291 unlikely a sun bear could survive long term in such as small patch, these areas might serve as  
292 stepping stones between larger forest areas. We resampled the predicted distribution to a resolution  
293 of 100 x 100 m raster grid cells using the *raster* package. We then used the *igraph* package (Csardi  
294 & Nepusz, 2006) to identify and remove isolated fragments that were 1 x 1 km or smaller in size.

295 To define a lower limit of sun bear occupancy, we compared three different methods: 5<sup>th</sup> percentile,  
296 10<sup>th</sup> percentile and maximum sensitivity and specificity. For the first two methods, we extracted  
297 the cell occupancy values from the distribution raster for each camera station that recorded a sun  
298 bear. We then used the percentile cut-off as the lower limit for sun bear occupancy. For the third  
299 method, we first extracted occupancy values for all camera stations, then used the occupancy  
300 values to generate a new set of detection/non-detection data. We applied the *optimal.thresholds*  
301 function from the R package *PresenceAbsence* (Freeman & Moisen, 2008) on these simulated data  
302 to obtain a lower limit for sun bear occupancy.

### 303 *Prediction of sun bear distribution under future forest degradation and loss*

304 To predict sun bear distribution under the future forest degradation scenarios in production forest  
305 reserves and state and alienated land, we used the above-ground carbon density rasters generated  
306 for those scenarios with the coefficient estimates from the best-ranked occupancy model. We then  
307 removed areas of the raster we were not able to predict to as well as areas below the minimum  
308 occupancy cut-off using the methods described above. To predict sun bear distribution under the  
309 low and high forest loss scenarios, we first overlaid the relevant scenario raster over the current  
310 sun bear distribution raster. We then removed areas of sun bear distribution that corresponded with  
311 cell values of “0” from the scenario raster. As we were unable to calculate 95% confidence  
312 intervals for the forest loss scenarios, we did not calculate them for the forest degradation scenarios  
313 either. Instead, we use our scenarios to highlight potential changes to current sun bear distribution.  
314 We further rounded area estimates to the hundreds to highlight the uncertainty of these estimates.

## 315 **Results**

316 Sun bears were detected at 375 out of 1,151 camera trap stations (33 %) across Sabah, with a total  
317 sampling effort of 130,078 camera trap days. We obtained 677 sun bear detections across eight  
318 15-day occasions for all stations. The AIC-best ranked model included above-ground carbon  
319 density and settlement density (Table 2). The model estimated occupancy (habitat use) to be 0.51  
320 (95% CI: 0.46 – 0.56) and detection estimates were generally low but varied considerably by  
321 researcher (0.07 to 0.39; Table S1). Above-ground carbon density was positively related to sun  
322 bear habitat use, while settlement density had a negative effect (Figure 2).

323 Sun bear occupancy lower limits for the 10<sup>th</sup> percentile (0.43) and maximum sensitivity and  
324 specificity (0.52) resulted in large areas of known sun bear distribution being removed (Table S2).  
325 As such, we used the 5<sup>th</sup> percentile (0.38) as our lower limit of occupancy. We predicted that sun  
326 bears currently occupy approximately 27900 km<sup>2</sup> of forest in Sabah, encompassing all the major  
327 forested landscapes (Figure 3). Totally protected areas (parks, wildlife sanctuaries and the  
328 following classes of forest reserves: wildlife, virgin jungle, amenity and protection) accounted for  
329 ~49% of the area occupied while production forest reserves and state and alienated land forest  
330 comprised ~43% and ~8% of the area occupied, respectively (Table 3).

331 Our scenarios showed that conventional selective logging in production forest reserves could  
332 reduce the total area occupied by sun bears by ~4%, while logging in state and alienated land  
333 forests would result in a ~1% reduction (Table 3, Figure S2). The low forest loss scenario in  
334 production forest reserves reduced the area occupied by sun bears by ~11% in production forest  
335 reserves and ~5% total. The high forest loss scenario meanwhile reduced the area occupied by  
336 ~24% in production forest reserves and ~11% total. In the scenarios with forest loss in state and  
337 alienated land, the total area occupied reduced by approximately ~1% (low forest loss) and ~2%  
338 (high forest loss; Table 3, Figure S2). Of all our scenarios, the high forest loss in production forest  
339 reserves scenario resulted in the most apparent loss of sun bear habitat in central and southwest  
340 Sabah (Figure 3). Similarly, the scenario involving conventional selective logging in production  
341 forest reserves did reduce the habitat suitability in central and southwest Sabah (Figure 3).

**342 Discussion**

343 We analysed the largest camera trap dataset compiled on sun bears in Malaysia that spanned a  
344 gradient of forest conditions, from primary to very degraded selectively logged. Our occupancy  
345 models identified above-ground carbon density as an important determinant of sun bear habitat  
346 use. Even at low above-ground carbon density values (i.e. very degraded forest areas), sun bear  
347 habitat use was estimated to be fairly high ( $> 0.25$ ; Figure 2), and increased in areas with higher  
348 above-ground carbon density (i.e. more intact forest areas). This resilient nature of sun bears  
349 surviving in human-altered forests has been well documented (Brodie, Giordano, & Ambu, 2015;  
350 Sollmann et al., 2017; Wearn et al., 2017; Deere et al., 2018; Guharajan et al., 2018; Jati et al.,  
351 2018).

352 Settlement density, a proxy for poaching pressure, was another important determinant of sun bear  
353 habitat use on a large scale. Negative associations between sun bears and human features such as  
354 villages and roads have been shown by other studies (Nazeri et al., 2012; Wai-Ming Wong &  
355 Linkie, 2012; Nazeri et al., 2014; Guharajan et al., 2018; Tee et al., 2021). The effects of poaching  
356 on sun bears are difficult to quantify, but it is reasonable to assume that bear populations are at  
357 risk from this threat and would avoid places they are likely to be in danger (Guharajan et al., 2018).  
358 Sun bears may be directly targeted by poachers or may be indirectly killed (i.e. by-catch from  
359 snaring). Poachers active in forest areas will use rural settlements as bases for their activities. Sun  
360 bears are primarily killed for their parts (Crudge et al., 2019), and within a two-year period (2015  
361 – 2017) Sabah authorities seized bear parts belonging to at least 10 individual bears (Or, Gomez,  
362 & Lau, 2017). It is widely assumed that the extent of killing is far greater than the number of dead  
363 sun bears indicated by seizures of bear parts (Crudge et al., 2019). Elsewhere in mainland  
364 Southeast Asia, poaching through the use of snares has seemingly extirpated sun bears in otherwise  
365 intact forests (Tilker & Abrams et al., 2019). As such, effective strategies against poaching are  
366 essential in ensuring that sun bears are protected across their range in Sabah.

367 Sun bears are predicted to be widespread across the natural forest landscapes of Sabah, and these  
368 predictions were similar to expert-derived range maps produced earlier, in which presence points  
369 and forest cover were used to map potential occurrence of sun bears (Scotson, Fredriksson, Augeri,  
370 et al., 2017; Crudge et al., 2019). The large areas of nearly contiguous forest in central and south-  
371 western Sabah are strongholds for the species. The highland areas along the west coast are also  
372 important for sun bear populations while large suitable areas in eastern Sabah are isolated from  
373 other forest blocks. Smaller pockets of forest ( $\geq 1 \text{ km}^2$ ) deemed suitable for sun bears were  
374 identified; however, due to the size and isolation of these fragments, it is uncertain if sun bears  
375 actually occur there and even if they do, the long-term viability of these individuals is questionable.  
376 However, these pockets may possess some value as stepping stones for sun bears travelling  
377 between larger forested areas.

378 Effective management of Sabah's totally protected areas should continue to be a priority  
379 conservation action for sun bears in Sabah. This is because the totally protected area network in

## Sun bear distribution

380 Sabah, which currently covers approximately 26% of Sabah's forested landscape, encompasses  
381 half the predicted sun bear distribution. It is commendable that the Sabah government is pushing  
382 to increase the protected area network to at least 30% of Sabah's forests by 2025 (Sabah Forestry  
383 Department, 2018) - this would serve to permanently secure more habitat in sun bear range,  
384 although a large proportion (~40%) of sun bear distribution would likely still fall outside totally  
385 protected areas. Law enforcement to reduce and prevent poaching in these protected areas is of  
386 paramount importance, to prevent the reduction of sun bear populations as observed in other  
387 protected areas across the species range (Tilker & Abrams et al., 2019).

388 Sustainable management of production forest reserves is important for the long-term survival of  
389 sun bears in Sabah, as we have shown that ~43% of predicted sun bear distribution lies within  
390 these forests. Sabah currently employs the sustainable forest management model in production  
391 forest reserves, utilising reduced impact logging techniques and ensuring that high conservation  
392 value areas are maintained (Sabah Forestry Department, 2018). This means that our scenarios  
393 involving the more destructive conventional selective logging are unlikely to happen. However,  
394 the degradation resulting from conventional logging appeared to have a weak impact on overall  
395 sun bear distribution in Sabah (~4% reduction in area), with the estimated reduction likely to be  
396 zero. Despite having higher occupancy in better-quality forests, sun bears seem able to adapt to  
397 habitat alterations caused by selective logging (S. T. Wong, Servheen, & Ambu, 2004; Brodie et  
398 al., 2015; Lindsell et al., 2015; Yue et al., 2015; Adila et al., 2017; Wearn et al., 2017; Jati et al.,  
399 2018; Hwang et al., 2021).

400 Our scenarios with industrial tree plantation expansion (deforestation) in production forest reserves  
401 had the biggest impact on sun bear distribution. Industrial tree species are now the main commodity  
402 available to be grown in Sabah, given restrictions on oil palm planting, and are thus the most likely  
403 to replace forests. Certain areas within production forest reserves in north, central and eastern  
404 Sabah have already been converted to these plantations. Rates of plantation expansion could  
405 possibly increase as climate change makes higher elevation areas more amenable to lowland tree  
406 production (Brodie, 2016).

407 The area occupied by sun bears in state and alienated land forests was small, due to the overall  
408 small size and fragmented nature of these forests. Future activities involving either conventional  
409 selective logging or the expansion of industrial tree plantation in these forests are unlikely to have  
410 much of an impact on overall sun bear distribution in Sabah. However, with the goal of expanding  
411 and connecting Sabah's protected area network, state and alienated land forests could serve as  
412 corridors. Although the area occupied by sun bears in these forests is small, replacing these areas  
413 with monocultures could still have a negative impact on sun bears, in particular reducing  
414 connectivity and gene flow between populations.

415 Other studies that investigated the impacts of forest loss on sun bears noted somewhat similar  
416 trends to our results but differed in scale. A study in Sumatra that used camera trap data found  
417 some evidence for a reduction in bear habitat use in one area undergoing rapid deforestation (W-

418 M. Wong, Leader-Williams, & Linkie, 2012). Another study projected forest loss in insular  
419 Southeast Asia (including Malaysia) from 2000 to 2030 and estimated that sun bear populations  
420 would decline by 50% (Scotson, Fredriksson, Ngoprasert, et al., 2017). However, this particular  
421 study inferred constant forest loss rates from 2000 to 2030 which resulted in more drastic  
422 reductions in Sabah compared to predictions from this study. Sabah's (and Malaysia's) current  
423 forest loss rates is much lower than in the last decade (Weisse & Goldman, 2021), largely due to  
424 policies limiting current commodity expansion. Therefore, these more extreme forest loss  
425 predictions are highly unlikely to happen. In our scenarios, we combined future deforestation to  
426 certain parts of production forest reserves to provide a more realistic scenario, as forest loss is very  
427 unlikely to take place in totally protected areas (which now account for ~26% of forested areas).  
428 In general however, the results of these other studies together with ours highlight how careful  
429 planning and thought is needed when converting forest to industrial tree plantations, as this will  
430 certainly have profound impacts on sun bears and other species in the long run.

431 One caveat of our study was that we used camera trap data from studies spread over a long period  
432 (2007 – 2018), with a possibility that sun bear populations at some surveyed areas might have  
433 undergone changes (i.e. subjected to increased poaching pressure) since the time of the study. In  
434 such cases, our predictions would not be entirely accurate for those areas. Similarly, our  
435 predictions for western Sabah may be biased as we only had limited camera trap data from this  
436 region. Upcoming camera trap surveys in western Sabah will be able to test the accuracy of our  
437 predictions for this region. We were also limited to covariates obtained from years 2014-2016,  
438 which did not temporally overlap all camera trap data. Our forest degradation and loss scenarios  
439 were each assumed to occur simultaneously, with no specific time frame for each scenario due to  
440 a lack of information on future land use change. This only allows for a general interpretation of  
441 sun bear habitat change in the context of the scenarios. Lastly, we could not compile a large enough  
442 dataset to investigate the direct effects of commodity plantations (both oil palm and industrial tree)  
443 on sun bears. Interestingly, the 26 camera stations in oil palm (that were removed from the final  
444 analysis) had no sun bear detections. Another study in Sabah with camera traps in oil palm  
445 plantations close to natural forest obtained few detections of sun bears (0.08 detections / 100 trap  
446 nights) and was not able to estimate bear occupancy in plantations (Yue et al., 2015). In landscapes  
447 with industrial tree plantations, sun bears have only been recorded in or near natural forest patches  
448 (McShea et al., 2009; Yaap et al., 2016), with no evidence to suggest that bears can utilise only  
449 planted areas. Further studies within the planted areas of both oil palm and industrial tree  
450 plantations would serve to better elucidate sun bear responses towards these land cover types.  
451 However, based on studies implemented to date (Normua et al., 2004; S. T. Wong, Servheen, &  
452 Ambu, 2004; S. T. Wong et al., 2005; Wai-Ming Wong & Linkie, 2012; W-M. Wong, Leader-  
453 Williams, & Linkie, 2012; Scotson, Fredriksson, Ngoprasert, et al., 2017; Guharajan et al., 2018),  
454 it seems more prudent to focus conservation attention on sun bears in natural forest.

## 455 **Conclusion**

456 Our study has shown that Sabah still harbours large areas of suitable habitat for sun bears,  
457 highlighting bear distribution in forests outside protected areas. It is essential to exercise proper  
458 planning in expanding industrial tree plantations within production forest reserves, as this would  
459 certainly have a big impact on bears. The focus in sun bear research must shift away from pilot  
460 surveys to repeated surveys across different forest protection classes to more accurately monitor  
461 sun bear habitat suitability in the face of land-use changes and potential increases in poaching. We  
462 commend the focus on enhancing the protection of Sabah's forests (i.e. increasing the amount of  
463 protected areas). Most importantly, it is crucial that sufficient resources are channelled towards  
464 enforcement activities.

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#### 468 **Competing interests**

469 The authors have no competing interests to disclose.

#### 470 **Author contributions**

471 RG, JFA, BG and AW conceived the study. NKA, HYL, NJD, MJS, BG, PCG, JFB, AG, SWT,  
472 AJH, JR, DWM, AM, and STW (Seth T. Wong) contributed data. RG, JFA and NJD conducted  
473 the analysis. RG, JFA, GRC and AW wrote the manuscript with comments provided by all authors.

#### 474 **Data availability**

475 Data for this study came from multiple institutions each with their own set of restrictions, and thus  
476 we are unable to make the raw data available for this study.

#### 477 **Compliance with ethical standards**

478 Our study did not involve human or animal subjects.

#### 479 **Consent to publish**

480 All authors consent to this study being published.

#### 481 **Plant reproducibility**

482 We did not use any live samples for this study.

#### 483 **Clinical trials registration**

484 Our study does not include clinical trials.

#### 485 **References**

## Sun bear distribution

- 486 Adila, N., Sasidhran, S., Kamarudin, N., Puan, C. L., Azhar, B., & Lindenmayer, D. B. (2017). Effects of peat  
487 swamp logging and agricultural expansion on species richness of native mammals in Peninsular Malaysia.  
488 *Basic Appl. Ecol.* **22**, 1–10.
- 489 Ancrenaz, M., Oram, F., Ambu, L., Lackman, I., Ahmad, E., Elahan, H., Kler, H., Abram, N. K., & Meijaard, E.  
490 (2015). Of Pongo, palms and perceptions: a multidisciplinary assessment of Bornean orang-utans *Pongo*  
491 *pygmaeus* in an oil palm context. *Oryx* **49**, 465–472.
- 492 Asner, G. P., Brodrick, P. G., Philipson, C., Vaughn, N. R., Martin, R. E., Knapp, D. E., Heckler, J., Evans, L. J.,  
493 Jucker, T., Goossens, B., Stark, D. J., Reynolds, G., Ong, R., Renneboog, N., Kugan, F., & Coomes, D. A.  
494 (2018). Mapped aboveground carbon stocks to advance forest conservation and recovery in Malaysian  
495 Borneo. *Biol. Conserv.* **217**, 289–310.
- 496 Augeri, D. M. (2005). On the biogeographic ecology of the Malayan sun bear (PhD dissertation). University of  
497 Cambridge.
- 498 Azhar, B., Lindenmayer, D. B., Wood, J., Fischer, J., & Zakaria, M. (2014). Ecological impacts of oil palm  
499 agriculture on forest mammals in plantation estates and smallholdings. *Biodivers. Conserv.* **23**, 1175–1191.
- 500 Brodie, J. F. (2016). Synergistic effects of climate change and agricultural land use on mammals. *Front. Ecol.*  
501 *Environ.* **14**, 20–26.
- 502 Brodie, J. F., Giordano, A. J., & Ambu, L. (2015). Differential responses of large mammals to logging and edge  
503 effects. *Mamm. Biol. - Z. Für Säugetierkd.* **80**, 7–13.
- 504 Brodie, J. F., Giordano, A. J., Zipkin, E. F., Bernard, H., Mohd-Azlan, J., & Ambu, L. (2015). Correlation and  
505 persistence of hunting and logging impacts on tropical rainforest mammals: Logging, Hunting, and  
506 Mammal Diversity. *Conserv. Biol.* **29**, 110–121.
- 507 Brozovic, R., Abrams, J. F., Mohamed, A., Wong, S. T., Niedballa, J., Bhagwat, T., Sollmann, R., Mannan, S.,  
508 Kissing, J., & Wilting, A. (2018). Effects of forest degradation on the moonrat *Echinosorex gymnura* in  
509 Sabah, Malaysian Borneo. *Mamm. Biol.* **93**, 135–143.
- 510 Cheah, C. P. I. (2013). The ecology of Malayan sun bears (*Helarctos malayanus*) at the Krau Wildlife Reserve,  
511 Pahang, Malaysia and adjacent plantations (PhD dissertation). Universiti Putra Malaysia.

## Sun bear distribution

- 512 Clements, G. R., Lynam, A. J., Gaveau, D., Yap, W. L., Lhota, S., Goosem, M., Laurance, S., & Laurance, W. F.  
513 (2014). Where and How Are Roads Endangering Mammals in Southeast Asia's Forests? (L. Kumar,  
514 Ed.)*PLoS ONE* **9**, e115376.
- 515 Crudge, B., Lees, C., Hunt, M., Steinmetz, R., & Garshelis, D. L. (2019). Sun bears: Global status review &  
516 conservation action plan, 2019-2028. IUCN SSC Bear Specialist Group / IUCN SSC Conservation  
517 Planning Specialist Group / Free the Bears / TRAFFIC.
- 518 Csardi, G., & Nepusz, T. (2006). The igraph software package for complex network research. *InterJournal Complex*  
519 *Syst.* **1695**.
- 520 Curtis, P. G., Slay, C. M., Harris, N. L., Tyukavina, A., & Hansen, M. C. (2018). Classifying drivers of global forest  
521 loss. *Science* **361**, 1108–1111.
- 522 Deere, N. J., Guillera-Aroita, G., Baking, E. L., Bernard, H., Pfeifer, M., Reynolds, G., Wearn, O. R., Davies, Z. G.,  
523 & Struebig, M. J. (2018). High Carbon Stock forests provide co-benefits for tropical biodiversity. (A.  
524 Magrach, Ed.)*J. Appl. Ecol.* **55**, 997–1008.
- 525 Evans, J. S. (2018). *\_spatialEco\_*.
- 526 Fiske, I., Chandler, R., & others. (2011). unmarked: An R package for fitting hierarchical models of wildlife  
527 occurrence and abundance. *J. Stat. Softw.* **43**, 1–23.
- 528 Fredriksson, G. M. (2005). Human-sun bear conflicts in East Kalimantan, Indonesian Borneo. *Ursus* **16**, 130–137.
- 529 Fredriksson, G. M. (2012, November). Effects of El-Nino and large-scale forest fires on the ecology and  
530 conservation of Malayan sun bears (*Helarctos malayanus*) in East Kalimantan, Indonesian Borneo (PhD  
531 dissertation). Universiteit van Amsterdam.
- 532 Freeman, E. A., & Moisen, G. (2008). PresenceAbsence: An R Package for Presence-Absence Model Analysis. *J.*  
533 *Stat. Softw.* **23**, 1–31.
- 534 Gaveau, D. L. A., Locatelli, B., Salim, M. A., Yaen, H., Pacheco, P., & Sheil, D. (2019). Rise and fall of forest loss  
535 and industrial plantations in Borneo (2000-2017). *Conserv. Lett.* **12**, e12622.
- 536 Gaveau, D. L. A., Sheil, D., Husnayaen, Salim, M. A., Arjasakusuma, S., Ancrenaz, M., Pacheco, P., & Meijaard, E.  
537 (2016). Rapid conversions and avoided deforestation: examining four decades of industrial plantation  
538 expansion in Borneo. *Sci. Rep.* **6**.



## Sun bear distribution

- 539 Gaveau, D. L. A., Sloan, S., Molidena, E., Yaen, H., Sheil, D., Abram, N. K., Ancrenaz, M., Nasi, R., Quinones, M.,  
540 Wielaard, N., & Meijaard, E. (2014). Four Decades of Forest Persistence, Clearance and Logging on  
541 Borneo. (K. Bawa, Ed.)*PLoS ONE* **9**, e101654.
- 542 Granados, A., Brodie, J. F., Bernard, H., & O'Brien, M. J. (2017). Defaunation and habitat disturbance interact  
543 synergistically to alter seedling recruitment. *Ecol. Appl.* **27**, 2092–2101.
- 544 Gray, T. N. E., Hughes, A. C., Laurance, W. F., Long, B., Lynam, A. J., O'Kelly, H., Ripple, W. J., Seng, T.,  
545 Scotson, L., & Wilkinson, N. M. (2018). The wildlife snaring crisis: an insidious and pervasive threat to  
546 biodiversity in Southeast Asia. *Biodivers. Conserv.* **27**, 1031–1037.
- 547 Gray, T. N. E., Lynam, A. J., Seng, T., Laurance, W. F., Long, B., Scotson, L., & Ripple, W. J. (2017). Wildlife-  
548 snaring crisis in Asian forests. *Science* **355**, 255–256.
- 549 Guharajan, R., Abram, N. K., Maggana, M. A., Goossens, B., Wong, S. T., Nathan, S. K. S. S., & Garshelis, D. L.  
550 (2017). Does the Vulnerable sun bear *Helarctos malayanus* damage crops and threaten people in oil palm  
551 plantations? *Oryx* **53**, 611–619.
- 552 Guharajan, R., Arnold, T. W., Bolongon, G., Dibden, G. H., Abram, N. K., Teoh, S. W., Maggana, M. A., Goossens,  
553 B., Wong, S. T., Nathan, S. K. S. S., & Garshelis, D. L. (2018). Survival strategies of a frugivore, the sun  
554 bear, in a forest-oil palm landscape. *Biodivers. Conserv.* **27**, 3657–3677.
- 555 Hearn, A. J., Cushman, S. A., Ross, J., Goossens, B., Hunter, L. T. B., & Macdonald, D. W. (2018). Spatio-temporal  
556 ecology of sympatric felids on Borneo. Evidence for resource partitioning? (L. Bosso, Ed.)*PLOS ONE* **13**,  
557 e0200828.
- 558 Hearn, A. J., Ross, J., Bernard, H., Bakar, S. A., Goossens, B., Hunter, L. T. B., & Macdonald, D. W. (2017).  
559 Responses of Sunda clouded leopard *Neofelis diardi* population density to anthropogenic disturbance:  
560 refining estimates of its conservation status in Sabah. *Oryx* 1–11.
- 561 Hijmans, R. J. (2019). raster: Geographic Data Analysis and Modeling.
- 562 Jackson, C. H. (2011). Multi-State Models for Panel Data: The msm Package for R. *J. Stat. Softw.* **38**, 1–29.
- 563 Jati, A. S., Samejima, H., Fujiki, S., Kurniawan, Y., Aoyagi, R., & Kitayama, K. (2018). Effects of logging on  
564 wildlife communities in certified tropical rainforests in East Kalimantan, Indonesia. *For. Ecol. Manag.* **427**,  
565 124–134.

## Sun bear distribution

- 566 Lindsell, J. A., Lee, D. C., Powell, V. J., & Gemita, E. (2015). Availability of large seed-dispersers for restoration of  
567 degraded tropical forest. *Trop. Conserv. Sci.* **8**, 17–27.
- 568 Luskin, M. S., Christina, E. D., Kelley, L. C., & Potts, M. D. (2014). Modern Hunting Practices and Wild Meat  
569 Trade in the Oil Palm Plantation-Dominated Landscapes of Sumatra, Indonesia. *Hum. Ecol.* **42**, 35–45.
- 570 MacKenzie, D. I., Nichols, J. D., Royle, J. A., Pollock, K. H., Bailey, L. L., & Hines, J. E. (2006). Occupancy  
571 Modelling and Estimation. San Diego, CA: Academic.
- 572 McShea, W. J., Stewart, C., Peterson, L., Erb, P., Stuebing, R., & Gimán, B. (2009). The importance of secondary  
573 forest blocks for terrestrial mammals within an Acacia/secondary forest matrix in Sarawak, Malaysia. *Biol.*  
574 *Conserv.* **142**, 3108–3119.
- 575 Mohamed, A., Sollmann, R., Wong, S. T., Niedballa, J., Abrams, J. F., Kissing, J., & Wilting, A. (2019). Counting  
576 Sunda clouded leopards with confidence: incorporating individual heterogeneity in density estimates. *Oryx*  
577 **1–10**.
- 578 Nazeri, M., Jusoff, K., Madani, N., Mahmud, A. R., Bahman, A. R., & Kumar, L. (2012). Predictive Modeling and  
579 Mapping of Malayan Sun Bear (*Helarctos malayanus*) Distribution Using Maximum Entropy. (S. Walker,  
580 Ed.) *PLoS ONE* **7**, e48104.
- 581 Nazeri, M., Kumar, L., Jusoff, K., & Bahaman, A. R. (2014). Modeling the potential distribution of sun bear in Krau  
582 wildlife reserve, Malaysia. *Ecol. Inform.* **20**, 27–32.
- 583 Niedballa, J., Sollmann, R., Courtiol, A., & Wilting, A. (2016). camtrapR: an R package for efficient camera trap  
584 data management. *Methods Ecol. Evol.* **7**, 1457–1462.
- 585 Normua, F., Higashi, S., Ambu, L., & Mohamed, M. (2004). Notes on oil palm plantation use and seasonal spatial  
586 relationships of sun bears in Sabah, Malaysia. *Ursus* **15**, 227–231.
- 587 Or, O. C., Gomez, L., & Lau, C. F. (2017). Recent Reports of Seizures and Poaching of Sun Bears in Malaysia. *Int.*  
588 *Bear News* **26**, 17–18.
- 589 R Core Team. (2019). R: A language and environment for statistical computing. R Foundation for Statistical  
590 Computing, Vienna, Austria.
- 591 Ross, J., Hearn, A. J., & Macdonald, D. W. (2017). The Bornean carnivore community: lessons from a little-known  
592 guild. In D. W. Macdonald, C. Newman, & L. A. Harrington (Eds.), *Biol. Conserv. Musteloids*. pp. 326–  
593 339. Oxford: Oxford University Press.

## Sun bear distribution

- 594 Roundtable on Sustainable Palm Oil. (2018). Principles and criteria for the production of sustainable palm oil. Kuala  
595 Lumpur, Malaysia.
- 596 Sabah Forestry Department. (2018). Sabah Forest Policy 2018. Sandakan, Sabah, Malaysia.
- 597 Scotson, L., Fredriksson, G., Augeri, D., Cheah, C., Ngoprasert, D., & Wai-Ming, W. (2017). *Helarctos malayanus*.  
598 The IUCN Red List of Threatened Species 2017. International Union for Conservation of Nature.
- 599 Scotson, L., Fredriksson, G., Ngoprasert, D., Wong, W.-M., & Fieberg, J. (2017). Predicting range-wide sun bear  
600 population trends using tree cover and camera-trap bycatch data. *PLoS One* **12**, e0185336.
- 601 Seaman, D. J. I., Bernard, H., Ancrenaz, M., Coomes, D., Swinfield, T., Milodowski, D. T., Humle, T., & Struebig,  
602 M. J. (2019). Densities of Bornean orang-utans (*Pongo pygmaeus morio*) in heavily degraded forest and  
603 oil palm plantations in Sabah, Borneo. *Am. J. Primatol.*
- 604 Sollmann, R., Mohamed, A., Niedballa, J., Bender, J., Ambu, L., Lagan, P., Mannan, S., Ong, R. C., Langner, A.,  
605 Gardner, B., & Wilting, A. (2017). Quantifying mammal biodiversity co-benefits in certified tropical  
606 forests. (H. Regan, Ed.) *Divers. Distrib.* **23**, 317–328.
- 607 Tilker, A., Abrams, J. F., Mohamed, A., Nguyen, A., Wong, S. T., Sollmann, R., Niedballa, J., Bhagwat, T., Gray,  
608 T. N. E., Rawson, B. M., Guegan, F., Kissing, J., Wegmann, M., & Wilting, A. (2019). Habitat degradation  
609 and indiscriminate hunting differentially impact faunal communities in the Southeast Asian tropical  
610 biodiversity hotspot. *Commun. Biol.* **2**.
- 611 Tilker, A., Nguyen, A., Abrams, J. F., Bhagwat, T., Le, M., Van Nguyen, T., Nguyen, A. T., Niedballa, J.,  
612 Sollmann, R., & Wilting, A. (2018). A little-known endemic caught in the South-east Asian extinction  
613 crisis: the Annamite striped rabbit *Nesolagus timminsi*. *Oryx* 1–10.
- 614 Wearn, O. R., Rowcliffe, J. M., Carbone, C., Pfeifer, M., Bernard, H., & Ewers, R. M. (2017). Mammalian species  
615 abundance across a gradient of tropical land-use intensity: A hierarchical multi-species modelling  
616 approach. *Biol. Conserv.* **212**, 162–171.
- 617 Wong, S. T., Servheen, C., Ambu, L., & Norhayati, A. (2005). Impacts of fruit production cycles on Malayan sun  
618 bears and bearded pigs in lowland tropical forest of Sabah, Malaysian Borneo. *J. Trop. Ecol.* **21**, 627–639.
- 619 Wong, S. T., Servheen, C. W., & Ambu, L. (2004). Home range, movement and activity patterns, and bedding sites  
620 of Malayan sun bears *Helarctos malayanus* in the Rainforest of Borneo. *Biol. Conserv.* **119**, 169–181.

## Sun bear distribution

- 621 Wong, W.-M., Leader-Williams, N., & Linkie, M. (2012). Quantifying changes in sun bear distribution and their  
622 forest habitat in Sumatra: Sun bear population trends and deforestation in Sumatra. *Anim. Conserv.* **16**,  
623 216–223.
- 624 Wong, W.-M., & Linkie, M. (2012). Managing sun bears in a changing tropical landscape. *Divers. Distrib.* **19**, 700–  
625 709.
- 626 Yaap, B., Magrath, A., Clements, G. R., McClure, C. J. W., Paoli, G. D., & Laurance, W. F. (2016). Large Mammal  
627 Use of Linear Remnant Forests in an Industrial Pulpwood Plantation in Sumatra, Indonesia. *Trop. Conserv.*  
628 *Sci.* **9**, 194008291668352.
- 629 Yue, S., Brodie, J. F., Zipkin, E. F., & Bernard, H. (2015). Oil palm plantations fail to support mammal diversity.  
630 *Ecol. Appl.* **25**, 2285–2292.

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