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# Drivers of Bornean orangutan distribution across a multiple-use tropical landscape

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**Abstract:** Logging and conversion of tropical forests in Southeast Asia have resulted in the expansion of landscapes containing a mosaic of habitats that may vary in their ability to sustain local biodiversity. However, the complexity of these landscapes makes it difficult to assess abundance and distribution of some species using ground-based surveys alone. Here we deployed a combination of ground-transects and aerial surveys to determine drivers of the Critically Endangered Bornean Orangutan (*Pongo pygmaeus*) distribution across a large multiple-use landscape in Sabah, Malaysian Borneo. Ground-transects and aerial surveys using drones were conducted for orangutan nests and strangler fig trees (an important food resource) in 48 survey areas across 76 $km^2$, within a study landscape of 261 $km^2$. Orangutan nest count data were fitted to models accounting for variation in land use, above-ground carbon density (ACD; a surrogate for forest quality), strangler fig density, and elevation (between 117 and 675 m). Orangutan nest counts were significantly higher in all land uses possessing natural forest cover, regardless of degradation status, than in monoculture plantations. Within these natural forests, nest counts increased with higher ACD and strangler fig density, but not with elevation. In logged forest (ACD 14 – 150 Mg $ha^{-1}$), strangler fig density had a significant, positive relationship with orangutan nest counts, but this relationship disappeared in forest with higher carbon content (ACD 150- 209 Mg $ha^{-1}$). Based on an area-to-area comparison, orangutan nest counts from ground transects were higher than from counts derived from aerial surveys, but this did not constitute a statistically significant difference. Although the difference in nest counts was not significantly different, this analysis indicates that both methods under-sample the total number of nests present within a given area. Aerial surveys are therefore a useful method for assessing orangutan habitat use over large areas, however the under-estimation of nest counts by both methods suggests that a small number of ground surveys should be retained in future surveys using this technique, particularly in areas with dense understory vegetation. This study shows that even highly degraded forests may be suitable orangutan habitat as long as strangler fig trees remain intact after areas of forest are logged. Enrichment planting of strangler figs may therefore be a valuable tool for orangutan conservation in these landscapes.

**Keywords:** Aboveground carbon, aerial survey, drone, forest disturbance, ground-transect, land use, multiple-use landscape, strangler fig

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## 1. Introduction

**1. Introduction**

Tropical forests are home to two thirds of the world’s biodiversity, but are being lost or degraded due to the expansion of agriculture and logging [1]. Since 2000, the area of intact forest has been reduced by 7.2% globally, and South East-Asian forests specifically have shrunk by 13.9% [2]. As intact forest declines, species are forced to adapt to more degraded habitat conditions and to mosaics of anthropogenic land use types. Understanding how species respond to human modified forests can inform land use decisions and species-specific management strategies.

Bornean orangutans (*Pongo pygmaeus morio*) are critically endangered due to hunting [3, 4], habitat loss arising from logging and conversion of forest to industrial oil palm plantations and other forms of agriculture [3]. It is estimated that habitat destruction, fragmentation and hunting drove a decline of approximately 100’000 Bornean orangutans between 1999 and 2015 [3] and that 78% of Bornean orangutan range lies outside protected areas, within logging concessions and partially forested oil palm and timber plantations [5]. This suggests that the capacity of orangutans to survive in human-modified habitats and across a mosaic of land use types is critical to their future persistence.

Orangutans construct a nest in the branches of trees on an almost daily basis, for resting overnight and sometimes during the day [6]. The traditional approach to surveying orangutan density is to make observations of their nests along ground-transects within discrete areas of homogenous habitat[7, 4] ]. However, unless multiple surveys can be conducted across a large area, information collected from ground-transects is based on orangutan activity within a narrow band of habitat, limited by the horizontal distance at which an observer can identify a nest under forest cover [6]. Moreover, in human-modified landscapes, the small size of forest fragments and presence of multiple land use types can result in a complex mosaic of habitats that are difficult to survey using a ground-transect approach.

An alternative method to overcoming the small-scale habitat complexity and large-scale sampling effort is to implement aerial surveys using helicopters or drones and to quantify the number of canopy-visible nests. Information gained from aerial surveys can capture data from a rapidly changing landscape and provides more extensive coverage at lower cost than ground-based surveys [8]. Helicopter surveys have been used to assess orangutan population densities for several years; however, helicopter flights are significantly more expensive than aerial surveys by drones and can be prohibitively expensive for small NGOs [9]. Helicopters are also in high demand and can therefore be difficult to secure for surveying purposes. Additionally, helicopter surveys do not generally collect precise information on nest locations, which is required for research on the fine-scale drivers of orangutan habitat choice. A comparison of these methods across a relatively small study area (5 km$^2$) in Sumatra found that orangutan nest counts were significantly lower in aerial surveys by drone than from ground-transects [8]. The aerial survey reported by Wich et al., (2016), was conducted at 150 m above ground-level with a 12 MP camera [29], whereas a similar study of chimpanzee nest detection by drone survey found that the nest detectability increased with image resolution [8]. Image resolution is therefore expected to have a strong effect on nest detection and therefore on the difference in nest encounter rates between aerial and ground-transects for nests. In this study we compare nest counts from aerial surveys and ground-transects over a much larger and more complex landscape to fully understand the strengths and weaknesses of each approach to sampling orangutan populations and to assess the conditions and resources associated with estimating orangutan population density.

Environmental variables known to affect orangutan nest distribution and habitat preference were mapped in order to determine the drivers of orangutan nest distribution within this landscape. It is well known that forest quality is a strong predictor of orangutan habitat suitability [10]. Forest degradation due to logging and agricultural conversion generally results in lower food resource availability and higher energetic costs associated with dispersal [11]. However, this relationship may not be linear, as low-intensity disturbance to forests can result in higher availability of fruit-producing tree species, providing greater foraging opportunities [12, 13]. Additionally, the highest recorded orangutan abundances in Borneo occur in selectively logged forests in Kalimantan and Sabah, and old growth forest in Sarawak [3]. However, high orangutan densities in degraded forest may also be the result of refugee crowding, as individuals flee from areas of active logging into neighbouring intact forest [14]. The relationship between forest quality and orangutan nest density in regions with multiple land uses is therefore worthy of further study. In this study, above-ground carbon density (ACD) was used as a surrogate for forest quality across the study landscape, which is justified by the sensitivity of ACD to logging intensity across our study region [15].

The highest orangutan densities occur within lowland habitats, and they are generally rare or absent at elevations over 500 m [14]. This elevational decline may be driven by changes in the abundance and phenology of important food sources such as strangler fig trees and fruit-producing lianas [16]. Strangler fig (*Ficus* spp.) trees are considered a keystone food resource for multiple frugivores in Bornean forests, including orangutans [17], providing a rich source of sugars, protein, carbohydrates, and calcium [18]. Bornean forests possess a distinct episodic reproductive phenology, characterised by irregular synchronous masting of canopy trees on cycles of 7-10 years [19]. Thus, it has been suggested that the carrying-capacity of orangutans in lowland dipterocarp forest is largely dependent on the amount of fall-back food resources available outside masting events, including leaves, bark, pith, and insects [20]. Fig trees are a key component of this resource as they produce fruit asynchronously throughout the year [21]. In Sumatran upland forests and Kalimantan peat swamp forests, orangutan density is positively related to strangler fig density [24]. However, the relationship between strangler fig abundance and the distribution of orangutan nests has not been studied in Bornean forests on mineral soils, which represent the majority of orangutan habitat in Borneo.

**The specific questions addressed by this study are as follows.**

1. **How do nest counts derived from aerial surveys compare to those derived from ground-transects?**

2. **How is orangutan nest density abundance affected by conversion of forests to alternative land uses?**

3. **How does the density of orangutan nests respond to variation in forest quality, strangler fig density and elevation within a multiple-use landscape in Borneo?**

## 2. Materials and Methods

### 2.1 Study Area

The study area (Figure 1 a) is a 261,264-ha multiple-use forest landscape located in Southeast Sabah, Malaysia (5.11394- 4.41325° N, 116.99576- 117.49802° E, Fig. 1). The study area has a rugged terrain lying between 94 and 1140 m, although most of the landscape lies below 500 m asl (Figure 1 b).

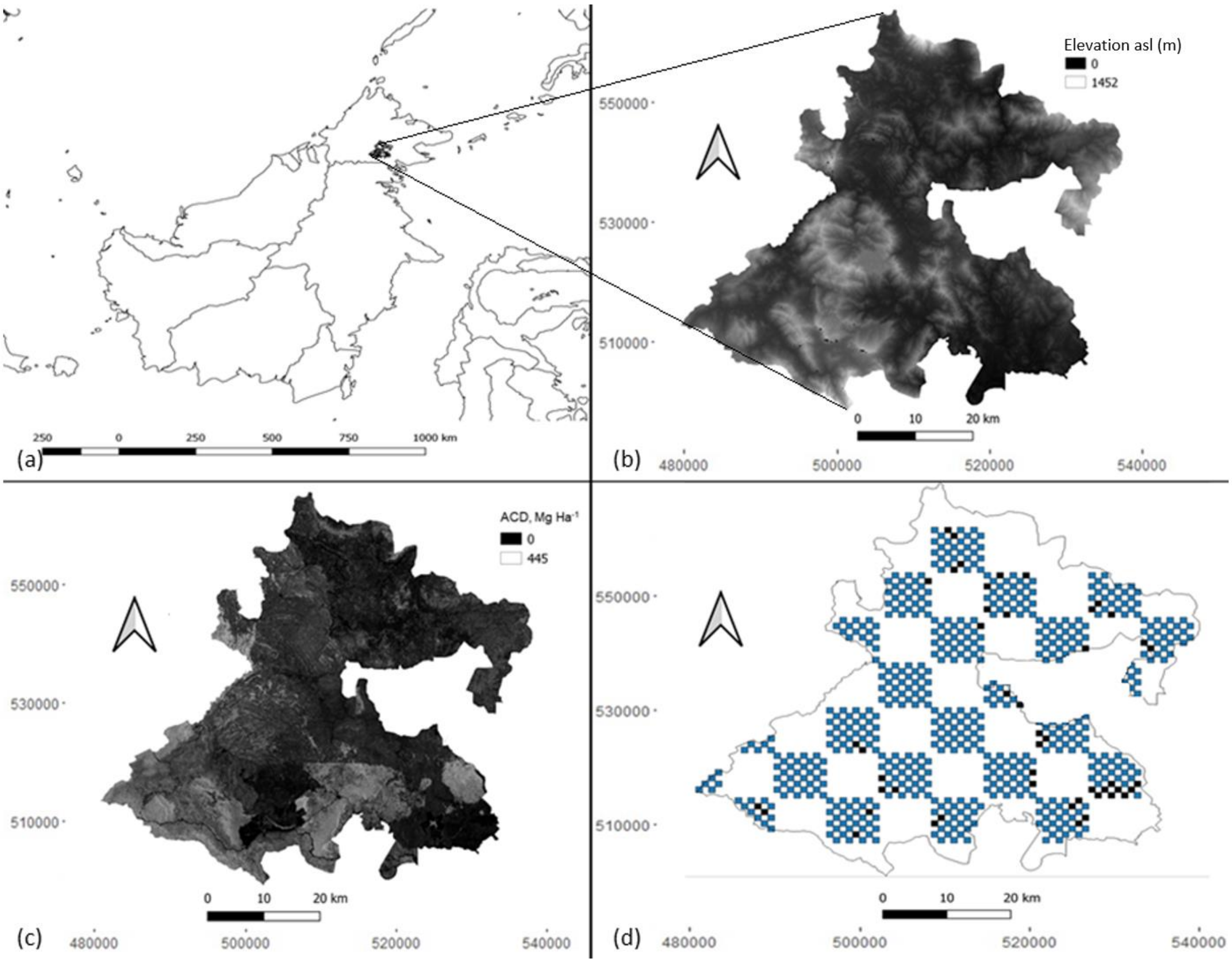

Figure 1. (a) Map of the study area in relation to the whole island of Borneo. (b) Map of elevation above sea level (asl) across the study area [15]. (c) Map of above-ground carbon (ACD) Mg ha$^{-1}$, derived from LiDAR survey across the study area [15]. (d) The grid system used to organise the distribution of aerial plots within the study area and provide a reference for the spatial random effect used in the model. Each blue square represents 1 km$^2$, with each black square representing the location of survey areas.

The multiple-use forest landscape was defined by the Sabah State government in 2012 to bring the management of protected areas and commercial land use types under a common management umbrella (Figure A1). Heavy historical timber extraction from forests in Sabah has resulted in a recent decline in logging revenue, and efforts are being made to create revenue from production forests by embedding short (8-15 yr) rotation plantations within existing logging concessions, referred to hereafter as Integrated Mosaic Planting (IMP) areas which cover 12.8% of the study area (33,512 ha). Approximately 56.7% of the study area (148,357 ha) is composed of protected Class 1 Forest Reserves, which contain a mix of logged and unlogged forest where logging and hunting are banned. A further 9.0% of the study area (23,977 ha) consists of unmanaged rubber (*Hevea brasiliensis)* and acacia (*Acacia mangium*) plantations. Approximately 9.0% of the study area (23,847 ha) is proposed for conversion to oil palm plantations, of which a quarter had been cleared and terraced by the mid-point of our sampling in 2017. Five separate forest fragments, amounting to 7,311 ha, or 2.8% of the total study area, are protected as 'Virgin Jungle Reserves', consisting mainly of unlogged primary forest on steep topography.

For the purposes of this analysis, five land uses were recognised: (i) Class 1 protected forest, (30 survey areas, 59.31 km$^2$), (ii) oil palm plantations (3 survey areas, 1.15 km$^2$), (iii) silvicultural plantations of rubber (3 survey areas, 3.23 km$^2$) or *Acacia mangium* (2 survey areas, 1.37 km$^2$ total) labelled 'silviculture' from hereon, (iv) integrated mosaic plantations (5 survey areas consisting of 1-5 hectare patches of timber trees, interspersed with remnant forest patches, 7.25 km$^2$ total) and small 'agroforestry' areas (2 survey areas, 2.98 km$^2$ total) labelled 'IMP areas' from hereon, and (v) natural riparian forest of roughly 100 m width embedded within oil palm plantations (3 survey areas, 1.1 km$^2$ total).

### 2.2 Sampling design and survey methods

Orangutan nests and large strangler fig trees (*Ficus* spp.) were surveyed across 48 areas. These survey areas were determined at random to sample at least three survey areas within all land use types (after combining Acacia and rubber plantations, due to similar land-cover characteristics) and subject to the constraint that surveys had to be accessible to sampling on foot and by drone (i.e., < 2.5 km from a road). Furthermore, land uses that covered larger areas were sampled more comprehensively based on their relative representation within the study landscape. On average, the 48 aerial surveys covered 149 ha (range 38 to 252 ha, SEM 0.083), for a total area of 76.39 km$^2$, or approximately 28% of the study landscape. Forty-four areas were surveyed using both aerial and ground-transect methods (Figure 1 d). A total of four areas, in Class I forest, integrated mosaic plantations were only surveyed by drone due to access limitations on the ground.

Aerial surveys were conducted using either fixed-wing or quadcopter drones. The fixed wing drone (Zeta Phantom FX 61 with HKPilot Mega 2.7 Flight Controller, Hobbyking, Fotan, Hong Kong) had a wingspan of 1550 mm, an approximate flight time of 50 minutes and average cruising speed of 25 kph. Images were acquired using a Canon S100 camera (Canon, Ōta, Tokyo, Japan), with a 12 MP resolution and image sensor size of 7.44 x 5.58 mm. The camera was triggered to take pictures at 2-s intervals using the Canon Hack Development Kit (CHDK) intervalometer (chdk.wikia.com/wiki/Adding_Firmware_Features). An internal GPS and barometer recorded information on position and altitude. The quadcopter (DJI Phantom 4 Pro quadcopter, Shenzhen, China 518057) was used for 46 of the 48 flights. It had a maximum dimension of 350 mm, using standard 127 mm DJI Phantom 4 rotors, with a flight time of approximately 26 minutes and a cruising speed of 50-72 kph. Images were acquired using an onboard 20 MP camera, with a sensor size of 12.8 mm x 9.6 mm.

For both drones, surveys were initially designed using Garmin Basecamp software (Garmin BaseCamp version 4.5.2, Garmin Europe Ltd, United Kingdom) to specify a 1.5 km$^2$ survey area. These coordinates were then uploaded to Mission Planner 1.3.46 software (Ardupilot.org/planner/), to calculate a safe flight altitude, defined as a minimum of 100 m above the highest point on the ground. For the fixed-wing drone, flight plans were uploaded directly to the vehicle using Mission Planner. For the quadcopter, coordinates for each corner of the survey area were uploaded to DJI Ground Station Pro (GSPro), and then sent to the drone. Each survey had a minimum of 75% overlap and 60% sidelap between captured images for mapping purposes. The coordinates of the outer corners of images along the survey boundary were used to calculate the full extent of the area covered by drone, incorporating variations in topography. Aerial surveys covered an average of 1.5 km$^2$, an area approximately 24 times larger than the ground-transects.

Ultimately, the fixed wing drone was only used for the aerial survey of one survey area of 1.4 km$^2$, with a secondary flight over this area by quadcopter. A total of 14,029 individual images were captured in the drone surveys. Each image was searched for orangutan nests and fig trees by a single experienced reviewer (SM) for a minimum of 30 seconds and repeated three times for the entire set of images. Images taken at higher altitude were searched for longer (up to 2 minutes) to account for the larger canopy surface area displayed in these images and were analysed three times in order to standardise methods.

A trigonometric approach was employed to georeference the locations of individual orangutan nests, fig trees, and boundaries of aerial surveys. Exiftool [23] was used to extract the GPS metadata recorded with each image, and the coordinates of any pixel of interest was determined by calculating the bearing from the pixel of interest to the centre of each image using the ‘bear’ function of the ‘Fossil’ package in R [24]. The bearing was then adjusted to account for the difference between the direction of the drone and true north. The distance between pixels on the ground was calculated using the ground-surface distance formula [25] and Vincenty’s Formula [26] was used to determine the GPS coordinates of the target pixel for each nest and fig tree. Given that every nest and fig tree detected in aerial surveys was geo-located, we were able to directly count the number of nests and fig trees detected from aerial surveys that were located within areas surveyed on foot during ground-transects. The spatial accuracy of GPS coordinates recorded by drone surveys were within 1.5 m [27].

Ground-transects were conducted prior to the aerial survey and were positioned in the centre of areas covered by aerial surveys. Ground-transects were based on a straight 1500 m distance in Garmin Basecamp, but undulations in the terrain consistently increased this distance. Tracks recorded using a Garmin GPSMAP 60CS GPS, (Garmin

Europe Ltd, United Kingdom) were used as the length measurement for calculating the actual distance covered during each transect. It is estimated that this model has an average positioning accuracy of 4.5 m [28]. Transect width was calculated using the Effective Strip Width (ESW) function of the 'Distance' package [29] in R version 2.15.3 (R Core Team, 2019), calculated by pooling data collected across all transects, using horizontal distances of all nest observations taken during the course of the survey and a truncation distance of 42.4 m. The transect ESW was multiplied by its length to produce a polygon covering the area surveyed.

Transects varied in length due to topographic variation at each site but averaged 42 m x 1523 m. At each nest, the nest decay status, height, perpendicular distance to the main transect line and GPS position were recorded. Mature strangler fig trees of ≥10 cm diameter at breast height (DBH) that had fully encompassed their hosts were also recorded. Locations were recorded by GPS, and perpendicular distance from the transect line was measured by tape measure.

A state-wide airborne LiDAR survey (ALS) in 2016 [15], was used to provide information about above-ground carbon density (ACD) as a surrogate for forest quality across the survey area. LiDAR reconstructs the three-dimensional structure of the forest canopy and provides data on mean top-of-canopy height (TCH, in m) from which ACD is derived using regression methods. Based on data from this survey, ACD and elevation were derived at 30 x 30 m resolution (Figure 1 c). All survey areas were then subdivided into polygons based on land use type and inferred barriers to orangutan dispersal. For example, wide rivers can pose a barrier to orangutan dispersal and impact habitat use [14] and were used to divide survey areas into discrete partitions. Areas of river, roads and settlements were excluded from calculations of mean ACD within survey areas, but roads were not treated as a direct barrier to dispersal as orangutans are known to be able to crossroads on foot. For each polygon representing a discrete land use type, or a subdivision defined by a river or road, we estimated the mean ACD and mean elevation, and extracted the number of nest and fig trees detected in these areas based on GPS coordinates. Orangutan nest and fig tree counts within these polygons were the response variables for the analyses described below.**2.4 Data analysis**

Question one addresses the difference in orangutan nest counts between aerial surveys and ground-transects. To answer this, the number of nests detected in ground-transects and aerial surveys were compared directly by identifying a polygon in the aerial surveys representing the transects surveyed on the ground and counting only nests and figs within those polygons. This allowed for a direct comparison between the number of nests and figs detected by the two methods within the same area. To accommodate spatial non-independence among samples, the entire study area was gridded at a resolution of 8 x 8 km (Figure 1 d) and data derived from within the same grid cell were regarded as spatially autocorrelated. Nest counts were fitted to a linear mixed-effects model with Poisson distributed residuals, using the 'glmer' function of the 'MASS' package in R. This model possessed fixed effects for survey method (drone survey vs ground-transect), mean ACD, the interaction between ACD and survey method and a random effect of the location of survey areas within the wider landscape, (represented as its 64 km$^2$ grid cell, Figure 1 d) to account for the nested structure of the data.

For question two, we assessed the effects of land uses (continuous forest, integrated mosaic plantation areas, oil palm plantations, oil palm riparian strips and silviculture areas) on nest counts, fig counts, and ACD within each aerial survey area. We used a generalised linear mixed model with a Poisson error structure for the count data and a linear mixed effects model for ACD, using the 'lmer' function in the 'lme4' package in R [30]. The location of samples within grids was included as a random effect to account for spatial autocorrelation as above. The log transformed area of each polygon used in this analysis was included using the 'offset' function, to account for differing polygon sizes.

For question three, we investigated how forest degradation affects orangutan nest density, estimating the influence of ACD, elevation, and strangler fig density on orangutan nest counts derived from aerial surveys, within the subset of polygons containing forest along a disturbance gradient. Survey areas covering monocultures and IMP were excluded, but those with riparian forest within oil palm plantations were included. This set of samples encapsulated an ACD range from 31 to 209 Mg ha$^{-1}$ that is assumed to reflect a gradient of forest quality, as tree species diversity is known to increase with aboveground carbon density in human modified landscapes [3**1**]. Data were fitted to generalised additive models (GAM) using the 'mgcv' package in R, assuming a negative binomial distribution of residuals. The model fitted the fixed main effects of ACD, elevation, and fig density per km$^2$ and the two-way interaction between ACD and fig density, which tests the hypothesis that the response of orang-utan nest density to forest quality depends on fig tree density. Locations of each polygon were included as a random effect, and a log transformation of the polygon area was included using the 'offset' function to account for the varying size of polygons. Tensors were used to account for differences in scaling between fig density and mean ACD, and splines were included to smooth the non-linear covariates comprising the main effects [32]. Finally, the values for the 25th and 75th percentiles of fig density from aerial surveys were fitted to this GAM and used to predict the effect of increasing ACD on orangutan nest counts. All models were validated by the inspection of residuals and Cook's distance.

## 3. Results

### 3.1 Orangutan nest density from aerial and ground surveys

In total, 813 individual orangutan nests and 360 strangler fig trees were identified in the 48 aerial surveys covering 75.5 km$^2$. The mean (± SEM) nest encounter rate from aerial surveys was 11.8 ± 3.4 km$^{-2}$ (median= 3.2 km$^{-2}$; range 0 – 93.6 km$^{-2}$; n = 48), the mean fig encounter rate was 5.14 ± 0.7 km$^{-2}$ (median= 1.6 km$^{-2}$; range 0.0 – 27.0 km$^{-2}$, n= 48). In the 43 ground-transects covering a total of 2.75 km$^2$, 64 orangutan nests and 18 fig trees were encountered. The mean nest encounter rate for ground-transects was 23.3 ± 9.1 km$^{-2}$ (median= 0.0 km$^{-2}$; range 0 – 98.3 km$^{-2}$; n = 43), and the mean strangler fig encounter rate was 6.5 ± 1.6 km$^{-2}$ (median= 0.0 km$^{-2}$, range= 0.0 – 3.0 km$^{-2}$, n= 43).

### 3.2 Effects of survey method on orangutan nest counts

Based on an area-to-area comparison of nest counts derived from each method, mean (± SEM) orangutan nest count derived from aerial surveys (0.402 ± 0.020 nests km$^{-2}$) was not significantly different ($F_{1,80}$ = 1.007, P= 0.773, Figure 2) to those recorded during ground-transects (1.488 ± 0.02 nests km$^{-2}$). Within this sample, ACD did not significantly affect the number of nests detected using either survey method ($F_{1,80}$ = 2.675, P= 0.144). The interaction between ACD and survey method type also did not have a significant effect on nest counts recorded ($F_{1,80} = 0.097$, P= 0.753).

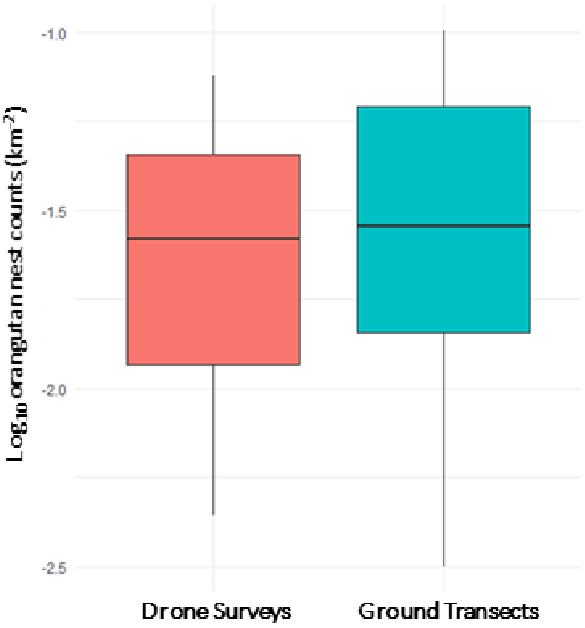

**Figure 2.** Boxplots of $\log_{10}$ (orangutan nest counts km$^{-2}$) nest counts, based on surveys from equal area surveys for ground-transects and UAV surveys.

### 3.3 Influence of land use on nest counts, strangler fig counts, and ACD in aerial surveys

Orangutan nest counts in continuous forest were significantly higher than in any other land use type studied, including integrated mosaic plantations, oil palm plantations, oil palm riparian strips or silviculture ($F_{4,\ 61.769} = 4.371$, $P < 0.003$, Figure 3 aa). Strangler fig counts were significantly lower in oil palm plantations than continuous forest, but they did not vary significantly among other land uses studied (P= 0.038, $F_{4,\ 47.15} = 2.761$, Figure 3 b). Mean ACD was significantly higher in continuous forest than any other land use type surveyed ($F_{4,\ 67.427} = 9.589$, $P < 0.001$, Figure 3 c), while the difference in ACD between rubber and acacia plantations and continuous was marginally non-significant (P= 0.052, Figure 3c).

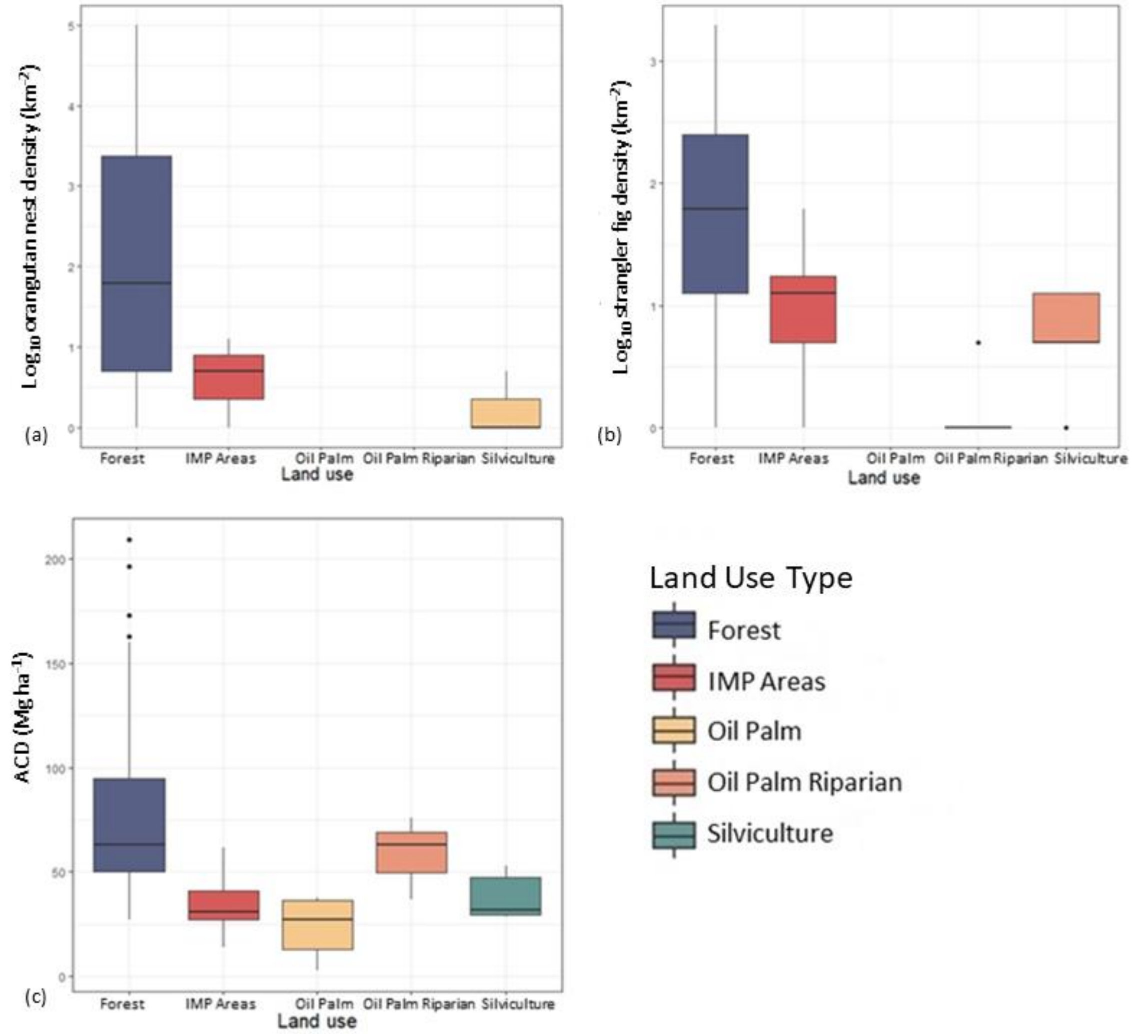

**Figure 3.** Boxplots showing (a) $\text{Log}_{10}$ orangutan nest counts ($\text{km}^{-2}$ on untransformed scale) from aerial surveys, (b) Log fig counts ($\text{km}^{-2}$ on untransformed scale) from aerial surveys and (c) ACD ($\text{Mg ha}^{-1}$) for different land use types within aerial survey areas: continuous forest, IMP areas, silviculture plantations, oil palm plantations, and riparian forest embedded within oil palm plantations. The horizontal lines represent the median values for each land use, the boxes represent the 25th to 75th percentile values and the whiskers represent the values outside of this range.

### 3.4 Effects of forest quality, strangler fig density, and elevation on orangutan nest counts in aerial surveys

Orangutan nest counts increased with the mean ACD of a survey area, although there were few survey areas with ACD greater than 150 $\text{Mg ha}^{-1}$ which expands the uncertainty associated with values in this range (Table 1, Figure 4 a). Strangler fig density also had a significant positive impact on orangutan nest counts in aerial surveys (Table 1, Figure 4 b). There was a marginally non- significant interaction between ACD and strangler fig density, which suggested that high fig densities may have had a stronger impact on nest counts in low ACD forest than in more intact forest with higher ACD (Table 1, Figure 4 c). Elevation had no significant impact on orangutan nest counts across the areas surveyed in this study (Table 1).

| Variables | edf | Ref.df | Chi.sq | p-value |
|---|---|---|---|---|
| Fig Density | 2.230 | 2.687 | 10.428 | 0.012 |
| Mean ACD | 1.603 | 1.864 | 21.999 | <0.001 |
| Mean Elevation | 1.000 | 1.000 | 1.365 | 0.243 |
| Fig Density * Mean ACD | 1.000 | 1.000 | 3.700 | 0.054 |
| Random Effect (Plot Location) | 12.806 | 15.000 | 165.475 | < 2e-16 |

Table 1: Results of the GAM used to predict the effects of mean ACD, strangler fig density, mean elevation and the interaction between fig density and ACD on aerial orangutan nest counts, including expected default frequency (edf), reference degrees of freedom (Ref.df) and Chi squared statistics (Chi.sq).

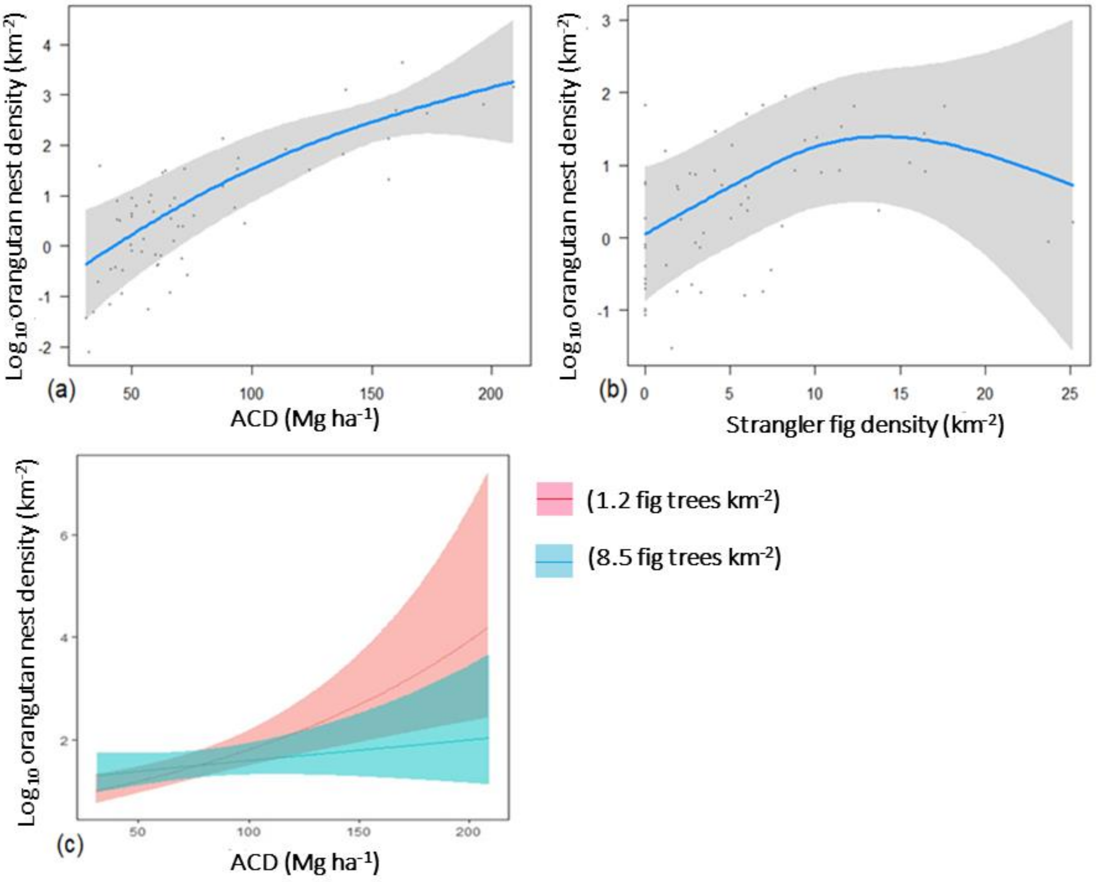

**Figure 4** (a) Predicted relationship (±95% confidence envelope) from a generalized additive model (GAM) fitting data on log-transformed orangutan nest counts to ACD in aerial surveys of forested areas, (b) predicted relationship (±95% confidence envelope) from a GAM fitting data on log-transformed orangutan nest counts to strangler fig density in aerial surveys of forested areas and (c) predicted relationships from a GAM fitting data on log-transformed orangutan nest density to ACD in aerial surveys of forested areas assuming either the 25th percentile value of strangler fig tree density (1.2 fig trees km$^{-2}$: pink line and shading showing 95% confidence envelope) or the 75th

percentile of strangler fig tree densities (8.5 fig trees km$^{-2}$: blue line and shading showing 95% confidence envelope).

## 4. Discussion

### 4.1 Comparison of survey methods

Mean orangutan nest count density did not differ between aerial surveys and ground-transects across our study area in Southeast Sabah. This result contrasts with previous research in Sumatra showing that orangutan nest counts were significantly lower in aerial surveys by fixed-wing drone than in ground-transects that sampled the same habitat [8]]. However, the aerial surveys in the Sumatran study were made from approximately 50 m higher than that adopted in our study, and using a 12 MP camera[8], which is significantly lower resolution than the 20 MP camera used for 96% of the surveys in this study. Therefore, it remains a possibility that the lower nest count density in the aerial surveys of the Sumatran study is a methodological artefact, resulting from the higher altitude surveys and use of a lower resolution camera.

Despite the absence of a difference in nest counts between the two survey methods, it is likely that both methods under-estimate the true density of Orangutan nests. This is because nests constructed on top of tree crowns, which are most visible in aerial surveys, are difficult to detect by an observer from the ground, and conversely, nests below the tree crown may be invisible in drone surveys. The under-estimation of nest counts in ground-transects may be particularly acute in the dense second vegetation typical of highly degraded forest, while aerial surveys might be expected to under-estimate nest counts in high quality forest with a more heterogeneous canopy structure [8]. However, the absence of a significant interaction between survey method and ACD in our study suggests that the relative success of the two survey methods does not vary in response to forest quality. In order to estimate the extent to which each survey method under-estimates true nest density, future studies should record precise coordinates of each nest and then overlay maps of nest locations to determine those that had been missed in each case. This would allow researchers to compute a local conversion factor for scaling nest counts from aerial surveys to total counts in each setting. In order to compute these conversion factors, ground transects are still required to complement aerial survey techniques in orang-utan nest surveys.

### 4.2 Effect of land use on orangutan nest counts, strangler fig counts and above-ground carbon density

Conversion of logged forest to create single-species plantations of oil palm, acacia, or rubber resulted in a reduction in orangutan nest counts, even when these plantations retained small patches of remnant forest. Only one nest was observed in 3.2 km$^2$ of rubber plantations surveyed, and none were observed in 1.5 km$^2$ of oil palm plantations, 0.21 km$^2$ of oil palm riparian strips or 1.4 km$^2$ of acacia plantations. Integrated mosaic plantation areas had higher median orangutan nest counts and fig density than monoculture plantations, but values were still substantially lower than in areas with a continuous cover forest, except where that forest was very heavily degraded. These data suggest that loss of forest cover reduces habitat quality for orangutans, even when natural forest cover is replaced by tree plantations equivalent in height and ACD to some natural forests. The factor that unites all the non-forest land uses compared here is the clearance of land prior to planting, and the creation of a woody vegetation with a much more homogeneous structure and species composition. Orangutans have been documented feeding on oil palm fruits within plantations, however agricultural monocultures are infrequently used by orangutans for nesting purposes [13] so nest construction in these land use types is unlikely even if orangutans are present. This study confirms this finding and extends it by recording limited use by orangutans of rubber and acacia plantations.

The low abundance of orangutan nests in silviculture plantations may arise for multiple reasons, including an inappropriate forest structure for nesting or arboreal dispersal[33], increased likelihood of disturbance or mortality of orangutans due to contact with humans and domestic animals [3] or an absence of food resources [34]. Our surveys showed that strangler fig density also declined following forest clearance and selective logging, as these trees are targeted for removal when the host tree is a valuable timber species [35]. Even though some strangler fig trees were left standing in silviculture and integrated mosaic plantations, the combination of these factors has resulted in a significant decrease in nest counts in converted areas.

No orangutan nests were encountered in 0.21 km$^2$ of riparian forest strips embedded within oil palm plantations, despite the presence of figs and intact forest in these areas. Isolated forest fragments within oil palm estates have been shown to be important orangutan habitats in adjacent areas of Sabah [36]. It is possible that the limited sampling of these areas coupled with unique characteristics of this study site explains the low number of nests recorded. In our study area, a major road passes between the single estate surveyed and neighbouring natural forest, therefore the riparian strips sampled are only connected to one fragment of continuous forest and they would not be able to function as uninterrupted dispersal corridors. *Ficus spp* have been observed growing in higher densities in riparian forest in Thailand [37], which may explain the high numbers observed in our study, despite the small area sampled. These observations suggest that the relationship between orangutan occupancy of a habitat and the availability of figs may be decoupled by the spatial structure of the habitat, as a lack of connectivity between these riparian strips and larger forest fragments makes dispersing for this food resource a less viable feeding strategy.

### 4.3 Variation in orangutan nest counts across a gradient of forest degradation

Orangutan nest density estimates derived from aerial surveys showed a positive relationship with ACD. The survey areas encompassed a wide gradient of forest degradation arising from variation in logging impacts, leading to a mosaic landscape composed of residual unlogged forest patches with high ACD embedded within a matrix of highly heterogeneous disturbed forest environments possessing lower and more variable values of ACD. This result contrasts with research in the Lower Kinabatangan Wildlife Sanctuary (LKWS) in Sabah [38, which showed that the correlation between nest density and ACD was weak and non-significant. However, this may be because the LKWS covers a smaller range of land use types, comprising primarily disturbed forest that possesses a narrower range of ACD values (0 – 150 Mg ha$^{-1}$), than those included in the multiple-use forest landscape we examined [38].

Higher nest counts in less degraded forest may arise because of orangutan preferences for specific forest structural characteristics that are modified by logging, combined with changes in food resource availability linked to logging disturbance. Tall and stable trees with a complex branching structure are preferred for nest building, possibly because they create a stable platform for nests in wind and rain and provide a useful vantage point over the forest [9]. Additionally, undisturbed forests have fewer canopy gaps [39], which are energetically expensive for orangutans to cross [5]. Disturbed forests also have a more uniform canopy height, which was negatively correlated with orangutan density in other studies in Sabah [36]. Further analysis of these metrics would help us to understand how forest structure drives orangutan nest site selection in a multiple-use landscape.

Our results revealed that orangutan dependence on strangler figs may be greater in more degraded forest (< 150 Mg ha$^{-1}$) than in relatively undisturbed forests. In higher quality forest, orangutan nest density became decoupled from strangler fig density, possibly because food derived from other fruiting tree species became more available. This finding supports previous research in Sumatra showing that the importance of fig trees to orangutan habitat usage increases in more degraded forest [33]. This may be associated with a decline in the abundance of other food sources, as fig trees are an important source of proteins, carbohydrates, lipids, and minerals for orangutans and other frugivores [39, 18]. Figs are also a reliable and consistent food resource, because different species fruit asynchronously and the intervals between fruiting events are short [40]. Consequently, they are highly sought after, and trees possessing large fruit crops can result in aggregations of orangutans and other frugivores [41].

Changes in food availability in response to logging may also be a significant driver of orangutan nest abundance. Mean fruit availability is a strong predictor of orangutan density [42] and disturbed forests are known to have lower food availability for orangutans [14]. This is reflected by the findings of this study, as nest counts generally increased with higher ACD. On the other hand, the five highest nest counts observed in this study were located in more disturbed forest (ACD < 150 Mg ha$^{-1}$). This partial decoupling may occur for several reasons. First, Bornean orangutans display considerable dietary flexibility, which allows them to extend their range into more disturbed environments when foraging for alternative food sources [12]. The fruits and leaves of pioneer species such as *Macaranga pearsonii* and *Neolamarckia cadamba* that are abundant in degraded forests across the study area are potentially important alternative food sources [12], while tree bark and insects also provide a reliable source of nutrients [43]. Secondly, in areas where food resources are scarce, orangutans are known to rest more frequently and construct day nests 44]. This study suggests that degraded forest (ACD < 150 Mg ha$^{-1}$) where mature strangler fig trees are left unlogged retains higher orangutan nest counts than forest of the same ACD range where fig trees have been removed. However, without location-specific phenological data on fig fruiting events we are not able to attribute high nest densities in low ACD forest to fig tree abundance directly. Lastly, high densities of strangler fig trees were observed in heavily logged forest, indicating that at least some large, mature trees were left intact and remained a viable food source in otherwise degraded areas.

Contrary to expectations, there was no evidence of a decline in orangutan nest counts across the range of elevations surveyed in this study (117 to 675 m). A possible explanation for this lack of effect of elevation is that our entire study area was above the threshold elevation of 100 m that makes a difference for orangutan abundance. For example, a previous study of Bornean orangutan populations in Kalimantan showed that densities declined beyond 100 m asl. [4]. That interpretation may also explain the generally low population densities of orangutans across our study area in Sabah (nest densities in the range 0 – 93.6 km$^{-2}$ in forested habitats) compared to populations examined in forests at lower altitudes (10- 20 m asl) where nest densities are in the range 87.5-1149.9 km$^{-2}$ in forested habitats [45].

## 5. Conclusions

This study highlights the drivers of orangutan distribution in a multiple-us landscape, based on the observation of nest counts across multiple survey areas within this landscape. Orangutan nest counts declined significantly in response to increasing intensity of land use (Fig 3 a), in conjunction with decreasing ACD (Fig 4 b). These results emphasize the importance of remnant forest, with low rates of human disturbance as important orangutan habitat in multiple-use forest landscapes. Strangler fig density was also shown to be a significant driver of orangutan nest density, with high nest counts observed in forest with a higher densities of strangler fig trees (Fig 4 b). The importance of strangler fig trees as food sources for orangutans in logged and degraded forests, which is supported by our study as well as others [18, 22,], justifies specific management interventions that might enhance the conservation of orangutans in these habitats. For example, enrichment planting of strangler fig trees might be an effective technique for increasing food availability and habitat quality in degraded secondary forests, especially when combined with other measures for restoring forest structure and species composition[46]. In addition, restrictions on cutting lianas with fleshy fruits consumed by orangutans would limit the reduction in strangler fig trees and fruit-producing lianas that occurs when generic climber cutting practices are used to aid regrowth of mature trees in logged forest [47]. In multiple-use landscapes, forest patches may be small and isolated, but they often possess sub-populations of orangutans that are vital to sustaining the viability of the regional metapopulation, distributed across a heterogeneous landscape [14]. The ability to conduct rapid surveys of forest fragments in their entirety across these landscapes may be a vital tool for monitoring the status of orangutan populations in the future. Our work demonstrates that drone surveys have the potential to play an important role in that effort.

Despite the under-estimation of orangutan nest density by both aerial surveys and ground-transects, the larger area sampled by drones than ground surveys for an equivalent effort expands the scope and accuracy of inferences about the drivers of orangutan abundance and distribution, particularly when sampling heavily disturbed environments or populations with low individual density. When coupled with an effective correction factor for under-sampling of nests, and high throughput image analysis, drone surveying could serve as an effective rapid assessment tool for monitoring orangutan populations [8]. However, the process of sorting through aerial images individually was time-consuming and prone to human error. Adopting a machine learning approach for identifying orangutan nests in aerial images may save time and improve standardisation in future surveys [48].

## 6. Supplementary Materials:

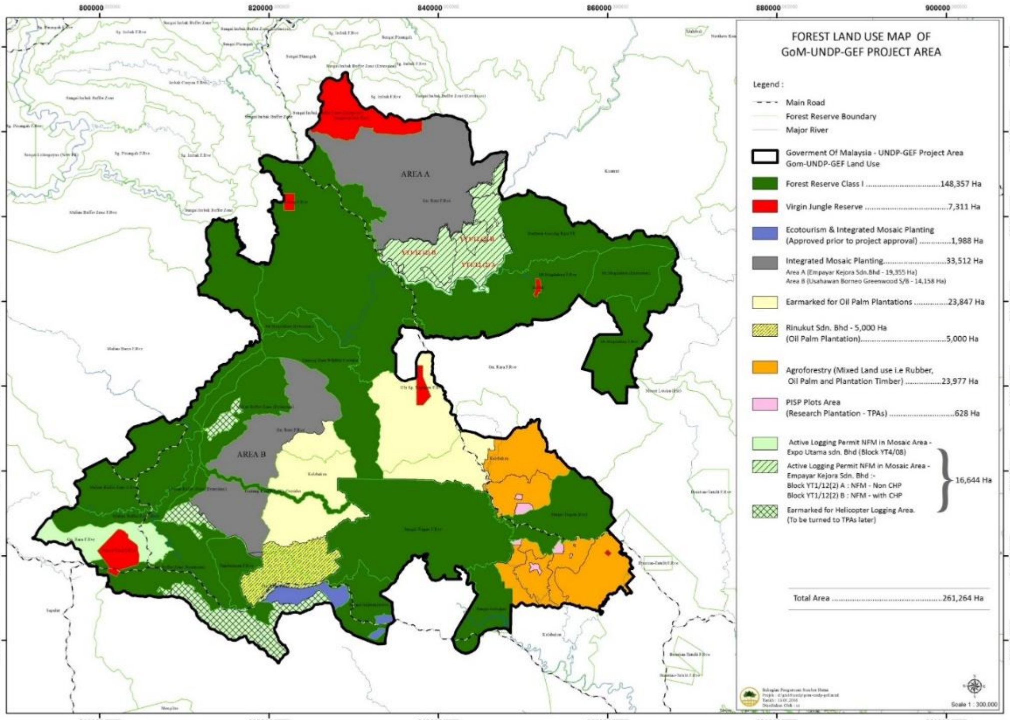

**Figure A1:** Land use map for the UNDP-GEF study area, comprised of proposed land uses for associated areas throughout the region, (Sabah Forestry Dept., 2016) [49].

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