



Canopy structure drives orangutan habitat selection in disturbed Bornean forests

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The conservation of charismatic and functionally important large species is becoming increasingly difficult. Anthropogenic pressures continue to squeeze available habitat and force animals into degraded and disturbed areas. Ensuring the long-term survival of these species requires a well-developed understanding of how animals use these new landscapes to inform conservation and habitat restoration efforts. We combined 3 y of highly detailed visual observations of Bornean orangutans with high-resolution airborne remote sensing (Light Detection and Ranging) to understand orangutan movement in disturbed and fragmented forests of Malaysian Borneo. Structural attributes of the upper forest canopy were the dominant determinant of orangutan movement among all age and sex classes, with orangutans more likely to move in directions of increased canopy closure, tall trees, and uniform height, as well as avoiding canopy gaps and moving toward emergent crowns. In contrast, canopy vertical complexity (canopy layering and shape) did not affect movement. Our results suggest that although orangutans do make use of disturbed forest, they select certain canopy attributes within these forests, indicating that not all disturbed or degraded forest is of equal value for the long-term sustainability of orangutan populations. Although the value of disturbed habitats needs to be recognized in conservation plans for wide-ranging, large-bodied species, minimal ecological requirements within these habitats also need to be understood and considered if long-term population viability is to be realized.

Bornean orangutan | Carnegie Airborne Observatory | conservation | Light Detection and Ranging | movement ecology

Large vertebrates perform disproportionately important roles in ecosystem functioning (1, 2), yet the conservation of the Earth's remaining large mammal fauna is becoming increasingly difficult, particularly in light of their wide-ranging habits (3–5). Human population growth and natural resource use continue to place tremendous pressure on these species and their remaining habitat (4, 6, 7). Previous strategies that relied almost exclusively on the preservation of pristine habitat for large mammal conservation are proving insufficient, with populations continuing to decline (4, 5). New strategies that complement the continued protection of pristine environments are urgently needed if we are to succeed in saving these charismatic and functionally important species.

The Bornean orangutan, *Pongo pygmaeus*, is highly illustrative of these challenges. Despite more than five decades of conservation effort, orangutan populations continue to decline throughout their range (8), with the species downgraded to critically endangered on the International Union for Conservation of Nature (IUCN) Red List in 2016 (9). Previous conservation strategies have focused on protecting primary forest, based on the idea that orangutans are dependent on pristine forest habitat (10, 11). However, recent work has found orangutans to be much more flexible in their behavior, and more resilient to anthropogenic disturbance than previously thought (12, 13). For example, contrary to previously held views, orangutans travel terrestrially in all forest types but display increased terrestrial activity in both heavily disturbed and primary forest, suggesting that not only can they adapt their behavior but

that anthropogenic disturbance is not necessarily the dominant driver of such behavioral adaptation (14).

Indeed, more than 70% of Bornean orangutans occur in fragmented, multiple-use, and human-modified forests, ranging from degraded forest with ongoing timber extraction to secondary forest, and even tree and oil palm plantations (13, 15, 16). Although it remains essential to conserve primary forest from conversion and degradation, for orangutans and many other conservation objectives, it is becoming apparent that this strategy alone is not enough to safeguard the species in the long term. Conservation efforts need to expand beyond focusing only on the protection of intact primary forest to include disturbed and fragmented forest where orangutans occur, as well as addressing the threats to these populations. Hunting, for example, is emerging as an even more important and imminent threat than forest disturbance, and there is an urgency to identify new approaches that will sustain existing orangutan populations in habitats that are not pristine, and where human activities are ongoing (8). Such approaches include recognizing the value and prioritizing the role of disturbed forest in orangutan conservation strategies. To achieve this goal, a well-developed understanding of how orangutans use these habitats is required to direct conservation efforts, forest restoration projects, and the identification of new protected areas. Although it is becoming clear that orangutans can survive in such forests over the short term, there is a need to identify the ecological requirements of these new habitats that will sustain viable populations into the future, which requires knowledge of orangutan behavior and the forest characteristics they require for survival in disturbed forest.

Despite their ability to engage in terrestrial locomotion, orangutans are predominantly arboreal, and as such, they spend most of their time in the forest canopy. Canopy characteristics, such as 3D structure and individual features (e.g., emergent trees, canopy gaps), would therefore be expected to be highly influential drivers

Significance

Bornean orangutans are critically endangered, and their numbers continue to decline despite decades of conservation effort. Management strategies aimed at protecting primary forest are proving insufficient, and new approaches are required to ensure the species' survival. Here, we use high-resolution laser remote sensing coupled with visual observations of wild orangutans to map canopy structure and quantify orangutan movement through disturbed forests in Borneo. Our findings provide crucial insights into the types of forest characteristics orangutans use in disturbed forests and are likely required for their continued survival in these fragmented landscapes, where most of the extant population occurs. Management and forest restoration efforts that foster these attributes are more likely to succeed at sustaining orangutan populations over the long term.

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of orangutan behavior and habitat selection. Animals, particularly arboreal primates, interact with 3D vegetation structure in direct (e.g., climbing, traveling) and indirect (e.g., selecting structurally induced microclimates) ways, making vegetation structure an important component of their habitat (17, 18). However, measuring canopy 3D structure is challenging, especially at spatial scales appropriate for large mammals. Light Detection and Ranging (LiDAR) is an effective remote sensing tool that overcomes many of these difficulties and provides detailed information on the 3D nature of canopies (17), and it has been successfully applied in primate ecology studies (19, 20).

The Lower Kinabatangan region of Sabah, Malaysia, on the island of Borneo, consists of highly fragmented and disturbed forest patches within a mosaic of oil palm plantations and human settlements (Fig. 1 *A* and *B*). Despite such disturbance, the region supports a relatively large orangutan population that has been continually studied since 1998, making it the longest uninterrupted wild orangutan study in Borneo, and an ideal population and location for investigating orangutan behavior in disturbed and fragmented forest (21). By combining high-resolution airborne LiDAR measurements of forest canopy structure with detailed field-based visual follows of wild orangutans, we quantified how 3D forest structure determines orangutan habitat use in disturbed forest. Specifically, we aimed to understand (*i*) how forest canopy structure affects orangutan movement behavior and (*ii*) how selection for canopy attributes might differ between orangutan age and sex classes. We predicted that tall and structurally complex

canopies would be selected more often because they would assist with vertical movement (climbing) and serve as anchors for large-diameter (>5 cm) woody lianas that facilitate lateral movement between trees (22). We further expected selection to differ among orangutan age and sex classes, with females being more conservative in their selection of movement pathways, opting to travel in directions of increased canopy height and cover that would provide stronger supports relative to males, which would take more risks (following refs. 23, 24). Alternatively, heavier males could be expected to select closed canopy that would aid lateral movement across the forest because they would require stronger supports and be less able to cross areas of sparse canopy, whereas females could be less selective of closed canopy and focus selection instead on structurally complex, tall canopies because their smaller, lighter bodies would enable them to cross sparser canopy.

Results and Discussion

Orangutans of all age and sex classes aligned their movement paths with structural attributes of the upper canopy in this disturbed forest system (canopy structure descriptions are provided in Table 1), moving in directions with increased canopy cover (closure), taller trees, and uniform height (Fig. 2 *A–C* and Table 2). Similarly, although responses were more varied, most orangutans avoided canopy gaps and were more likely to move toward emergent crowns (Fig. 2 *D* and *E* and Table 2). However, movement pathways were not determined by canopy vertical complexity (canopy shape or vertical layering) for any age or sex

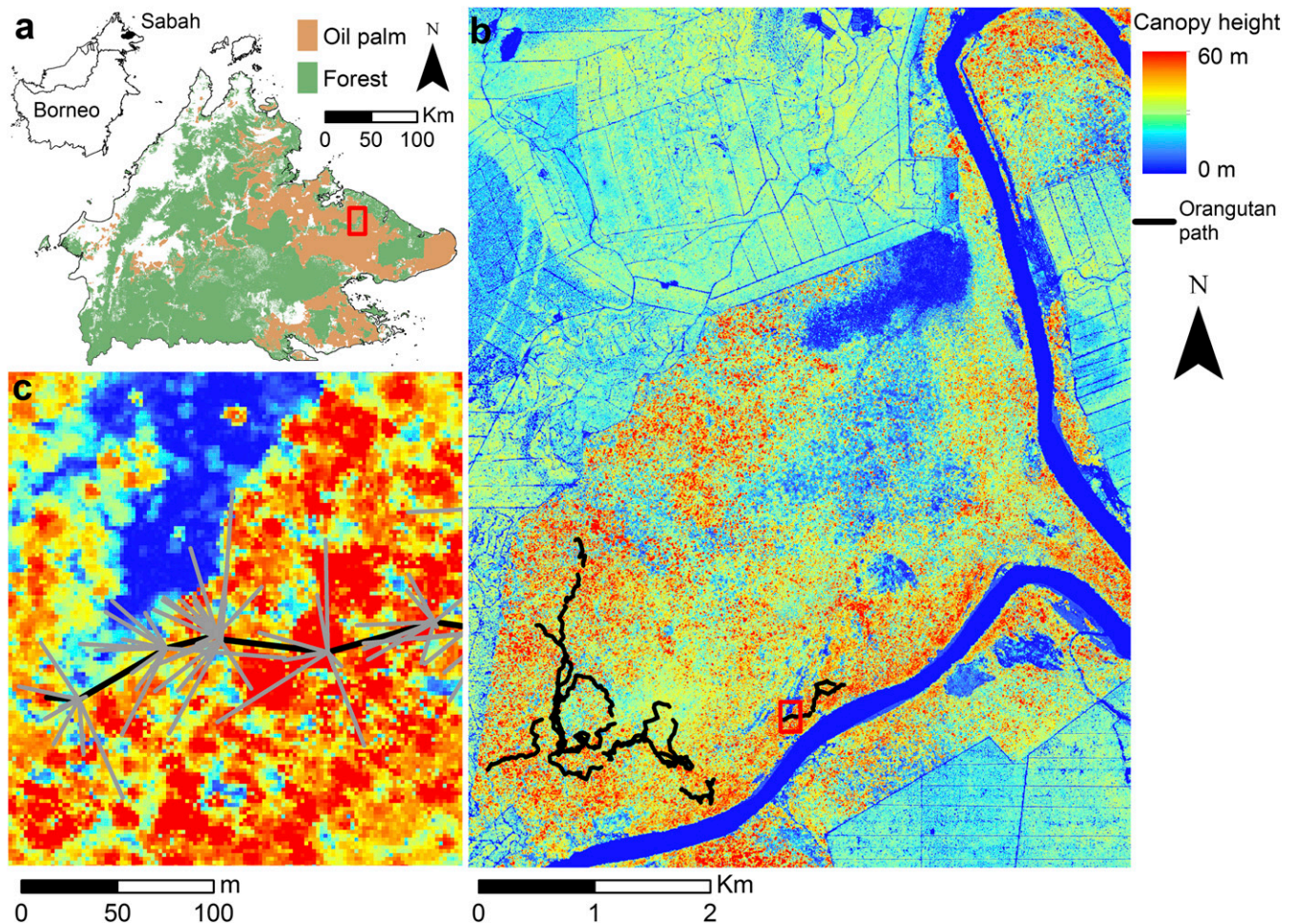


Fig. 1. (*A*) Location of the study site within Sabah, Malaysia. (*B*) Canopy height within and around the study site, Lot 2 of the LKWS, with an example of a flanged male orangutan movement path used in the analysis. (*C*) Depiction of an SSP generated along an example movement path (the black line depicts the observed movement, and the gray lines show the available steps the orangutan could have taken). Red blocks in *A* and *B* indicate zoomed-in areas in *B* and *C*, respectively.

Table 1. LiDAR-derived measurements of canopy structure modeled as covariates in conditional logistic regressions used to describe orangutan movement in the LKWS, Sabah, Malaysia

Structural property	Measurement	Resolution	Description
Upper canopy	Canopy cover	10 m	Proportion of 2×2 -m pixels containing vegetation above 10 m in height
	Canopy height	2 m	Vegetation height in each pixel
	Canopy height heterogeneity	2 m	SD of canopy height over the length of each observed and available step
Canopy features	Distance to emergent crown	2 m	Euclidean distance to the nearest emergent crown, defined as ≥ 2 contiguous pixels taller than 1.5 SDs of the mean canopy height
	Distance to gap	2 m	Euclidean distance to the nearest canopy gap, defined as an area $\geq 12 \text{ m}^2$ with a $\geq 50\%$ reduction in canopy height relative to the surrounding 1 ha
Vertical complexity	Canopy shape	5 m	Ratio of the height above ground where maximum canopy volume occurs to the 99th percentile of total canopy height
	Canopy layering	5 m	Number of vertical vegetation layers present in the canopy between the forest floor and the top of the canopy

class, as evidenced by the small variable importance values and β coefficients of these variables in the resource selection models (Fig. 2 *F* and *G* and Table 2). Step selection functions (SSFs), used to model orangutan movement, were reasonably robust [observed Spearman's rank correlation (r_s) > random r_s] for all individuals.

Taken together, these results suggest that although orangutans do make use of disturbed, degraded, and fragmented forest, they also select for certain canopy attributes within these forests, indicating that not all disturbed or degraded forest is of equal value for the long-term sustainability of orangutan populations. However, for most metrics, response strength and, to a lesser extent, direction varied among individuals (Fig. 2 and Table 2),

suggesting that there is a degree of flexibility in orangutan canopy use, and that no single canopy structural property proved overly dominant.

Canopy structure has previously been shown to have strong effects on habitat selection across a wide range of faunal species (17), including arboreal primates (19, 20). Moreover, forest structure (measured as canopy height) is a more important determinant of global primate species richness than productivity or rainfall (18). However, contrary to our predictions and findings for many other species (17), canopy vertical complexity was unimportant in orangutan habitat selection. Instead, elements of the upper canopy (cover, height, and canopy height heterogeneity) were determining factors (Fig. 2), properties that likely

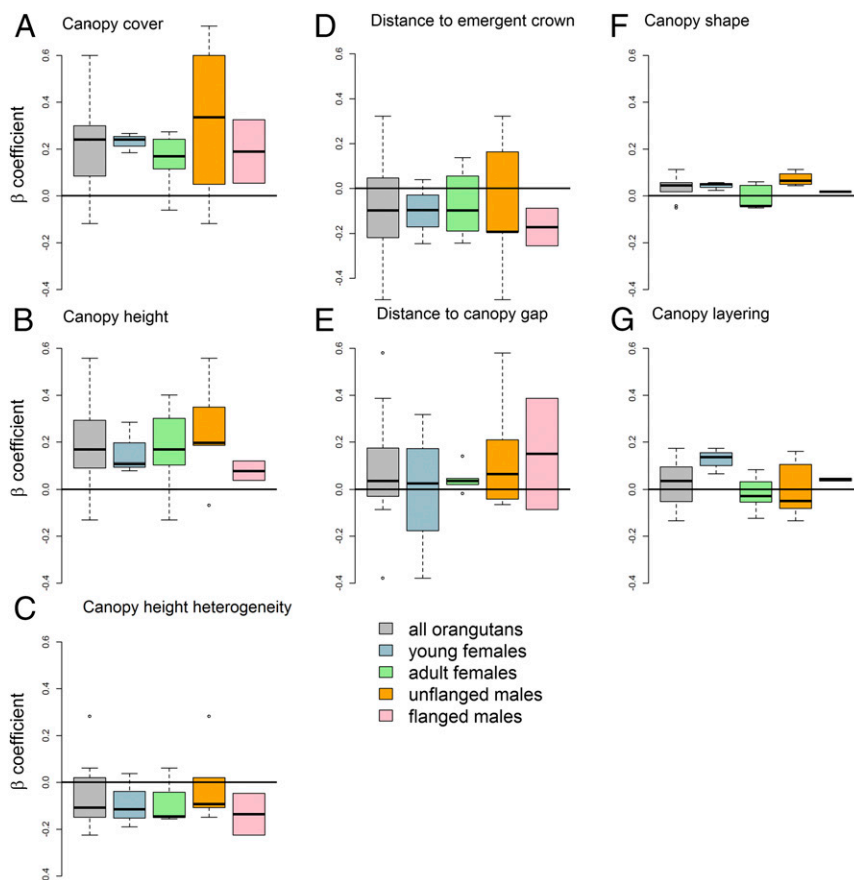


Fig. 2. (A–G) Box plots of model averaged β coefficients from all individuals and across orangutan age and sex classes derived from individually applied SSFs. The solid line in each box indicates the median for each age and sex class, whereas the top and bottom of the boxes depict the third and first quartiles, respectively. Whiskers denote the maximum and minimum values, or 1.5-fold the interquartile range (whichever is smaller), and dots represent outliers. Values above the solid line at zero (positive coefficients) indicate selection for a given covariate, whereas values below (negative coefficients) indicate selection against a given covariate.

Table 2. Model averaged coefficients ($\hat{\beta}$), SEs, and variable importance of LiDAR-derived structural metrics from conditional logistic regression models applied individually to each orangutan in the LKWS, Sabah, Malaysia

Orangutan age and sex class	Canopy cover			Canopy height			SD of height			Distance to emergent canopy			Distance to canopy gap			PI/H ratio			No. of canopy layers		
	$\hat{\beta}$	SE	Imp	$\hat{\beta}$	SE	Imp	$\hat{\beta}$	SE	Imp	$\hat{\beta}$	SE	Imp	$\hat{\beta}$	SE	Imp	$\hat{\beta}$	SE	Imp	$\hat{\beta}$	SE	Imp
Young	<i>0.184</i>	<i>0.107</i>	<i>0.80</i>	0.109	0.105	0.21	0.038	0.074	0.09	-0.096	0.126	0.11	0.025	0.128	0.08	0.023	0.080	0.08	0.136	0.116	0.22
females	0.266	0.166	0.61	0.079	0.129	0.04	-0.190	<i>0.111</i>	<i>0.72</i>	-0.245	0.158	0.59	<i>0.318</i>	<i>0.166</i>	<i>0.80</i>	0.049	0.115	0.03	0.174	0.129	0.38
males	0.241	0.205	0.20	0.285	0.138	0.92	-0.114	0.132	0.20	0.039	0.292	0.07	-0.379	0.240	0.75	0.056	0.136	0.08	0.066	0.178	0.08
Adult	<i>0.169</i>	<i>0.096</i>	<i>0.78</i>	<i>0.168</i>	<i>0.092</i>	<i>0.77</i>	-0.145	0.065	1.00	0.138	0.146	0.19	-0.018	0.111	0.07	0.045	0.071	0.16	-0.054	0.085	0.09
females	0.239	0.072	1.00	0.099	0.076	0.41	0.063	0.051	0.35	-0.105	0.082	0.33	0.025	0.072	0.04	-0.044	0.063	0.13	-0.121	0.075	0.64
males	0.047	0.084	0.13	0.339	0.080	1.00	0.005	0.067	0.11	-0.039	0.156	0.11	0.044	0.104	0.12	-0.047	0.071	0.13	0.019	0.090	0.11
males	0.273	0.079	1.00	-0.130	0.083	0.57	-0.155	0.044	1.00	-0.243	0.083	1.00	0.140	0.068	0.93	0.060	0.059	0.33	0.084	0.061	0.43
Unflanged	0.600	0.216	1.00	-0.068	0.200	0.10	-0.108	0.140	0.13	0.163	0.198	0.14	-0.041	0.232	0.10	0.075	0.160	0.11	-0.134	0.158	0.14
males	0.725	0.204	1.00	0.186	0.167	0.22	0.020	0.128	0.07	0.322	0.253	0.36	-0.065	0.220	0.07	0.044	0.133	0.08	0.160	0.136	0.24
males	0.335	0.104	1.00	0.197	0.093	0.89	-0.092	0.063	0.48	-0.193	0.139	0.48	0.066	0.101	0.13	0.112	0.074	0.49	-0.082	0.085	0.24
males	-0.118	0.146	0.22	0.349	0.155	1.00	0.282	0.119	1.00	-0.194	0.216	0.24	0.210	0.169	0.40				0.107	0.160	0.11
males	0.049	0.181	0.09	0.559	0.121	1.00	-0.149	0.119	0.28	-0.495	0.240	0.91	<i>0.581</i>	<i>0.314</i>	<i>0.79</i>	0.054	0.134	0.10	-0.049	0.171	0.09
Flanged	0.325	0.095	1.00	0.119	0.092	0.31	-0.046	0.064	0.12	-0.256	<i>0.139</i>	<i>0.85</i>	-0.086	0.112	0.12	0.018	0.068	0.09	0.048	0.087	0.11
males	0.054	0.167	0.13	0.038	0.146	0.13	-0.225	0.114	0.87	-0.088	0.156	0.14	0.387	0.157	1.00				0.036	0.123	0.13

Bold font indicates significant ($P < 0.05$) variables, and italics represent variables where $P < 0.1$. Model coefficients indicate the strength of selection for or against a given covariate, with positive coefficients indicating selection for and negative coefficients indicating selection against. Variable importance (Imp) is a measure of the relative importance of each covariate, calculated as the sum of the Akaike weights (w_i) over all models (used in the model averaging) in which the covariate appears.

enhance lateral movement across the canopy. Orangutans are the world's heaviest arboreal mammal and need sufficiently strong branches to cross gaps, with jumping being rare, biomechanically difficult, and energetically expensive (25). They must either descend to the ground (or lower levels of the canopy) or select gap-free pathways (i.e., continuous canopy cover) and tall trees that contain sufficiently strong branches and/or woody lianas to support their weight (24). Tall trees (including emergent crowns) are also important nesting locations (26, 27) and concentrated fruiting sites (11, 28), especially in disturbed forests (29), likely contributing to their selection. Although orangutans can and do descend to the ground to cross gaps (14), this activity is energetically expensive because it requires descending and reascending the canopy (25), and also exposes orangutans to increased pathogens and predation risk (14). Remaining in the upper canopy is therefore a more astute strategy, which is further aided by uniform canopy height. When canopies are irregular or structurally complex, lateral canopy movement can become even more energetically expensive than terrestrial locomotion because of the required increase in vertical movement (14). In contrast, uniform canopies enable orangutans to remain at the same height, thereby enhancing lateral movement.

There were no significant differences in the way age and sex classes used canopies (Kruskal-Wallis test, $P > 0.05$ for all structural metrics) (Fig. 2), suggesting that structural drivers influence orangutans in similar ways despite pronounced sexual dimorphism and adult male bimaturism, as well as observed age and sex differences in terrestrial activity and branch use (14, 24; but see refs. 22, 23, where no differences in locomotion between age and sex classes were detected). Our sample sizes were relatively small, however, so detecting statistical differences in responses is difficult. Notwithstanding these considerations, there was a tendency for unflanged males to display more variation in their responses to most structural metrics (Fig. 2 and Table 2). Unflanged adult males are less territorial (30), making it reasonable to assume that they would travel more, and therefore be less familiar with their surroundings, as opposed to more territorial flanged males, especially flanged males in consort with philopatric females (30–32). Indeed, mean daily distance traveled for unflanged males was longest at 856.56 m, compared with 546.70 m for flanged males, 729.20 m for subadult females, and 694.45 m for adult females. Movement decisions by unflanged males could also be more variable due to their social plasticity and need to find mates while simultaneously avoiding flanged males (30, 33), which could take precedence over energetic costs.

Although we found canopy structure to influence orangutan movement, other factors not examined here could also be potentially important. For example, food resources and mineral licks are known to influence orangutan densities and distributions (11, 34, 35), and could similarly affect finer scaled movement decisions. Although emergent tree crowns can be viewed as surrogates for large fruiting trees, such as *Ficus* and *Dracontomelon* spp., more direct measures that also account for fruiting phenology will likely be illuminating. Similarly, the distribution of conspecifics, such as potential mates and/or hostile individuals, could be an important consideration (36). Knowledge of the simultaneous locations of other individuals will be useful for understanding the influence of these drivers, although this information is particularly difficult to obtain for orangutans, given the difficulties with fitting global positioning system (GPS) tracking devices or following several individuals simultaneously. Nevertheless, understanding how canopy structural properties influence movement is an important first step for predicting suitable forest as potential orangutan habitat.

Although orangutans can and do occupy disturbed and degraded forest, as also shown in this study, it is unknown whether these habitats can secure their long-term survival and persistence. In similar ways to how orangutans can occupy oil palm plantations only if there is sufficient natural forest in close proximity (16), some degraded forests can probably sustain orangutans in the short term, but there are likely to be some minimal ecological requirements necessary for the long-term survival of viable breeding populations in these landscapes. Large-scale timber extraction in Kinabatangan started in the 1970s, and conversion to agriculture started in the mid-1980s. The forests of the floodplain have therefore been fragmented and degraded for a considerable time (>40 y), but still support a significant breeding orangutan population. It is thus reasonable that the canopy elements found to be important here can be viewed more broadly as useful measures of such minimum requirements. In Kinabatangan, orangutans across age and sex classes selected tall, closed canopy forest with relatively uniform height and few gaps. Restoration projects that promote these canopy attributes in combination with other aspects required for orangutan survival, such as sufficient food resources (e.g., fruiting trees) and reduced hunting, are therefore more likely to have long-term success at sustaining populations. Moreover, activities that promote forest fragmentation and an opening up of the canopy (both at the landscape and within-forest-patch scales) should be discouraged for orangutan conservation. Notwithstanding these minimal forest attributes, it is becoming clear that orangutans are more robust and adaptable to human disturbance than previously

thought, and that they are relatively flexible in their use of the canopy, making use of a wide range of canopy conditions as also demonstrated through the range of observed responses to structural metrics in this study. Disturbed forests, with these minimal ecological conditions, should therefore be considered as a high priority in orangutan conservation planning if we are to secure the successful long-term survival of these iconic great apes (8).

Beyond orangutans, there is a need to recognize and understand the conservation value of degraded and disturbed lands, and how priority species, and biodiversity more broadly, use and persist in these landscapes. As anthropogenic pressures continue to grow and exert pressure on animal habitat, especially in the developing tropics, these fragmented and disturbed areas will become more and more typical of available habitat. Moreover, many of these species require large areas already beyond the scope of the current protected area network to be viable in the long term, and conservation planning needs to include such landscapes. If we do not adequately understand how they are used by animals, current and future conservation strategies will likely be largely ineffective for enabling charismatic and functionally important species, such as orangutans and many others, to survive over the long term.

Methods

Orangutan Movement Data. Orangutan movement data were collected in the Lower Kinabatangan Wildlife Sanctuary (LKWS), Sabah, Malaysia. These fragmented forest patches consist mostly of mixed lowland dipterocarp forests along the Kinabatangan River, all of which have been repeatedly logged over the past century but are now protected within either the wildlife sanctuary or other types of protected forest. The orangutan population in the region was estimated at ~1,100 animals in the early 2000s (21), but this population had declined to an estimated 800 individuals by 2015 due to continuous forest loss and dispersal into nonforest habitat. This study was conducted in the intensive study site used by the Kinabatangan Orangutan Conservation Project, which covers ~7.4 km² of Lot 2 of the LKWS (118°17' to 118°20' E and 5°34' to 5°33' N). The 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. 1B). The entire site is below 50 m above sea level and consists of a mosaic of degraded mixed lowland dipterocarp and freshwater swamp forests, with low overall tree density (332 stems per hectare), a short canopy (>80% of trees are <20 m in height), large canopy gaps, and significant soil disturbance (21).

Each day, a team of orangutan researchers enters the study site and systematically surveys the area for the presence of wild orangutans (29). When found, focal animals are followed from nest to nest (dawn until dusk), and the GPS location of the followed individual is recorded each time the animal moves to a new tree, resulting in a complete movement pathway for each day an orangutan is followed. GPS accuracy in this environment was estimated to be between 2 and 8 m. For this study, we used location data collected over a 3-y period from 2014 to 2016. Only individuals with at least 94 observed locations (80 movement steps, defined as the straight-line path between successive trees through which orangutans moved) were included. The final dataset comprised 222 d of direct follows of 14 individual orangutans, resulting in a total of 4,765 observed steps over a total distance of 142.34 km [584 steps over 27 d from three subadult females (independently ranging offspring 7–12 y old), 2,603 steps over 126 d from four adult females, 975 steps over 38 d from five unflanged males (estimated ≥15 y of age), and 603 steps over 31 d from two flanged males].

Airborne LiDAR and Structural Metrics. We mapped the study area with discrete-return airborne LiDAR in April 2016 using the Carnegie Airborne Observatory-3 (CAO) (37). The CAO LiDAR subsystem provides 3D structural information on vegetation canopies and the underlying terrain. The GPS inertial measurement unit (IMU) subsystem provides 3D position and orientation data for the sensors, allowing for highly precise and accurate positioning of LiDAR observations on the ground. For this study, the CAO data were collected from 3,600 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 3.20 laser shots per square meter. Horizontal and vertical error estimates were 16 cm and 7 cm root-mean-square-error, 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 georeferenced 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 yields a digital canopy model (DCM). The final ground elevation and woody canopy height models were derived at a spatial resolution of 2 m.

From the processed LiDAR data, we extracted structural metrics expected to influence orangutan canopy movement (Table 1). We derived measurements of upper canopy attributes (canopy cover, canopy height, and the heterogeneity of canopy height) and canopy features (emergent tree crowns and canopy gaps) from the DCM and metrics of canopy vertical complexity (canopy shape and canopy layering) from the vertical distribution of the LiDAR points. Canopy cover was defined as the proportion of area occupied by vegetation above a height of 10 m [i.e., 1 (full cover) – canopy gap fraction (the area above 10 m clear of vegetation)]. A horizontal plane was created through the DCM at a height of 10 m aboveground, following which the number of pixels for which the DCM was above this plane was counted and divided by the total number of pixels over a 10 × 10-m area. An aboveground height of 10 m was chosen because the mean canopy height in the study area was 17.3 m, and orangutans in Kinabatangan are known to travel mostly in the top half of the canopy. Canopy height was measured as the interpolated height of the DCM at a resolution of 2 m, and the heterogeneity of canopy height was defined as the SD of canopy height between two observed or available orangutan movement steps. Emergent tree crowns were expected to influence orangutan movement because they represent large trees that are used as nesting, foraging, and vantage points in these forests (29). These emergent tree crowns were defined as clumps of two or more contiguous pixels (from the DCM) with a height greater than 1.5-fold the SD of the mean canopy height across the study area (i.e., emergent crowns were >28.2 m tall and ≥8 m² in area) (modified from ref. 38). Orangutans were expected to avoid canopy gaps because of the increased energetic costs of descending and ascending the canopy to cross them (25). Canopy gaps were defined as areas of at least three contiguous DCM pixels (i.e., 6 m in length and 12 m² following refs. 10, 11, 14, which classified gaps as being ≥5 m in length) that had a relative height of –0.5 to –1.0, or 50–100%, below the mean canopy height of the surrounding 1 ha (modified from ref. 39).

For metrics of canopy vertical complexity, we binned the vertical distribution of LiDAR points into volumetric pixels (voxels) of 5 × 5-m horizontal spatial resolution and 1-m vertical resolution, with the DTM used to standardize the vertical datum at the horizontal center 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 percentage of vegetation present in each 1-m height category. We then counted the number of 1-m layers in each column that contained vegetation as a measure of canopy vertical complexity (i.e., the number of 1-m canopy layers where vegetation was present). Finally, we computed a canopy shape parameter for each voxel, the *PIH* ratio (following ref. 40), that reduces a large amount of vertical profile information into a simple metric depicting the overall architecture of the canopy. The *PIH* ratio is defined as the ratio of the height above ground where the maximum canopy volume (*P*) occurs relative to the 99th percentile of total canopy height (*H*). A high *PIH* ratio indicates that the majority of foliage is positioned high in the canopy, independent of overall canopy height, whereas a low *PIH* ratio indicates a groundward tendency of foliar distribution (40).

Analysis. SSFs were used to identify canopy structural metrics that influenced orangutan movement (41, 42). SSFs are a case-control resource selection function where the step (defined as the straight-line path between successive GPS locations) is the dependent variable. The probability of an individual orangutan selecting a step was estimated by comparing each observed step with a matched sample of 10 randomly drawn available steps (Fig. 1C). Available steps for each individual orangutan were generated by randomly drawing step lengths and turning angles from the movement distributions of all other observed orangutans, thereby avoiding issues of circularity (41). Each day of orangutan observation (nest-to-nest focal following) was processed separately to ensure that each sample represented an actual step (movement), and was not affected by the possibility that the GPS tracking of the orangutan began a few hours after it had already left the nest and started moving the next day. Predictor variables (canopy structural

metrics are provided in Table 1) were measured as their length-weighted mean, or SD in the case of canopy height heterogeneity, along the length of each observed and available step. SSF models are not based on the stringent assumption that the animal traveled the sampled straight-line path, only that the environmental characteristics between the starting and ending points influenced movement and the location of the end point (42).

Predictor variables were scaled and centered before analysis, following which candidate sets of conditional logistic regression models were constructed for each individual orangutan. These candidate sets consisted of a global model containing all predictor variables (Table 1) and reduced versions of this model. We did not include interaction terms because we had no biological basis for doing so. SSFs were applied separately to each orangutan to account for individual variation, and to enable inferences about age- and sex-specific behaviors (41). Collinearity between predictor variables was assessed using generalized variance inflation factors (GVIFs), with all GVIF scores <3 , and most <2 , in all models. Models were ranked and assessed using sample size-corrected Akaike information criteria (AICc) and Akaike weights (w_i). Because of close convergence between top models (small changes in AICc scores and w_i between models), model averaging was implemented using the coefficients from the models with a delta AICc <2 relative to the most parsimonious model (43). Robustness of the best-performing model was assessed using a k-fold cross-validation technique for conditional logistic regression that evaluates the performance of the model by comparing scores of observed steps with random ones (44). To achieve this assessment, an SSF was built by randomly selecting 80% of the strata, and then comparing the results with the withheld 20%. This procedure was repeated 100 times, with the observed steps ranked

against random ones. A Spearman's rank correlation (r_s) was then calculated to evaluate how well the training data explained the testing data. Finally, we tested for differences in selection between the four age and sex classes (using the variable coefficients from the model averaging as the dependent variable) using a Kruskal–Wallis test.

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- Duffy JE (2003) Biodiversity loss, trophic skew and ecosystem functioning. *Ecol Lett* 6: 680–687.
- Dunne JA, Williams RJ, Martinez ND (2002) Network structure and biodiversity loss in food webs: Robustness increases with connectance. *Ecol Lett* 5:558–567.
- Ceballos G, Ehrlich PR, Soberón J, Salazar I, Fay JP (2005) Global mammal conservation: What must we manage? *Science* 309:603–607.
- Hoffmann M, et al. (2011) The changing faces of the world's mammals. *Philos Trans R Soc Lond B Biol Sci* 366:2598–2610.
- Ripple WJ, et al. (2016) Saving the world's terrestrial megafauna. *Bioscience* 66: 807–812.
- Ripple WJ, et al. (2016) Bushmeat hunting and extinction risk to the world's mammals. *R Soc Open Sci* 3:160498.
- Schipper J, et al. (2008) The status of the world's land and marine mammals: Diversity, threat, and knowledge. *Science* 322:225–230.
- Meijaard E, Wich S, Ancrenaz M, Marshall AJ (2012) Not by science alone: Why orangutan conservationists must think outside the box. *Ann N Y Acad Sci* 1249:29–44.
- Ancrenaz M, et al. (2016) Pongo pygmaeus. The IUCN Red List of Threatened Species 2016: e.T17975A17966347. Available at dx.doi.org/10.2305/IUCN.UK.2016-1.RLTS.T17975A17966347.en. Accessed March 15, 2017.
- Knop E, Ward PI, Wich SA (2004) A comparison of orangutan density in a logged and unlogged forest on Sumatra. *Biol Conserv* 120:183–188.
- Felton AM, Engström LM, Felton A, Knott CD (2003) Orangutan population density, forest structure and fruit availability in hand-logged and unlogged peat swamp forests in West Kalimantan, Indonesia. *Biol Conserv* 114:91–101.
- Ancrenaz M, et al. (2010) Recent surveys in the forests of Ulu Segama Malua, Sabah, Malaysia, show that orangutans (*P. p. morio*) can be maintained in slightly logged forests. *PLoS One* 5:e11510.
- Meijaard E, et al. (2010) Unexpected ecological resilience in Bornean orangutans and implications for pulp and paper plantation management. *PLoS One* 5:e12813.
- Ancrenaz M, et al. (2014) Coming down from the trees: Is terrestrial activity in Bornean orangutans natural or disturbance driven? *Sci Rep* 4:4024.
- Wich SA, et al. (2012) Understanding the impacts of land-use policies on a threatened species: Is there a future for the Bornean orangutan? *PLoS One* 7:e49142.
- Ancrenaz M, et al. (2015) Of Pongo, palms and perceptions: A multidisciplinary assessment of Bornean orangutans *Pongo pygmaeus* in an oil palm context. *Oryx* 49: 465–472.
- Davies AB, Asner GP (2014) Advances in animal ecology from 3D-LiDAR ecosystem mapping. *Trends Ecol Evol* 29:681–691.
- Gouveia SF, Villalobos F, Dobrovolski R, Beltrão-Mendes R, Ferrari SF (2014) Forest structure drives global diversity of primates. *J Anim Ecol* 83:1523–1530.
- McLean KA, et al. (2016) Movement patterns of three arboreal primates in a Neotropical moist forest explained by LiDAR-estimated canopy structure. *Landscape Ecol* 31: 1849–1862.
- Palminteri S, Powell GVN, Asner GP, Peres CA (2012) LiDAR measurements of canopy structure predict spatial distribution of a tropical mature forest primate. *Remote Sens Environ* 127:98–105.
- Ancrenaz M, Goossens B, Gimenez O, Sawang A, Lackman-Ancrenaz I (2004) Determination of ape distribution and population size using ground and aerial surveys: A case study with orangutans in lower Kinabatangan, Sabah, Malaysia. *Anim Conserv* 7:375–385.
- Manduell KL, Harrison ME, Thorpe SKS (2012) Forest structure and support availability influence orangutan locomotion in Sumatra and Borneo. *Am J Primatol* 74:1128–1142.
- Thorpe SKS, Crompton RH (2005) Locomotor ecology of wild orangutans (*Pongo pygmaeus abelii*) in the Gunung Leuser Ecosystem, Sumatra, Indonesia: A multivariate analysis using log-linear modelling. *Am J Phys Anthropol* 127:58–78.
- Thorpe SKS, Holder R, Crompton RH (2009) Orangutans employ unique strategies to control branch flexibility. *Proc Natl Acad Sci USA* 106:12646–12651.
- Thorpe SKS, Crompton RH, Alexander RM (2007) Orangutans use compliant branches to lower the energetic cost of locomotion. *Biol Lett* 3:253–256.
- van Casteren A, et al. (2012) Nest-building orangutans demonstrate engineering know-how to produce safe, comfortable beds. *Proc Natl Acad Sci USA* 109:6873–6877.
- Sugardjito J (1983) Selecting nest-sites of sumatran orang-utans, *Pongo pygmaeus abelii* in the Gunung Leuser National Park, Indonesia. *Primates* 24:467–474.
- Leighton M (1993) Modeling dietary selectivity by Bornean orangutans: Evidence for integration of multiple criteria in fruit selection. *Int J Primatol* 14:257–313.
- Ancrenaz M, Calaque R, Lackman-Ancrenaz I (2004) Orangutan nesting behavior in disturbed forest of Sabah, Malaysia: Implications for nest census. *Int J Primatol* 25: 983–1000.
- Utami SS, Goossens B, Bruford MW, de Ruiter JR, van Hooff JA (2002) Male bimatrimony and reproductive success in Sumatran orang-utans. *Behav Ecol* 13:643–652.
- Goossens B, et al. (2006) Philopatry and reproductive success in Bornean orang-utans (*Pongo pygmaeus*). *Mol Ecol* 15:2577–2588.
- Spillmann B, Willems EP, van Noordwijk MA, Setia TM, van Schaik CP (2017) Confrontational assessment in the roving male promiscuity mating system of the Bornean orangutan. *Behav Ecol Sociobiol* 71:20.
- Knott CD, Thompson ME, Stumpf RM, McIntyre MH (2010) Female reproductive strategies in orangutans, evidence for female choice and counterstrategies to infanticide in a species with frequent sexual coercion. *Proc R Soc Lond B Biol Sci* 277: 105–113.
- Matsubayashi H, et al. (2011) Natural-licks use by orangutans and conservation of their habitats in Bornean tropical production forest. *Raffles Bull Zool* 59:109–115.
- Kanamori T, Kuze N, Bernard H, Malim TP, Kohshima S (2017) Fluctuations of population density in Bornean orangutans (*Pongo pygmaeus morio*) related to fruit availability in the Danum Valley, Sabah, Malaysia: A 10-year record including two mast fruitings and three other peak fruitings. *Primates* 58:225–235.
- Marzec AM, et al. (2016) The dark side of the red ape: Male-mediated lethal female competition in Bornean orangutans. *Behav Ecol Sociobiol* 70:459–466.
- Asner GP, et al. (2012) Carnegie Airborne Observatory-2: Increasing science data dimensionality via high-fidelity multi-sensor fusion. *Remote Sens Environ* 124:454–465.
- Balzotti CS, et al. (2017) Topographic distributions of emergent trees in tropical forests of the Osa Peninsula Costa Rica. *Ecography* 40:829–839.
- Marvin DC, Asner GP (2016) Branchfall dominates annual carbon flux across lowland Amazonian forests. *Environ Res Lett* 11:094027.
- Asner G, et al. (2014) Landscape-scale changes in forest structure and functional traits along an Andes-to-Amazon elevation gradient. *Biogeosciences* 11:843–856.
- Thurfjell H, Ciuti S, Boyce MS (2014) Applications of step-selection functions in ecology and conservation. *Mov Ecol* 2:4.
- Fortin D, et al. (2005) Wolves influence elk movements: Behavior shapes a trophic cascade in Yellowstone National Park. *Ecology* 86:1320–1330.
- Burnham KP, Anderson DR (2002) *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach* (Springer, New York), 2nd Ed, p 488.
- Fortin D, et al. (2009) Group-size-mediated habitat selection and group fusion-fission dynamics of bison under predation risk. *Ecology* 90:2480–2490.