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

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Abstract

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

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

Introduction

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

The sun bear ranges from eastern India and southern China to Sumatra and Borneo (Scotson, Fredriksson, Augeri, et al., 2017). Although the species has been negatively impacted by deforestation (W-M. Wong, Leader-Williams, & Linkie, 2012; Scotson, Fredriksson, Ngoprasert, et al., 2017), it persists in selectively logged forests (Brodie et al., 2015; Lindsell et al., 2015; Adila et al., 2017; Jati et al., 2018), including those undergoing active timber extraction (Sollmann et al., 2017). Sun bears are able to survive in oil palm (Yue et al., 2015; Deere et al., 2018; Guharajan et al., 2018) and industrial tree plantations (McShea et al., 2009; Yaap et al., 2016; Wong et al., unpublished data), as long as forested areas are present. While sun bears are tolerant of certain levels of habitat degradation and modification, they show a general avoidance of humans (Augeri, 2005; Brodie et al., 2015; Guharajan et al., 2018). Even when depredating human-grown crops, sun bears minimise their activity during hours when people are active (Fredriksson, 2005; Cheah, 2013; Guharajan et al., 2017; Ross, Hearn, & Macdonald, 2017).

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

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

Materials and Methods

Study area

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

Data collection

We examined multiple camera trap surveys across Sabah that were conducted during 2007 – 2018 (Table 1; Figure 1). Surveyed areas were mostly in eastern and central Sabah, with minimal effort in western Sabah especially and no surveys in coastal areas (i.e. mangroves). Despite this spatial bias in the data, our surveyed areas were somewhat representative of conditions across Sabah (Figure S1), with surveys generally in forests of lower above-ground carbon density (logged) and further from anthropogenic features. This was expected as surveys were targeted in large, more remote forested areas (most of which have been logged) that corresponded with important natural habitats of sun bears in Sabah. The surveys were led by different researchers, but cameras were generally set up in locations that maximised detections of large mammals, such as wildlife trails, logging roads, skid trails and ridgelines. Camera traps were set perpendicular to the ground, at a height between 20 and 80 cm. Each station comprised 1- 5 camera traps, with a range of models used, including Reconyx RM45, HC500, PC800 and PC850; Bushnell TrophyCam; Cuddeback Expert and Capture; PantheraCam V3 and Snapshot Sniper P41. For stations with more than one camera trap, we pooled detections from all cameras and treated them as one sampling unit. We did not include camera trap stations that were placed in oil palm plantations (n = 26), because none of these had detections of sun bears and the overall low sampling effort precluded us from making reasonable predictions.

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

Preparation of occupancy covariates

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

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

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

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

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

Preparation of future forest degradation rasters

We simulated forest degradation through conventional selective logging in: (1) production forest reserves and (2) state and alienated land forests. Production forest reserves are managed either for selective logging or for some form of commodity plantation. State and alienated land forests are largely unprotected forest areas, with the only difference being that alienated lands have a title issued. State and alienated land forests are generally small and isolated, while production forest reserves are often large and form contiguous forest blocks with protected areas. In reality, conventional selective logging is extremely limited in its use today and is being phased out, with many forests logged using reduced-impact techniques. However, we are unable to accurately measure the real impact of reduced impact logging, as many forests logged using this technique were earlier logged conventionally. With these constrains, we use a simplified general approach and simulated how conventional selective logging effects might further degrade forests. We further assumed that this degradation would happen simultaneously, as we did not have any way to specify a time period.

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

Preparation of future forest loss rasters

We simulated potential forest loss in production forest reserves and in state and alienated land forests. Future forest loss in Sabah is likely to be driven by the conversion of forest to industrial tree plantations, as the state government has imposed restrictions on the expansion of oil palm plantations. In general, planters will establish new industrial tree plantations in degraded areas within each production forest reserve, although factors such as access to roads will also influence planting area choice. As we did not have information on where exactly these plantations would be established, we therefore relied on above-ground carbon density to identify these potential areas. For each individual production forest reserve, we selected the lowest 15% (low forest loss scenario) and 30% (high forest loss scenario) of above-ground carbon density raster values (representing the most degraded forests within each production forest reserve) and reduced them to “0”. We reduced the values to “0” as the expansion of tree plantations required a clear cut, resulting in complete forest loss. As we did not have camera trap stations located within established industrial tree plantations, we were not able to assess future sun bear distribution in these areas and limited our inference only to the impact of future clear cutting on sun bear distribution. We then merged the new “0” values with the original above-ground carbon density raster using the R package *raster* (Hijmans, 2019) to create unique rasters for low forest loss and high forest loss scenarios in production forest reserves. We repeated the process for the whole area of state and alienated land forests, creating rasters for a low forest loss and high forest loss scenario respectively. Our scenarios created a matrix of forested areas and deforested areas in each production forest reserve and across state and alienated land. Similar to the forest degradation rasters, we were not able to specify a timeline of forest loss due to a lack of information on when tree plantations would be established across Sabah. Instead, we assumed that plantation expansion would happen simultaneously.

Occupancy analysis

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

We ran single-season occupancy models (MacKenzie et al., 2006) to investigate sun bear habitat use across Sabah using the R package *unmarked* (Fiske, Chandler, & others, 2011). We kept two covariates permanently on the detection component of the model (researcher and survey effort). We then ran two sets of occupancy models. The first set was to choose an appropriate circular spatial area radius for settlement density (10 km, 15 km and 20 km) to then use in the second set of models. For the first set, we ran three models where each had a different settlement density circular spatial area radius as a covariate. We compared model Akaike's Information Criterion (AIC), and selected the 15 km bandwidth as it was ranked highest.

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

Predictions of sun bear distribution

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

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

Prediction of sun bear distribution under future forest degradation and loss

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

Results

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

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

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

Discussion

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

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

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

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

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

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

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

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

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

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

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

Conclusion

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

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Competing interests

The authors have no competing interests to disclose.

Author contributions

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

Data availability

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

Compliance with ethical standards

Our study did not involve human or animal subjects.

Consent to publish

All authors consent to this study being published.

Plant reproducibility

We did not use any live samples for this study.

Clinical trials registration

Our study does not include clinical trials.

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