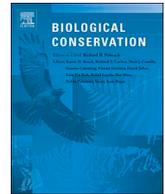




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Combining behavioural and LiDAR data to reveal relationships between canopy structure and orangutan nest site selection in disturbed forests

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ABSTRACT

Primary tropical forests are becoming increasingly disturbed and fragmented, making it critically important to understand the conservation value of degraded forests. Many populations of even the largest and most iconic species are now found outside of primary habitats, and the long-term survival of these and many other species depends on appropriate management of degraded areas, whether protected or not. However, for conservation in degraded habitats to be successful, an adequate understanding of the minimal ecological requirements necessary for species persistence within them is required. We combined ground and helicopter nest surveys of critically endangered Bornean orangutans with high-resolution measurements of forest canopy structure from airborne Light Detection and Ranging (LiDAR) to understand orangutan nest site selection across multiple spatial scales in degraded forests of the Lower Kinabatangan region, Malaysian Borneo. We found orangutans to be selective when choosing nest sites, with nests more likely to be observed in canopies of tall and uniform height and closer to full canopy gaps, which was consistent across spatial scales and orangutan age and sex classes. These sites likely offer orangutans an improved vantage point and/or shelter from wind and rain. In contrast, no discernible relationships between nest site selection and canopy complexity, or nest abundance and landscape forest structure or aboveground carbon density were recorded. Our findings suggest that although orangutans do nest across a range of forest conditions, their optimum requirement for nesting strongly depends on forest patches with sufficient tall canopy of uniform height. These results serve to inform degraded forest conservation strategies across Borneo, particularly where orangutans are a focal species.

1. Introduction

Protecting pristine primary forests remains a cornerstone of biodiversity conservation in the tropics (Gibson et al., 2011). However, primary forests are rapidly declining in extent and remain severely threatened by increasing rates of deforestation and degradation, even within protected areas (Laurance et al., 2012). Non-protected areas surrounding protected forests, as well as degraded forests more generally, are therefore becoming increasingly important for successful conservation strategies (Edwards et al., 2013). It is widely acknowledged that these areas can retain significant levels of biodiversity (Edwards et al., 2011; Turner and Corlett, 1996), even for large iconic and wide-ranging species (Ancrenaz et al., 2010; Athreya et al., 2013; Chapron et al., 2014), and that they warrant improved management and protection (Santika et al., 2015). An integral prerequisite of such

management action, however, is an adequate understanding of the minimal ecological requirements necessary for species to persist in these degraded forests, thereby maximising their biodiversity value.

Critically endangered Bornean orangutans (*Pongo pygmaeus*) exemplify this need for increased attention and understanding of the conservation value of degraded forests. Today, > 70% of Bornean orangutans survive in degraded forests (protected or not) that have been exploited recently or are still being used by people (Ancrenaz et al., 2015; Meijaard et al., 2010; Wich et al., 2008). However, despite their ability to survive in disturbed forests, orangutans remain susceptible to changing forest characteristics and likely require minimal ecological attributes to persist in transformed forests over the long term. Structural elements of the canopy, for example, act as important drivers of orangutan movement in disturbed forest and suggest that forests with taller canopies, increased canopy closure and uniform height are most

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suitable for orangutan conservation (Davies et al., 2017). However, a better understanding of other ecological requirements is also necessary to realize the full capability of degraded forests for orangutan conservation.

Provisioning of suitable nest sites is one such requirement. Orangutans sleep in well-engineered, arboreal nests that are usually freshly built every evening using the branches within a single tree, although in some cases branches from surrounding trees are incorporated (Prasetyo et al., 2009; van Casteren et al., 2012). Although not yet fully understood, proposed reasons for nest-building by orangutans and other great apes include avoidance of predators and other night time disturbances, resource access and defence, thermoregulation and protection from adverse weather, and the need for fully recumbent, restful sleep (Anderson, 1998; Prasetyo et al., 2009; Samson and Shumaker, 2015; Stewart and Pruetz, 2013). Regardless of the primary reason for their construction, orangutans sleep in nests for approximately 13 h a day (i.e. more than half their life), with nest site availability therefore critical for their survival. Despite this, there is a paucity of knowledge about relationships between forest structure and nest site selection by orangutans. Studies investigating nest site selection have found orangutans to nest in taller trees and to be selective in the tree species chosen (Ancrenaz et al., 2004a). Tree species with greater branching complexity (more branches along the trunk) are preferred (Prasetyo et al., 2009), as well as those characterized by stilt or buttress roots, vertical rather than angled central trunks, and with larger trunk diameters, likely due to enhanced stability against wind (Cheyne et al., 2013). Avoidance of trees that are in fruit, likely to evade disturbance by nocturnal foragers (Sugardjito, 1983), and trees that produce copious amounts of latex (Gibson, 2005) has also been recorded. Forest structure could similarly be expected to influence nest site selection because wild orangutans, in contrast to other great apes, build their nests almost exclusively in the tree canopy. Nest densities are also conventionally used as a proxy for orangutan abundance (Ancrenaz et al., 2004b, 2005; Johnson et al., 2005; Kuehl et al., 2008), even though nest abundance does not always correlate with high patch use for other activities, such as foraging (Ancrenaz et al., 2004a; Sugardjito, 1983). Therefore, an understanding of how forest structure affects both nest site selection and nest abundance will yield important insights for orangutan ecology, conservation and population monitoring.

Adequate understanding of the relationship between forest structure and nest site selection requires the measurement of forest structure at multiple scales. Canopy structure at individual nest sites will inform the types of trees orangutans select for nesting, and measurements of canopy structure surrounding nest sites will provide insights into the types of forest they are able to nest in and that are required for orangutan population persistence, especially as tropical forests become increasingly fragmented and degraded. However, measuring forest structure at multiple scales is challenging to achieve with ground surveys and/or satellite-based remote sensing. Airborne Light Detection and Ranging (LiDAR), an active remote sensing technique capable of measuring vegetation structure and the underlying terrain in three-dimensional space, overcomes many of these difficulties. Airborne LiDAR provides highly detailed information on forest canopy structure across large areas, and, when combined with behavioural and/or distributional data, can be a powerful tool in animal ecology studies (Davies and Asner, 2014), including those focused on primates (Davies et al., 2017; McLean et al., 2016; Palminteri et al., 2012).

Here, we combine ground and aerial surveys of orangutan nest sites and abundance with high-resolution airborne LiDAR measurements of forest canopy structure to quantify how forest structure affects orangutan nest site selection and abundance in disturbed forests of the Lower Kinabatangan region of Malaysian Borneo. Specifically, we aimed to quantify how structural characteristics of forest canopies: i) drive nest site selection across different spatial scales, from the nest site to a 1-ha area surrounding the nest, ii) differentially influence nest site selection across orangutan age and sex classes, and iii) drive orangutan

nest abundance, and hence population size, across the region. Orangutans in the Kinabatangan have been previously found to preferentially move in directions of increased canopy height, greater canopy closure and uniform canopy height, as well as avoid canopy gaps and move toward emergent tree crowns. Structural attributes of the lower canopy (e.g. canopy layering and canopy shape) did not affect orangutan movement (Davies et al., 2017). We aimed to test whether the same forest structural attributes are also important for nest site selection and whether they can therefore be prioritised in orangutan conservation projects, or if alternative structural metrics are important for nesting, in which case a wider range of forest attributes are required to sustain orangutan populations in disturbed forests.

2. Methods

2.1. Study site

The Lower Kinabatangan region of Sabah, Malaysia, consists of highly fragmented and disturbed forest patches within a mosaic of oil palm plantations and human settlements (Fig. 1). Remaining forest patches consist mostly of evergreen freshwater swamp and floodplain forests on mineral soils (Azmi, 1998). Low-stature forests and open areas occur in backswamp areas, whereas riparian and logged mixed lowland dipterocarp forests are found in some drier areas along river banks and on higher terraces. The dry lowland forest patches that remain have been repeatedly logged over the past century but protected since 2005 within either the Lower Kinabatangan Wildlife Sanctuary (LKWS) or other types of protected forest (Abram et al., 2014). The region experiences a warm, humid climate throughout the year: mean monthly temperature ranges between 21° and 34 °C, and mean annual precipitation is approximately 3000 mm (Ancrenaz et al., 2004a).

Ground surveys (nest count transects and orangutan follows) were conducted in the Kinabatangan Orangutan Conservation Programme (KOCPP) intensive study site within Lot 2 of the LKWS, which covers ~7.4 km² (118° 17' to 118° 20' E and 5° 34' to 5° 33' N). The KOCPP study site is bordered to the north and east by natural forests, to the south by the Kinabatangan River, and to the west by oil palm plantations (Fig. 1c). The entire study site is below 50 m above mean sea level and consists of a mosaic of degraded mixed lowland dipterocarp and freshwater swamp forests, with low tree density (332 stems per ha), a short canopy (> 80% of trees are < 20 m in height), large canopy gaps and significant soil disturbance. See Ancrenaz et al. (2004a) for a complete site description.

Despite high levels of disturbance and transformation, the Lower Kinabatangan region supports a relatively large orangutan population that was estimated at ~1100 individuals in the early 2000s (Ancrenaz et al., 2004b), but had declined to an estimated 800 individuals by 2015 (KOCPP, unpublished data). The orangutan population in the LKWS has been continually studied since 1998, making it the longest uninterrupted wild orangutan study in Borneo (Bruford et al., 2010), and an ideal population and location for studying orangutan behaviour and distribution in disturbed and fragmented forests.

2.2. Orangutan nest sites

We compiled a dataset of orangutan nest sites using three methods. In July 2015, a series of 20 1-ha plots spaced 200 m apart were surveyed by a team of five experienced nest spotters within a permanent transect grid system in the KOCPP study site. Each plot was 500 m long and extended 10 m either side of a centre transect line for a total width of 20 m per plot. Locations of all observed nests were recorded with a Global Navigation Satellite System (GNSS) (Fig. 1c–d). GNSS accuracy was estimated to be between 2 and 8 m. To ensure a wider spatial sampling of nests, we augmented this dataset of 153 nest sites with 118 nest locations recorded during full day focal follows of wild orangutans conducted in the study site between 2014 and 2017 (see Ancrenaz

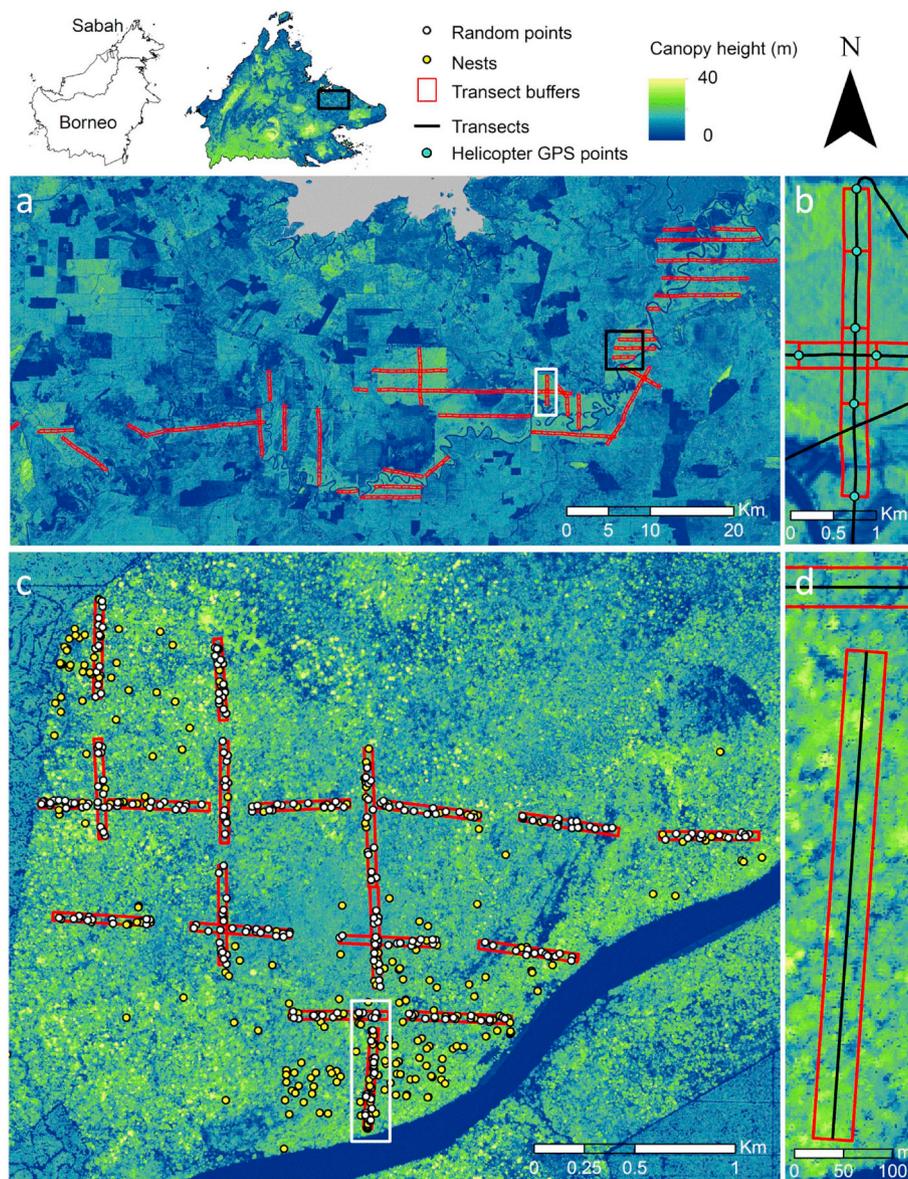


Fig. 1. a) Location of the helicopter surveys used for counts of orangutan nest throughout the Lower Kinabatangan region of Sabah, Malaysia. b) Zoom (corresponding to the white rectangle in a) of the helicopter surveys showing the helicopter flight lines and associated GNSS points and polygons. c) The intensive study site within Lot 2 of the LKWS (corresponding to the black rectangle in a) where the ground surveys of orangutan nests were conducted. d) Zoomed in area (corresponding to the white rectangle in c) of the ground line transects and associated buffers.

et al., 2004a; Davies et al., 2017). We chose this four-year time period as a balance between increasing nest sample size and reducing the time prior to and since the LiDAR data acquisition, which took place in April 2016. No timber extraction or illegal encroachment has occurred within the study site since 1998, and no significant change in forest structure, apart from natural processes such as stochastic treefall and regeneration, was recorded over the study period (2014 to 2017). Wild orangutans were followed from the morning nest site to the following evening nest site, with location and behavioural data recorded throughout the day, including the nest locations, using a GNSS. The identity, age and sex, of all but two of the nest builders was known and associated with each nest site. We identified the following age-sex classes from 26 habituated wild study subjects: adult females with dependant offspring (59 nest sites), adult females without dependant offspring (14 nest sites), flanged adult males (23 nest sites), subadults (independently ranging, immature offspring [female or male] who build their own nests 7–14 years old (van Noordwijk and van Schaik, 2005), 7 nest sites), and unflanged adult males (estimated ≥ 15 years of

age, 13 nest sites). The final ground-based dataset used for analysis consisted of 271 nest sites (153 from transects and 118 from follows). We did not record nest type (see Prasetyo et al., 2009) during the surveys, but almost all nests in our study site were observed to consist of types 1–3, with most being type 2 or 3 (KOCOP, unpubl. data). Ground nests have never been recorded in the Kinabatangan.

In addition to the ground surveys, we utilised nest count data from aerial surveys conducted in June 2015 as part of routine orangutan population and distribution monitoring in the remaining forest patches of the Lower Kinabatangan region. A Bell 206 Jet Ranger helicopter was used, with helicopter speed maintained at ~ 40 knots and height kept constant at 60–80 m above the forest canopy during all flights, following Ancrenaz et al. (2005). The copilot recorded the precise flight path location with a GNSS every 30 s. From the back seats, two observers searched for orangutan nests on either side of the helicopter and recorded all visible nests. A nest recorder seated between the nest spotters noted the number of nests detected by the observers per 30 s flying period. Trailing tapes placed on the aircraft windows limited the

observer's field of view to an approximately 150 m wide strip on either side of the helicopter. After each flight, data collected by the copilot and the nest recorder were matched to determine the location of all nest sightings along the aerial line transect precisely. The same observers, all with 10–20 years of experience, conducted all aerial surveys to limit inter-observer bias. Nevertheless, it was not possible to accurately estimate the impact of nest age on detection probability, and very fresh, green nests (a few days old) and those at the very last stages of decay (when only a few bare broken branches are visible) were likely underreported.

2.3. Airborne LiDAR and forest structural metrics

We mapped the study area with discrete-return airborne LiDAR using the Carnegie Airborne Observatory-3 (CAO) (Asner et al., 2012) in April 2016. The CAO LiDAR subsystem provides 3D structural information of vegetation canopies and the underlying terrain. The Global Positioning System-Inertial Measurement Unit (GPS-IMU) subsystem provides 3D position and orientation data for the CAO sensors, allowing for highly precise and accurate positioning of LiDAR observations on the ground. For this study, the CAO data were collected from 3600 m above ground level, using a scan angle of 36° and a side overlap of 30%. The aircraft velocity was 150 knots and the LiDAR pulse frequency was set to 150 kHz, resulting in an average point density of 3.2 laser shots per m². Horizontal and vertical error estimates were 16 cm and 7 cm root-mean-square-error (RMSE), respectively.

Laser ranges from the LiDAR were combined with the embedded GPS-IMU data to determine the 3D locations of laser returns, producing a 'cloud' of LiDAR data. The LiDAR data cloud consists of a large number of geo-referenced point elevation estimates, where elevation is relative to a reference ellipsoid. Initially, the LiDAR data points were processed to identify which laser pulses penetrated the canopy volume and reached the ground surface. We used these points to interpolate a raster digital terrain model (DTM) for the ground surface. A second digital surface model (DSM) was based on interpolations of all first-return points (i.e. including top of canopy and, where only ground returns exist, bare ground). Measurement of the vertical difference between the DTM and DSM yielded a digital canopy model (DCM), derived at 2 m spatial resolution. See Asner et al. (2018) for a full description of the LiDAR data processing.

For analysis of orangutan nest site selection from the ground-based surveys, we extracted metrics of canopy structure from the processed LiDAR data hypothesized to influence nest site selection, following those used by Davies et al. (2017). We derived measurements of upper canopy attributes (canopy cover, canopy height and the heterogeneity of canopy height) and canopy features (canopy gaps and emergent tree crowns) from the DCM, and metrics of canopy vertical complexity (canopy shape and canopy layering) from the vertical distribution of the LiDAR points. Canopy height was measured as the interpolated height of the DCM at a 2 m resolution. Canopy cover was defined as the proportion of a 10 × 10 m area covered by vegetation above a height of 10 m. An aboveground height of 10 m was chosen because orangutans in Kinabatangan are known to nest mostly in the top half of the canopy (Anczenaz et al., 2004a), which had a mean height of 17.3 m across the study area. Heterogeneity of canopy height was defined as the standard deviation of canopy height over a defined area, which varied depending on the scale of analysis (see below). We measured two types of canopy gaps: full gaps, defined as areas of at least three contiguous DCM pixels (i.e. 12 m²) that contained canopy below 2 m in height, and relative gaps, defined as areas of at least three contiguous DCM pixels that had a relative height of −0.5 to −1.0 (50–100%) below the mean canopy height of the surrounding 1 ha. Emergent tree crowns were defined as clumps of two or more contiguous DCM pixels with a height > 1.5 times the standard deviation of the mean canopy height across the study area (i.e. emergent crowns were > 28.2 m tall and ≥ 8 m² in area). For metrics of canopy vertical complexity, we binned the vertical

distribution of LiDAR points into volumetric pixels (voxels) of 5 × 5 m horizontal resolution and 1 m vertical resolution, with the DTM used to standardize the vertical datum at the horizontal centre of each voxel. The number of LiDAR points in each voxel was then divided by the total number of LiDAR points in that column, yielding the percentage of points in each voxel, and therefore the vertical distribution of vegetation in the canopy. We then counted the number of 1-m layers in each column where vegetation was present as a measure of canopy vertical complexity (i.e. the number of canopy layers). We also computed a canopy shape parameter from the voxel data, defined as the ratio of the height above ground where maximum canopy volume (P) occurs to the 99th percentile of total canopy height (H), thereby reducing a large amount of vertical profile information into a simple metric depicting the overall architecture of the canopy (Asner et al., 2014). A high $P:H$ ratio indicates that most foliage is positioned high in the canopy, independent of overall canopy height, whereas a low $P:H$ ratio indicates a groundward tendency of foliar distribution.

For analysis of orangutan nest densities from the helicopter surveys, we first defined polygons reflecting the area over which nests were counted by creating a 150-m buffer either side of the flight lines. We then intersected these polygons by constructing a line through each GNSS point recorded by the pilot per 30 s interval (Fig. 1a–b). The nest count associated with each GNSS point was then assigned to the relevant polygon. For each polygon, we extracted mean canopy height, mean canopy cover and heterogeneity of canopy cover, defined as the standard deviation of canopy height throughout the polygon, from the LiDAR data. We also measured the gap proportion of each polygon, defined as the proportion of polygon area where canopy height was below 2 m. Only polygons that contained adequate LiDAR data coverage, defined as those whose centroid overlaid LiDAR data, were included in the analysis ($n = 192$). In addition, we extracted mean aboveground carbon density (ACD) for each polygon using Sabah-wide ACD maps developed by Asner et al. (2018), only including polygons that completely overlaid ACD data ($n = 257$). Polygons dominated by mangroves were excluded due to no ACD data.

2.4. Analysis

We used binomial logistic regression models, using a generalised linear model fit, to develop resource selection functions (RSF, proportional to the probability of resource use by an animal) for analysis of orangutan nest site selection from the ground-based surveys. The dependent variable was nest presence, 1, contrasted with random points that represented available nest sites, 0. Fourteen random points, spaced at least 10 m apart, were generated within each ground transect buffer (Fig. 1c–d) for a total of 280 random points, thereby creating a close to balanced dataset of nest sites and random points. We chose to place random points within only the transect buffers because we knew that there were no nests present in the selected locations when the transects were walked, with the random points therefore representing true absence at the time of the surveys. We then extracted forest structural metrics, described above, around each point (nest and no nest) at three different spatial scales: the value at the point (corresponding to the value of the pixel on which the point was located), the mean value over the surrounding 0.1 ha (corresponding to the mean value within a circular buffer of 17.84 m radius around each point) and the mean value over the surrounding 1 ha (mean value within a circular buffer of 56.42 m radius around each point). We assessed collinearity between factors in each dataset prior to analysis using variance inflation factors (VIF) and spearman rank correlation tests. Distance to the nearest emergent tree crown was excluded from further analysis due to collinearity with canopy height. Once this factor was excluded, VIF scores for all factors were < 2.

We then modelled the probability of an orangutan selecting a nesting site (1 vs. 0) as a function of canopy height, canopy cover, distance to the nearest full canopy gap, distance to the nearest relative

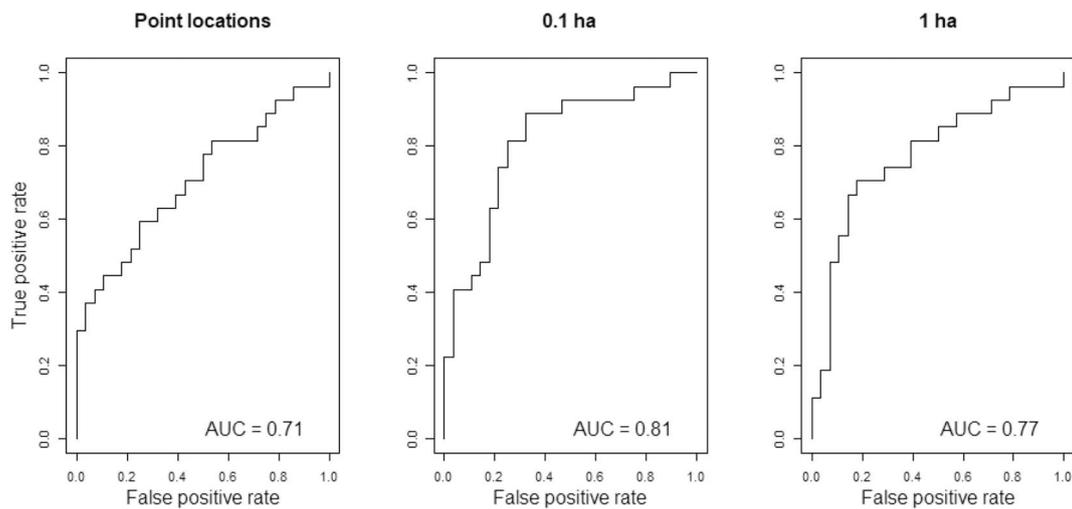


Fig. 2. Receiver operating characteristic (ROC) curves and area under the curve (AUC) calculations for the binomial logistic model ensembles used to predict orangutan nest site selection from ground-based surveys at three spatial resolutions.

canopy gap, the number of canopy layers and the canopy *P:H* ratio. For analyses at the 0.1 and 1 ha scales, we also included heterogeneity of canopy height as a factor in the models. We included two-way interactions between factors representing canopy structure (height, cover and heterogeneity of canopy height when applicable) and canopy complexity (the number of canopy layers and the *P:H* ratio), and interactions between these factors and canopy features (distance to the nearest full gap and distance to the nearest relative gap). We did not include interactions between the two measures of distance to canopy gaps (see Tables S1–S3 for full model constructions). All predictor variables were scaled and centred before analysis. We performed model selection on the constructed global models using Akaike Information Criteria corrected for sample size (AICc) and the model Akaike weights (AICwi). There was close convergence between top models for all datasets (small changes in AICc scores and AICwi between models), and conditional model averaging was therefore implemented using the coefficients from the models with a delta AICc ≤ 2 relative to the most parsimonious model (Burnham and Anderson, 2002). We assessed the predictive ability of the resulting model ensemble using cross validation. We divided the respective datasets into training (90% of the data) and testing (the remaining 10% of the data) sets and assessed the trained model ensemble's predictive ability on the unused test set, which we evaluated using the true to false positive rate plotted as a receiver operating characteristics (ROC) curve and the resulting area under the curve (AUC) calculations. To visually assess the influence of each significant predictor variable on the probability of orangutan nest site selection, we varied each significant covariate from the model ensemble across its range of values while keeping all other variables constant at their mean. We repeated this procedure for each significant interaction term, holding one of the two interacting variables at its minimum and, separately, maximum value while keeping all other predictor variables constant at their mean, to illustrate how nest site selection varied in contrasting environments. We also implemented a non-linear random forest model on each dataset and compared its performance relative to the logistic regressions using the same cross validation approach.

To assess potential differences in nest site selection across orangutan age and sex classes, we used the nest sites identified from the orangutan follows that had associated age-sex class data ($n = 116$). We grouped these nest sites into the five age-sex classes defined above and performed an analysis of variance (ANOVA) or Kruskal-Wallis test, depending on the distribution of the data (normalized or not), on each forest structural metric across the groups. We performed these analyses at each of the three spatial scales used above. Where significant

differences were detected (canopy height only), we performed a Tukey HSD posthoc test to assess between-group differences.

We used a linear model to analyse drivers of orangutan nest densities obtained from the helicopter surveys. The number of nests counted in each polygon was first divided by the helicopter flight length through the polygon to generate an aerial index of nest density per km (AI). Prior to analysis, we assessed collinearity between factors using VIF and spearman rank correlation tests. There were high levels of collinearity between canopy height, canopy cover and gap proportion ($r = 0.94$ for height vs. cover, $r = -0.69$ for height vs. gap proportion and $r = -0.76$ for cover vs. gap proportion). Therefore, we only included mean canopy height and canopy height heterogeneity (standard deviation of canopy height) in the models, with VIF being < 2 for both. We then modelled nest AI as a function of mean canopy height and canopy height heterogeneity, as well as the interaction between these two factors, which were scaled and centred before analysis. We again performed model selection using AICc and AICwi and used the most parsimonious model for further analysis (Burnham and Anderson, 2002). We assessed model fit by plotting the model predicted values against the measured values. We also implemented a random forest model and compared its performance relative to the linear model following the same approach. All statistical analyses were performed using R software version 3.5.0.

3. Results

3.1. Nest site selection

Models of orangutan nest site selection performed relatively well but performance varied with spatial grain size, hereafter referred to as study scale (Fig. 2). We were best able to predict nest sites at the 0.1 ha scale, followed by the 1 ha scale. These results suggest that orangutans consider spatial context when selecting nest sites, which was further demonstrated by the stronger response to canopy height at spatial grain sizes of 0.1 and 1 ha relative to the point locations (Tables 1–3, Fig. 3a–c). Across scales, canopy height was the strongest driver of orangutan nest site selection, appearing in all models used in the ensemble and with the highest β coefficient after model averaging (Tables 1–3). Nests were found in areas with taller canopy at all scales (Fig. 3a–c).

Distance to both full and relative canopy gaps were the next most important drivers of nest site selection across scales. Distance to full canopy gaps was present in all models across scales and distance to relative canopy gaps (defined as areas of at least 50% lower canopy

Table 1

Model-averaged parameter estimates from the point scale analysis of orangutan nest site selection. Models that had a $\Delta AIC_c \leq 2$ compared with the top performing model were included in the model ensemble (see Table S1). Significant variables are in italics.

Variable	β	SE (adjusted)	Z value	P value	Importance
<i>Canopy height</i>	<i>0.428</i>	<i>0.119</i>	<i>3.586</i>	<i>< 0.001</i>	<i>1.00</i>
<i>Distance to full gap</i>	<i>-0.347</i>	<i>0.098</i>	<i>3.547</i>	<i>< 0.001</i>	<i>1.00</i>
Canopy cover	0.321	0.178	1.799	0.072	1.00
Distance to 50% gap	0.218	0.121	1.797	0.072	1.00
Number of layers	0.061	0.104	0.587	0.557	1.00
<i>Distance to 50% gap: canopy height</i>	<i>0.300</i>	<i>0.129</i>	<i>2.334</i>	<i>< 0.05</i>	<i>1.00</i>
<i>Number of layers: Canopy height</i>	<i>-0.309</i>	<i>0.1010</i>	<i>3.105</i>	<i>< 0.01</i>	<i>1.00</i>
P: H ratio	-0.031	0.107	0.288	0.773	0.17
Distance to full gap: number of layers	-0.096	0.101	0.959	0.338	0.13
Canopy cover: distance to 50% gap	0.239	0.264	0.904	0.366	0.12
Canopy cover: number of layers	0.057	0.111	0.506	0.613	0.09
Distance to full gap: Canopy height	0.057	0.114	0.495	0.626	0.09
Canopy cover: Canopy height	0.065	0.140	0.465	0.642	0.09
P: H ratio: canopy height	0.141	0.097	1.461	0.144	0.09
Distance to 50% gap: number of layers	0.036	0.123	0.295	0.768	0.08

Table 2

Model-averaged parameter estimates from the 0.1 ha scale analysis of orangutan nest site selection. Models that had a $\Delta AIC_c \leq 2$ compared with the top performing model were included in the model ensemble (see Table S2). Significant variables are in italics.

Variable	β	SE (adjusted)	Z value	P value	Importance
<i>Canopy height</i>	<i>0.870</i>	<i>0.154</i>	<i>5.654</i>	<i>< 0.001</i>	<i>1.00</i>
<i>Distance to full gap</i>	<i>-0.381</i>	<i>0.101</i>	<i>3.779</i>	<i>< 0.001</i>	<i>1.00</i>
<i>Standard deviation of canopy height</i>	<i>-0.339</i>	<i>0.118</i>	<i>2.880</i>	<i>< 0.01</i>	<i>1.00</i>
Number of layers	-0.047	0.122	0.384	0.701	1.00
<i>Number of layers: canopy height</i>	<i>-0.318</i>	<i>0.109</i>	<i>2.924</i>	<i>< 0.01</i>	<i>1.00</i>
Distance to full gap: number of layers	0.191	0.117	1.637	0.102	0.63
Distance to full gap: canopy height	0.102	0.134	0.763	0.445	0.30
Canopy cover	-0.089	0.244	0.365	0.715	0.14

height than the surrounding ha) was present in all models at both the point and 1-ha scale. Distance to relative canopy gaps was excluded from modelling at 0.1-ha due to collinearity with canopy height heterogeneity. However, canopy height heterogeneity, which is analogous to distance from relative gaps based on their collinearity, was a prominent driver of nest site selection at this scale. Distance to full and relative canopy gaps, as well as canopy height heterogeneity, also had a relatively strong effect on nest site selection (high β coefficients) across scales (Tables 1–3). However, orangutan nest site selection varied with distance from gap type. Nests were built closer to full gaps at all study scales (Fig. 3d–f), but further from relative gaps (point and 1-ha scales) or, similarly, where canopy height heterogeneity was lower (0.1-ha scale) (Fig. 3i–k).

Canopy cover was not a significant driver of nest site selection at any scale although nests were typically built in areas with high canopy cover. The lack of significance for canopy cover was likely driven by the generally high levels of cover across the study site (see Fig. S1 where

pairwise comparisons between nest and non-nest sites are shown). Similarly, neither metric of canopy complexity (the number of canopy layers or the P:H ratio) was a significant driver of nest site selection (Tables 1–3), although the P:H ratio was not included in models at the 0.1- or 1-ha scale due to collinearity with canopy cover and canopy height heterogeneity.

There was a significant interaction between canopy height and canopy layering (measured as the number of layers in the canopy) at both the point and 0.1-ha scale. At both these scales, nests were more likely to be found in areas of complex canopy (more layers) where the canopy was short, whereas in areas of tall canopy, nests were more likely found in simpler canopies with fewer layers. However, areas with the highest probability for nest sites at both scales were in tall but simple canopies (Fig. 3g–h). At the 1-ha scale, the interaction between canopy layering and the distance to the nearest relative canopy gap was significant, with the highest probability of nest occurrence in complex canopies far from relative gaps (Fig. 3i). In contrast, although it was relatively unlikely to

Table 3

Model-averaged parameter estimates from the 1 ha scale analysis of orangutan nest site selection. Models that had a $\Delta AIC_c \leq 2$ compared with the top performing model were included in the model ensemble (see Table S3). Significant variables are in italics.

Variable	β	SE (adjusted)	Z value	P value	Importance
<i>Canopy height</i>	<i>0.583</i>	<i>0.165</i>	<i>3.532</i>	<i>< 0.001</i>	<i>1.00</i>
<i>Distance to full gap</i>	<i>-0.445</i>	<i>0.128</i>	<i>3.472</i>	<i>< 0.001</i>	<i>1.00</i>
Canopy cover	-0.093	0.207	0.447	0.655	1.00
<i>Distance to 50% gap</i>	<i>0.772</i>	<i>0.148</i>	<i>5.233</i>	<i>< 0.001</i>	<i>1.00</i>
Number of layers	-0.075	0.130	0.581	0.561	1.00
<i>Canopy cover: distance to 50% gap</i>	<i>-0.415</i>	<i>0.154</i>	<i>2.693</i>	<i>< 0.01</i>	<i>1.00</i>
<i>Distance to 50% gap: number of layers</i>	<i>0.248</i>	<i>0.114</i>	<i>2.172</i>	<i>< 0.05</i>	<i>0.88</i>
Distance to full gap: number of layers	0.238	0.124	1.912	0.056	0.80
Number of layers: Canopy height	-0.191	0.124	1.532	0.125	0.66
Canopy cover: distance to full gap	0.253	0.165	1.537	0.124	0.61
Canopy cover: Canopy height	0.174	0.133	1.306	0.192	0.23
Canopy cover: number of layers	0.082	0.213	0.385	0.700	0.16

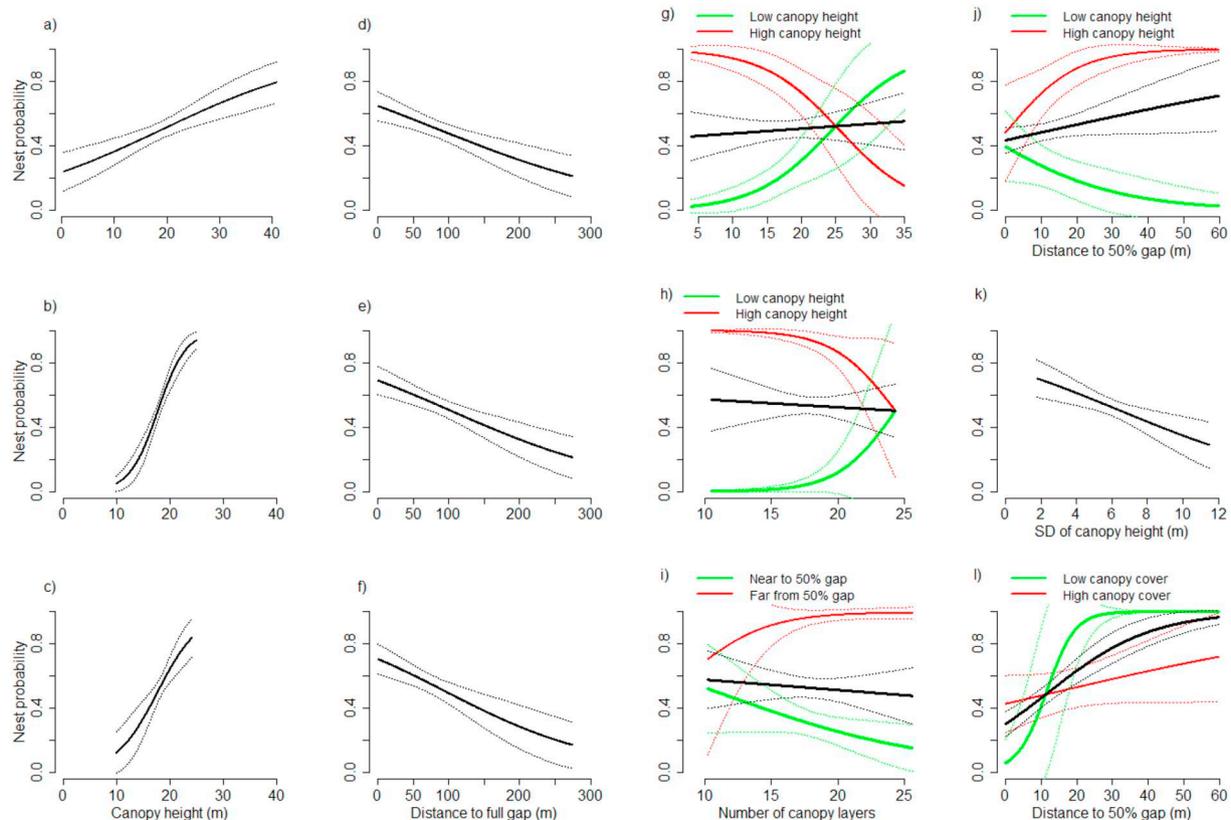


Fig. 3. Relationships between the probability of an orangutan selecting a nest site and significant covariates of forest structure measured in the LKWS, Sabah, Malaysia. Results are derived from averaged predictions from binomial logistic models. Dotted lines represent 95% confidence errors around predictions.

observe nests close to relative gaps, when this did occur, they were more likely to occur in canopies with fewer layers. However, this was possibly an artefact of few canopy layers nearer relative gaps due to the lower canopy height around gaps and therefore a lower capacity for a high number of canopy layers. The highest probability of nest occurrence at this scale remained in complex canopies far from relative gaps (Fig. 3i). The interaction between the distance to relative canopy gap and canopy height was also significant at the point location scale (Table 1). At this scale, nests in taller canopies were more likely to be far from relative gaps, whereas nests in shorter canopies were more likely to be closer to relative gaps (Fig. 3j). This effect could, however, be an artefact of relative gaps comprising short canopy. Finally, the interaction between canopy cover and distance from the nearest relative gap was significant at the 1-ha scale (Table 3). Although nests were more likely to be further from relative gaps regardless of canopy cover at this scale, this relationship was strongest where canopy cover was low (Fig. 3l).

3.2. Age-sex class differences

Nest site characteristics were similar across orangutan age-sex classes for all structural metrics apart from canopy height, and this result was consistent for both the point and 0.1 ha spatial scales, and tended toward significance at the 1 ha scale (ANOVA of canopy height for point locations: $F_{(4,111)} = 3.214, p < 0.05$; 0.1 ha: $F_{(4,111)} = 4.887, p < 0.01$; 1 ha: $F_{(4,111)} = 2.393, p = 0.055$). Tukey HSD posthoc tests revealed that nests built by unflanged males were in taller canopy than adult females with dependent offspring at both the point and 0.1 ha scales ($p < 0.05$ and $p < 0.01$ for point and 0.1, respectively), higher in canopy than adult females without dependent offspring at point and 0.1 ha scales ($p < 0.01$ and $p < 0.001$ for point and 0.1, respectively) and in higher canopy than flanged males at point locations ($p < 0.05$). Nests of unflanged males were not found in significantly taller canopy

than subadults at any scale of analysis, nor were subadult nests in significantly taller canopy than other age-sex classes (Figs. 4, S2).

3.3. Nest densities

Correlations between forest structural characteristics and orangutan nest densities were weak and not significant for all measured structural metrics (Fig. 5), and both the linear and random forest models applied to the dataset performed poorly (Fig. S3). Similarly, the correlation between nest density and ACD was weak and not significant (Fig. 6).

4. Discussion

Our combination of high-resolution remote sensing and field-derived behavioural data revealed that orangutans in disturbed Bornean forests are selective when deciding where to build night nests. Using only forest structural metrics, we predicted orangutan nest sites with relatively high accuracy across multiple spatial scales. This multi-scaled approach also showed that orangutans are cognisant of surrounding forest structure when choosing a nest site, with model performance increasing when spatial context was considered (model performance was improved at the 0.1 and 1 ha scale relative to the point scale). However, the improved model performance at coarser scales could also be due, at least in part, to a likely improvement in the spatial match between the LiDAR and field data at these scales. The handheld GNSS accuracy was lower than the GPS-IMU onboard the CAO and it is possible that the match between some nest sites and the LiDAR pixels were offset slightly, potentially leading to a mis-match at the point scale that would be smoothed at the 0.1 ha scale of analysis.

In contrast, we did not record any discernible relationship between nest abundance and forest structure or aboveground carbon density at a regional scale (across the Lower Kinabatangan region), suggesting that structural data collected at this scale (or resolution) are not informative

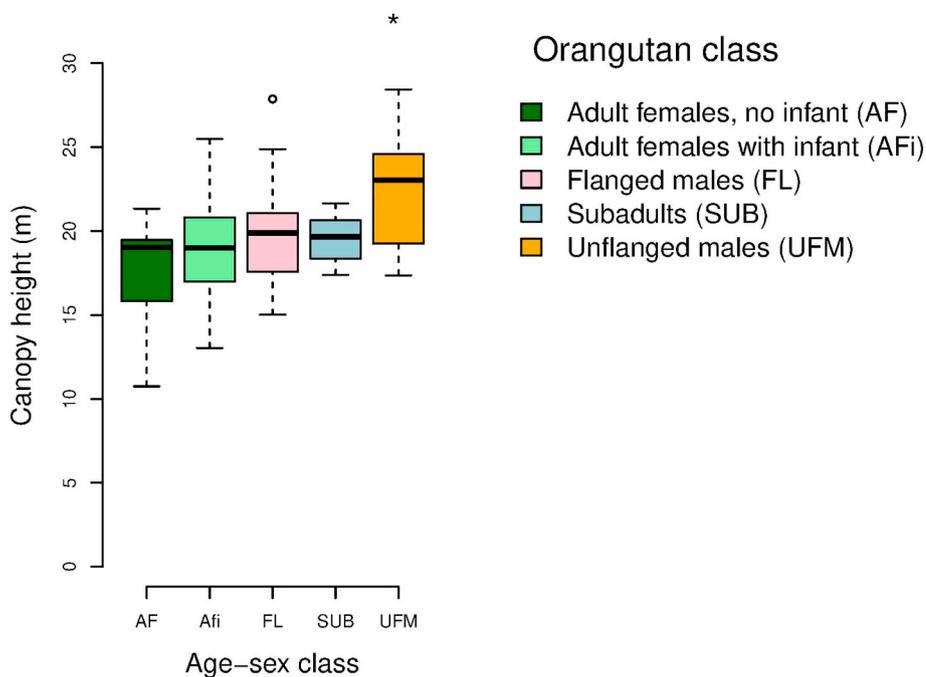


Fig. 4. Boxplot depicting canopy height of nest sites across orangutan age and sex classes. The solid line in each box indicates the median for each age and sex class, whereas the top and bottom of the boxes depict the third and first quartiles, respectively. Whiskers denote the maximum and minimum values, or 1.5-fold the interquartile range (whichever is smaller), and dots represent outliers.

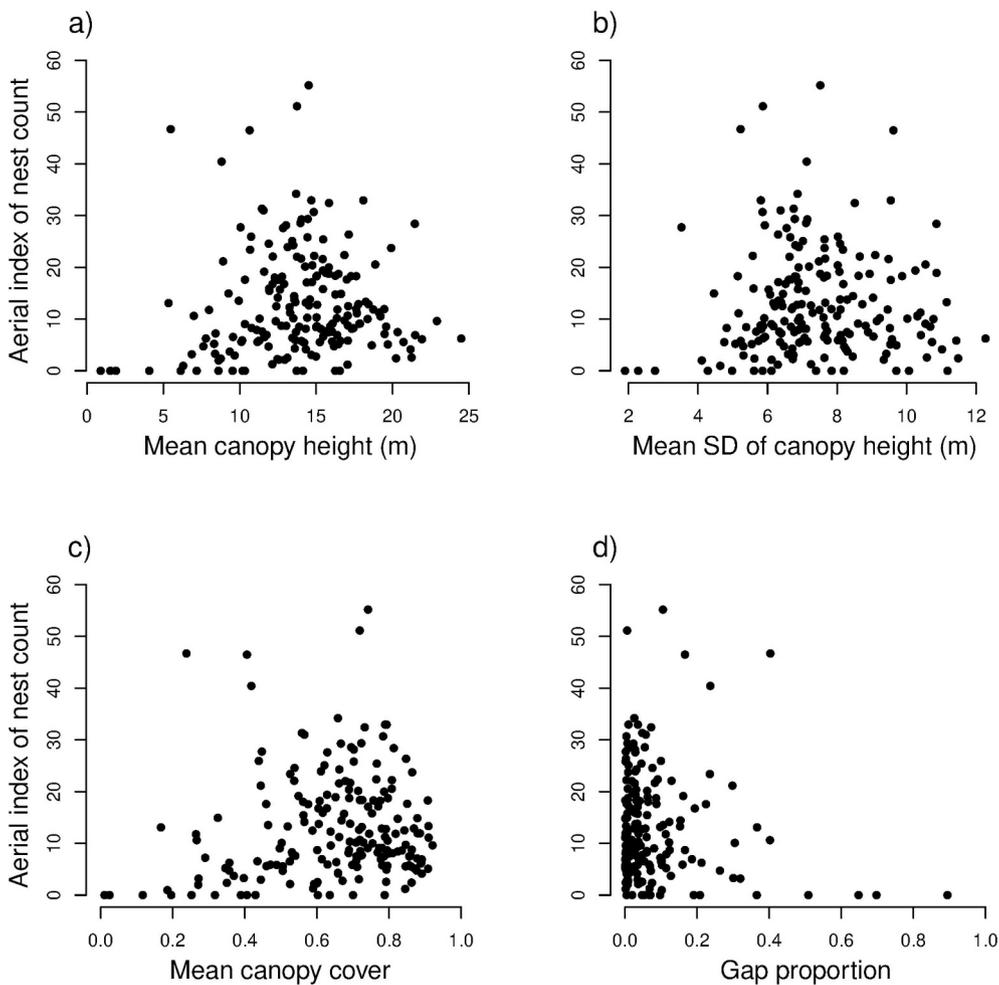


Fig. 5. Scatterplots depicting the correlation between orangutan nest densities and a) mean canopy height, b) the standard deviation of canopy height, c) mean canopy cover and d) gap proportion per polygon from the helicopter surveys.

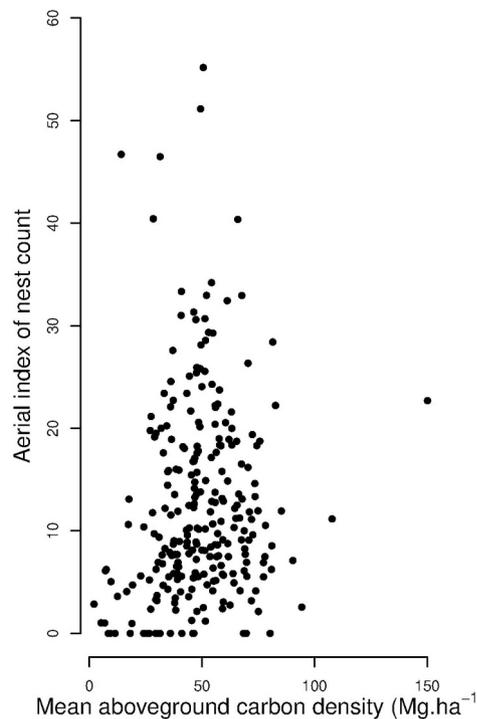


Fig. 6. Correlation between orngutan nest densities and mean aboveground carbon density per polygon from the helicopter surveys.

for orngutan abundance or nest site selection, and that orngutan spatial decision making is responsive to finer-scaled variation in canopy structure. Orngutans, at least in the Kinabatangan, do not seem to seek areas with specific forest-wide structural attributes as nest sites, but rather make spatial decisions about the best available site where they are when ready to nest. Notwithstanding this finding, orngutan densities have been shown to differ between regions with variable forest conditions (e.g. primary vs. degraded forest) (Ancrenaz et al., 2005; Felton et al., 2003; Husson et al., 2009) and comparisons of forest structure and/or other variables, such as food availability, across regions will likely support such differences in broad-scale orngutan abundance. Our study was restricted to the disturbed forests of the Lower Kinabatangan region, and should be seen in the context of orngutan distribution and behavioural patterns in disturbed forests, which can still support important orngutan populations provided minimal ecological conditions are met (Ancrenaz et al., 2004b, 2010; Davies et al., 2017).

Orngutan nest site selection was driven primarily by forest canopy height at all three spatial scales tested, with nests found in areas with taller canopy than random, as shown previously (Ancrenaz et al., 2004a; Prasetyo et al., 2009). Furthermore, nests were found more often where canopy height was relatively uniform, evidenced by the higher probability of observing nest sites with increasing distance from relative canopy gaps and where canopy height heterogeneity was lower. Selection for tall canopy could be driven by enhanced visibility at these higher positions, aiding in detection of ambush predators, such as clouded leopards and reticulated pythons, and/or conspecifics (Prasetyo et al., 2009), as well as increased comfort provided by what are likely more mature and stable (broader) trees (Cheyne et al., 2013). A primary reason for nest building in great apes is thought to be driven by the need for fully recumbent sleep provided by comfortable sleeping platforms (Stewart, 2011; van Casteren et al., 2012). Larger, taller trees provide more branching support for nest building and taller trees are also often broader and more stable at their base, providing resistance to wind disturbance (Prasetyo et al., 2009). Areas with uniform canopy height are likely to provide further protection from wind because they

experience lower wind speeds relative to areas with heterogeneous canopy height, such as forest edges, or exposed emerging crowns (Laurance and Curran, 2008; Smith et al., 2018). Orngutans typically build nests in the upper half of the canopy but below the very tops of the trees, allowing for maximum protection from wind as well as rain or sun. The tendency for nests to be found in areas with high levels of canopy cover, although not significantly different from random, could also be due to the added protection high canopy cover affords from wind and rain, as well as potentially decreasing detection by predators, particularly human hunters (see Meijaard et al., 2011; Voigt et al., 2018).

In contrast to avoidance of relative gaps, orngutan nests were more likely to be located close to full canopy gaps (12 m^2 areas of canopy height $< 2\text{ m}$). Although this may be counterintuitive given the propensity of orngutans to select nest sites in areas of tall, uniform canopy, sites near full gaps could provide some benefits. Visibility is likely enhanced at these sites, allowing orngutans to space themselves and thereby avoid conflict (van Schaik, 1999). Predators (e.g. clouded leopards and pythons) are also less likely to be near or attack from gaps. Increased sunlight penetrating gaps and their surroundings could also provide useful feeding opportunities by favouring the growth of pioneer plants and climbers that produce edible young shoots throughout the year. Nesting close to full gaps could, however, also simply be an energy saving behaviour. When orngutans begin searching for a suitable nest site, it is conceivable that they could be unwilling to cross or skirt a gap given the energetic costs of descending and then re-ascending the canopy, rather leaving such energetically demanding activity for the next day. Although orngutans have been observed to move out of fruiting trees when nesting at the end of the day, they rarely travel far to build a nest, often selecting a neighbouring tree (Sugardjito, 1983), which is suggestive of some aversion to high energy expenditure late in the day.

There were few differences in nest site selection across orngutan age and sex classes, with the use of taller trees by unflanged adult males being the only significant difference. Adult males, being the dispersing sex, are more mobile than adult females, which are highly philopatric (Arora et al., 2012). However, flanged males are also highly territorial and make use of long call vocalisations as a spacing mechanism to minimise direct conflict (Spillmann et al., 2017). Conversely, unflanged adult males, who lack the secondary sexual characteristics needed to produce long call vocalisations (Delgado, 2007; Mitani, 1985), are less territorial than flanged males (Utami et al., 2002). Unflanged males also need to more socially flexible than flanged males to maximise mating opportunities with females while simultaneously avoiding flanged males (Knott et al., 2010; Utami et al., 2002). This social flexibility, combined with their non-territoriality, makes it reasonable to assume that they would be less familiar with their surroundings compared with adult females or flanged males (Goossens et al., 2006; Spillmann et al., 2017). This unfamiliarity, coupled with their more clandestine mating strategy could lead unflanged males to nest in taller trees because of the enhanced visibility these sites offer, whereas flanged males are likely to be less reliant on high nesting sites as vantage points. Rayadin and Saitoh (2009) also recorded few differences between orngutan age and sex classes in terms of nest locations and characteristics of nesting trees. Flanged males did, however, build larger nests in more stable and lower locations than immature individuals, presumably because of their larger and heavier body size. Of all age and sex classes investigated by Rayadin and Saitoh (2009), unflanged males built nests in the upper section of a tree most often, corroborating our findings of their selection for higher nesting sites in taller trees. In contrast, females, especially those with infants, likely select nest sites with increased shelter to protect their more vulnerable young from predators (including human hunters) and adverse weather (Arora et al., 2012).

Although we were able to successfully predict nest site selection by orngutans using only structural metrics of the forest canopy, other factors are likely also important. Orngutans have been shown to select

certain tree species over others for nesting (Ancrenaz et al., 2004a; Prasetyo et al., 2009) and tree species composition, as well as the distribution of food resources (Felton et al., 2003; Kanamori et al., 2017) likely interact with canopy structure in driving nest site selection. Orangutans could also be expected to avoid areas of increased human disturbance and hunting (Marshall et al., 2006), especially given their increased vulnerability while sleeping. The proximity of other orangutans could similarly affect nest placement with either avoidance or attraction of conspecifics depending on hierarchical structure and social bonds. Nest construction is also a learned behaviour, with nest structural differences and site selection based on habitat type as well as cultural differences between orangutan groups in different regions. For example, orangutans in peat swamps tend to build predominantly type 4 nests (where branches of one or more trees are tied together to form the nest structure) (Prasetyo et al., 2009), whereas orangutans at other sites, including the Kinabatangan, tend to build nests in single trees, consisting of nest types 1–3. These differences in nest construction are likely due to forest structural differences between trees in peat swamps compared with other habitats, which then lead to cultural traditions that are transmitted across generations (Prasetyo et al., 2009). It is also possible that sites with the structural attributes important for nest site selection (e.g. tall trees) are limited in the fragmented and disturbed Kinabatangan forests relative to other sites, leaving fewer ideal nest sites for orangutans here. Orangutans in the Kinabatangan could therefore be forced to be less selective than orangutans elsewhere, leading to a broader selection of nest sites. Investigation of orangutan nest site selection in relation to forest structure elsewhere, especially in intact dipterocarp forests such as Danum Valley, Sabah or Gunung Palung, Kalimantan, would be informative.

Nevertheless, differences in forest structure are an important component of disturbed forests and understanding how structure influences nest selection is useful for predicting the conservation value of disturbed forest areas for orangutans. Forest structure can, for example, be measured relatively easily using appropriate remote-sensing technology and could serve as a useful proxy for assessing the conservation value of different forest areas for orangutans. Indeed, the recent launch of the Global Ecosystem Dynamics Investigation (GEDI) will greatly increase the availability of spaceborne LiDAR data across the tropics and could be used to assess forest quality across the entire distribution of orangutans.

Given the selection of certain canopy structural attributes by orangutans for nesting sites, what does this tell us about broader forest conservation in Borneo? An obvious implication is that if orangutan conservation is a goal, forest patches need to have sufficient tall canopy of uniform height to provide the best nesting opportunities. However, a lack of suitable natural nesting sites does not necessarily mean an absence of orangutans since they are known to nest in industrial tree plantations (Meijaard et al., 2010), oil palm plantations (Ancrenaz et al., 2015) and even single trees within agricultural landscapes (KOC, unpubl. data). However, our results suggest that sites with tall canopies of uniform height are essential for the long-term sustainability of orangutans in disturbed forests, and that these areas should be prioritised. Equally revealing is our finding that canopy complexity is not a major driver of nest site selection in the Kinabatangan, in much the same way that it does not drive orangutan movement here (Davies et al., 2017). Our results therefore suggest that leaving secondary forest stands, even if they are less structurally complex than primary forests, is of great importance provided they have sufficient canopy height and uniformity. The strong influence of uniform canopy height on orangutan nesting also indicates, however, that some small forest fragments may not be ideal for providing nesting opportunities due to a lack of tall, uniform canopy within them (Edwards et al., 2010). Yet, forest fragments, even of the smallest size, still retain some level of biodiversity (Lucey et al., 2014) and can be used by orangutans for dispersal or as food sources when moving across agricultural landscapes and should still be considered in orangutan conservation planning

(Ancrenaz et al., 2015). Likewise, narrow corridors between larger forest fragments might be useful in assisting dispersal but are likely insufficient for orangutan nesting if not wide enough to provide suitable nesting opportunities. Corridor width and forest structural characteristics should therefore be considered in landscape management strategies (see also Gray and Lewis, 2014).

Beyond considerations of forest structural requirements for orangutans, our study highlights the need to recognise the conservation value of disturbed tropical forests and to manage them appropriately (Meijaard et al., 2005). Disturbed habitats are becoming increasingly prevalent across the globe, including in non-tropical regions, and failure to prioritise and understand species use of these new environments will likely lead to conservation failures in the long term. Our approach of combining high-resolution spatial and behavioural data to understand orangutan habitat selection in disturbed forests will hopefully serve as a useful template for similar studies across a range of species and ecosystems, providing key insights to effectively balance landscape change and wildlife adaptation. Such approaches are becoming increasingly essential if free-ranging wildlife populations are to co-exist in a progressively human-transformed world.

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.biocon.2019.01.032>.

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