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Abstract

Knowledge of fundamental aspects of ecology such as species richness and distribution, and the factors affecting them, is increasingly used to identify priority areas for conservation and to effectively manage threatened species. We investigated the species richness and distribution pattern of nonhuman primate communities inhabiting 10 sampling sites in four different habitat classes corresponding to increasing habitat disturbance level, that is, old growth forest, twice logged forest, repeatedly logged forest, and oil palm plantation, in and around Kalabakan Forest Reserve, in central Sabah, Malaysian Borneo. By using direct and indirect survey methods, we confirmed the existence of 9 out of the total 10 primate species, found in Sabah, within the surveyed areas. Based on the monthly number of primate species detected, our results indicated a general trend of decreasing primate species richness with increasing habitat disturbance level. However, the response within the disturbed forest sites showed some variations with some sites in repeatedly logged forest displaying comparable primate species number to that of the undisturbed forest sites. We also found that within the forest habitats, tree density is a good predictor of the richness of the primate community with a positive effect. Hence, tree density may be a key indicator for evaluating primate communities in forest habitats. Overall, the results of our study suggest that although not equivalent to areas of undisturbed forest, degraded forests—including those that have been repeatedly logged—are still valuable for primate conservation. In contrast, oil palm plantations have mainly negative effects on the primate community.

Keywords

disturbed habitat, logging, oil palm plantation, primate species richness, SAFE project

Introduction

Knowledge of species richness and distribution, and the factors affecting them, is essential to set areas of conservation priorities, including for assessing the risk of species extinction and to effectively manage threatened species (Kay, Madden, VanSchaik, & Higdon, 1997). Primates are an important taxonomic group among tropical arboreal fauna, and one of the most dominant in terms of overall biomass (e.g., Eisenberg & Lockhart, 1972; Tashiro, 2001). Collectively, primates use a diverse array of resources, for example, fruits, seeds, flowers, leaves, invertebrates, and fungi (Corlett, 2009), indicating that they play a pivotal role in the complicated network of interactions among animal and plant species in the tropical forest ecosystems. Thus, an understanding of the structure of primate communities in different habitat types and conditions is important for developing conservation strategies,

not only for primates but also for the broader network of species with which they interact. Indeed, the Bornean primate community is suggested to be a good indicator of lowland diversity (Meijaard & Nijman, 2003).

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Previous studies have considered the influence of a variety of factors affecting the number of species in local communities and the abundance of each species (e.g., Eeley & Lawes, 1999; Hillebrand, 2004; Takyu, Kubota, Aiba, Seino, & Nishimura, 2005). Although there are exceptions, these studies have revealed that there seems to be a general tendency for species richness to decrease with increasing latitude, both among animals and plants (Eeley & Lawes, 1999; Hillebrand, 2004; Takyu et al., 2005). More specifically for primates in general, species richness at broad macroecological scales has been shown to be positively associated with rainfall (Fleagle, Janson, & Reed, 1999), although more recent studies have indicated that the biomass and species richness of frugivorous primates is negatively associated with seasonality in food availability but positively associated with total annual food abundance (Hanya & Aiba, 2010; Hanya et al., 2011). On the other hand, in degraded habitat landscapes that consist of a complex mosaic of disturbance intensities, primate communities are more likely to be structured by local-scale habitat parameters such as aspects of forest structure (Cheyne, Thompson, & Chivers, 2013; Hamard, Cheyne, & Nijman, 2010) including local variations of food quality in terms of nutritional quality and abundance (Vogel et al., 2015). Thus, this suggests that uncovering these local-scale habitat conditions necessary for primate persistence will be crucial to identify where suitable habitats are still present to preserve as many primate species as possible and for the construction of conservation and management action plans for primate species.

Borneo is a center of biodiversity and endemism (Woodruff, 2010), which is highly threatened from intensive logging practices and the large-scale conversion of forest to agriculture (Sodhi, Koh, Brook, & Ng, 2004). In the Malaysian state of Sabah in northern Borneo, much of the forests have already been logged at least once, and logged-over forests, especially highly degraded ones, are under pressure for conversion to agricultural plantations, mainly oil palm (*Elaeis guineensis*; Reynolds, Payne, Sinun, Mosigil, & Walsh, 2011). There are 10 nonhuman primate species found in the northern part of Borneo in the state of Sabah (Payne, Francis, & Phillips, 1985), including species of global conservation concern such as the Bornean orangutan (*Pongo pygmaeus morio*) and Bornean gibbon (*Hylobates muelleri fenerus*; IUCN, 2015). Here, we sought to describe the species richness and distribution patterns of primate species across a gradient of habitat disturbance from old growth forest to repeatedly logged forest to oil palm plantation in central Sabah, where data are generally lacking, and to determine the local-scale forest characteristics affecting primate species richness in this landscape. Faunal species richness is known to be typically higher in undisturbed forests compared with logged forests and

agricultural plantations (Berry et al., 2010; Sodhi et al., 2004; Yue, Brodie, Zipkin, & Bernard, 2015). Therefore, in our study, we predicted that primate species richness, as measured by monthly number of diurnal and nocturnal primate species detected, is higher in undisturbed forest as compared with disturbed forest and oil palm plantation. We also predicted that within the forest habitats, some aspects of forest characteristics would be good predictors to predict primate species richness and, hence, will be useful for evaluating primate community with respect to their conservation management and monitoring in degraded habitats.

Methods

Study Site

We conducted this study mainly at the SAFE project area (Stability of Altered Forest Ecosystems, www.safeproject.net, 4°33'N, 117°16'E), a large-scale (7,200 ha) ecological experiment investigating the effects of fragmentation of Southeast Asian rain forest and conversion to oil palm plantation (Figure 1; Ewers et al., 2011). The experimental area lies within the Kalabakan Forest Reserve in south central Sabah, Malaysian Borneo. Other sites include the Brantian Tantulit Virgin Jungle Reserve (VJR), Ulu Segama Forest Reserve (USFR), Maliau Basin Conservation Area (MBCA), and an oil palm plantation managed by Benta Wawasan Sdn. Bhd. With the exception of MBCA which is located approximately 65 km to the west of the SAFE project area, all other study sites were located within a 20-km radius in and around the SAFE project area.

The majority of the SAFE Project area has already undergone multiple (two or three times) intensive rounds of logging, beginning in 1978 and ongoing until the early 2000s (Konopik, Steffan-Dewenter, & Grafe, 2015; Struebig et al., 2013). As a result of this treatment, the remaining forest is generally heavily degraded and consists of a range of habitat types from grassy open areas and low scrub vegetation, to lightly logged forest on steep slopes and in rocky areas (Wearn, Rowcliffe, Carbone, Bernard, & Ewers, 2013). The VJR (2,200 ha) is a lowland dipterocarp rainforest, which is strictly protected as a site for forestry research and biodiversity conservation. Even so, while most of the VJR is undisturbed or near pristine old growth forest, some levels of disturbance are apparent particularly near access roads. The USFR (126,840 ha) is a lowland dipterocarp forest and was managed as a commercial forest reserve from 1961 but has since been gazetted as a protection forest reserve in 2014. Many parts of this forest reserve have been logged twice, between 1980 and 2000 (Ancrenaz et al., 2010). MBCA is a large (55,840 ha) totally protected area where logging is prohibited. Although in the past

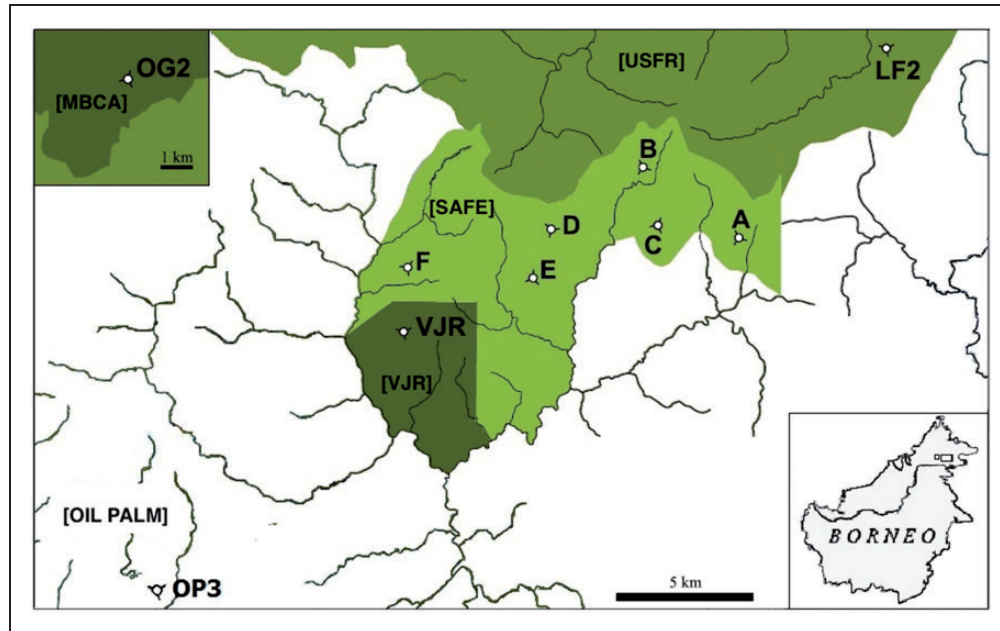


Figure 1. Location of 10 sampling sites (OG2, VJR, LF2, Blocks A–F, and OP3) in and around the Stability of Altered Forest Ecosystems project area (SAFE), BrantianTantulit Virgin Junge Reserve (VJR), Ulu Segama Forest Reserve (USFR), Maliau Basin Conservation Area (MBCA), and mature oil palm plantation (OIL PALM), in south central part of Sabah, Borneo, Malaysia, in 2011–2012. Note. dark shading = old growth forests; intermediate shading = twice logged forest; light shading = repeatedly logged forests; white areas = oil palm plantation; lines indicate rivers.

some logging activity has occurred in proximity to the MBCA in the early to mid-1990s, this area consists mainly of undisturbed lowland dipterocarp rainforest. The oil palm plantation used in this study consisted of 5- to 10-year-old oil palms in a large continuous plantation area (comprising recent plantings to >15-year-old palms) situated in the southwest of the SAFE project area, approximately 2 to 10 km from the nearest forests edges.

Primate Survey

To assess primate species richness and distribution, we surveyed 10 sampling sites representing four broad habitat categories. Three of these categories were previously defined by Struebig et al. (2013), based on logging disturbance history, that is, old growth forest, twice logged forest, and repeatedly logged forest, and one was additionally defined in the present study, that is, oil palm plantation. The old growth forest was represented by two sampling sites (OG2 and VJR) in the MBCA and VJR, respectively. Twice logged forest was represented by one sampling site (LF2) in USFR. Repeatedly logged forest was represented by six sampling sites (mainly within the proposed forest fragments of Blocks A to F and also included areas outside of these proposed fragments) within the SAFE Project area. Finally, oil palm plantation was represented by one sampling site (OP3) within the Benta Wawasan oil palm estates near

the SAFE Project area. The topography of all 10 sampling sites was generally very rough, with elevation ranging between 200 and 500 m. At the time of sampling, all sampling sites in the forest habitats (OG2, VJR, LF2, and Blocks A to F) were part of a large contiguous expanse of lowland dipterocarp forest (>1 million ha) in central Sabah (Reynolds et al., 2011).

We determined the presence of both diurnal and nocturnal nonhuman primates by conducting systematic surveys along pre-existing man-made trails, between 1.4 and 5.4 km long, in each of the 10 sampling sites. At each site, we walked the trails in the early morning from 6:00 a.m. to 12:00 p.m. and at night from 7:00 p.m. to 12:00 a.m. once every month (at around the first or second week of each month) for a total repeated surveys of at least 6 to 12 times per site between November 2011 and November 2012. Ideally, we would have surveyed all sampling sites equally, but logistical problems and unpredictable weather conditions during certain months prevented us from doing so. We conducted the surveys only during fine weather in a team of four to five researchers. The first person led the trail and cleared it when necessary. Two to three spotters followed the lead person, while the last person recorded data. To minimize intersite variation in primate detectability, we used the same spotters throughout the survey period, and all spotters had extensive experience in primate surveys in Sabah's forests. During the survey, we walked quietly at a speed of 1 to 1.5 km/h along the trails with brief stops (3–5 minutes) at every 50 m distance to

allow careful searching for primates at all heights of the canopy. We used red-light head lamps and spotlights during night walks to detect nocturnal primates. Whenever we spotted a primate individual or group, newly constructed nests of orangutan or heard gibbon vocalizations, we recorded the primate species name and location, and the approximate distance (m) of the primates or their signs from the observer. Distances were estimated by the naked eye or a range finder. Only when the primate species identity was known with high certainty, it was recorded. Accurate counts of individuals (or the primate group size) were not always possible due to the shyness of the animals. We regarded an animal or group of animals, newly constructed orangutan nests and gibbon vocalizations detected during each survey month, at a particular sampling site, as independent samples. We minimized the likelihood of double counting gibbons detected through vocalizations during each survey month by determining the approximate locations of the gibbon individuals or groups using a compass bearing and their approximate distances from the points of detection along the trails. Gibbon vocalizations detected from the same direction but estimated to be located at least 600 m apart were considered to be from two different individuals or groups based on the home range size (36 ha = 0.6 km × 0.6 km) of Bornean gibbon in Kutai National Park (Leighton, 1987), which appears to be consistent to that of the Bornean gibbon home range in Danum Valley, Sabah (range = 33–34 ha; Inoue, Sinun, & Okanoya, 2016). We defined newly constructed nests of orangutan as those in Class I and Class II following the ordinal index of orangutan nest age used by Ancrenaz, Calaque, and Lackman-Ancrenaz (2004). We assumed that each newly constructed orangutan nest was built by different individuals (Ancrenaz, et al., 2004). For consistency and to improve comparability of estimates of primate species number between sites, we recorded animals or their signs that were spotted only within an approximate distance <30 m from the trails, except when animals were detected through their calls, then we used an estimated distance of ca. 200 m radius as the cut off for data collection. The sampling methods used in our study are noninvasive and have been approved by Yayasan Sabah and the Forestry Department of Sabah. They do not violate any existing laws, rules, or regulations pertaining to animal study in the state of Sabah.

Vegetation Survey

To determine the habitat characteristics at each sampling site and investigate their effects on primate species number, we established ten 10 m × 10 m vegetation plots located at random along each of the trails used in the primate survey (total 0.1 ha plot per site). In the

vegetation plots, we tagged, counted, and recorded the species of all living trees with >10 cm dbh (diameter at breast height; 1.4 m above ground level). We also grouped them into six dbh classes using ordinal scales of 1–6, that is, dbh: 1, 10–20 cm; 2, 20–30 cm; 3, 30–40 cm; 4, 40–50 cm; 5, 50–60 cm; and 6 > 60 cm. The percentage of forest understory density, defined as all vegetation taller than 2 m, was estimated using a spherical densiometer measured from the center of each vegetation plot at all sites.

Data Analysis

We used the monthly number of primate species detected for each site in this study as an index of relative primate species richness. We compared graphically the monthly average of primate species richness weighted by trail length across all 10 sampling sites as well as between habitat types based on pooled data from the site level. As the data did not conform to a normal distribution (Klomogrov–Smirnov test, $p < .05$), we conducted the nonparametric Kruskal–Wallis test to compare the primate species richness across sampling sites and habitat types. We performed a generalized linear mixed-effects model (GLMM) analysis to determine whether primate species richness was affected by habitat type, using the R package “lme4” (Bates, Maechler, Bolker, & Walker, 2015). In this analysis, we used the monthly number of primate species detected at each site as a response variable, whereas habitat type—defined as (a) old growth forest, (b) twice logged forest, (c) repeatedly logged forest, and (d) oil palm plantation—was treated as categorical explanatory variable. To account statistically for the effects of differences in survey frequency, survey trail length, and understory density (logit transformed) affecting the detection of primate species number at each site, we included these variables as covariates (survey frequency and understory density) and random variable (trail length) in the model.

To detect the detailed effects of specific habitat characteristics on primate species richness, we performed another GLMM analysis. In this analysis, we considered sampling sites in the forest habitat only. We did not include the oil palm plantation because the specific habitat features recorded in our study were not relevant for this habitat, that is, no natural tree species were present in the oil palm plantation. We used the same response variable as with the earlier mentioned GLMM, and the three habitat characteristics, that is, tree density (defined as number of trees with >10 cm dbh per m²), tree dbh (>10 cm dbh: an index calculated as the sum of the averaged ordinal scales of each of the tree dbh classes), and tree diversity (calculated by the formula of Shannon–Wiener index of diversity based on the number of plant species and their frequencies found in the vegetation plots

in each site; Pielou, 1966) were used as continuous explanatory variables. We added survey frequency and understory density (logit transformed) as covariates and survey trail length as a random variable in the model to account statistically for the effects of differences in these variables on the detection of primate species across all forest sites.

For both GLMM analyses, we used Poisson as family object and we applied the *log* link function. From the GLMM analyses, we further examined a set of models with all possible combinations of the explanatory variables and ranked them by the Akaike Information Criterion (AIC) corrected for small sample size (AICc; Burnham & Anderson, 2002) to find the best models ($\Delta\text{AICc} < 2$). The analyses were performed in R using the dredge function in the “MuMIn” package, version 1.9.13 (Bartoń, 2012). All analyses were carried out using statistical software R, version 3.1.3 (R Development Core Team, 2015).

Results

Overall Results of Primate Survey

We covered a total cumulative distance of 578 km over the 12 months survey period (Table 1). Nine species of primates were detected, consisting of seven diurnal and two nocturnal species. All nine primate species were observed

directly, with the presence of two of the primate species were also detected indirectly either by their vocalization (Bornean gibbon) or from newly constructed nests (orangutan). Of the nine species detected, three are classified as *Endangered* on the IUCN (2015) Red List of Threatened Species (orangutan, *Pongo pygmaeus morio*; proboscis monkey, *Nasalis larvatus*; and Bornean gibbon, *Hylobates muelleri fenerus*), four are classified as *Vulnerable* (slow loris, *Nycticebus menagensis*; western tarsier, *Tarsius bancanus*; gray leaf monkey, *Presbytis hosei*; and pig-tailed macaque, *Macaca nemesterina*), and two species are regarded as *Least Concern* (red leaf monkey, *Presbytis rubicunda* and long-tailed macaque, *Macaca fascicularis*). The Bornean orangutan, the proboscis monkey, Bornean gibbon, gray leaf monkey, and red leaf monkey are all Bornean endemics (Payne et al., 1985).

The overall cumulative number of monthly independent detections of all primate species combined was 259 (Table 1), although the number of detections based on direct sightings was only 74 (or 29% of total detections): mean monthly detection rate of a primate species based on direct sightings was 0.51 (SD: 0.44, range: 0.08–1.25). The remaining 185 were based on indirect detection, that is, detections of orangutan nest: 138 (mean: 11.5, SD: 13.3, range: 0–36); detection of gibbon calls: 47 (mean, 3.9; SD, 4.6, range: 0–16). The two most frequently detected primate species were the orangutan and Bornean gibbon (a combined of 81% from total

Table 1. Cumulative Number of Monthly Independent Detections (via Direct and Indirect Observations) of Nine Primate Species.

Habitat type Primate species/Sampling site	OGF		TLF	RLF						OP	Total
	OG2	VJR	LF2	A	B	C	D	E	F	OP3	
<i>Pongo pygmaeus morio</i>	0	5	13	16	21	24	15	39	19	1	153
<i>Hylobates muelleri fenerus</i>	14	6	13	2	3	0	7	9	3	0	57
<i>Macaca nemesterina</i>	1	0	0	0	2	10	0	1	0	1	15
<i>Tarsius bancanus</i>	2	1	0	2	0	0	1	5	0	0	11
<i>Presbytis rubicunda</i>	2	1	0	1	0	0	1	2	1	0	8
<i>Nycticebus menagensis</i>	0	0	0	1	0	1	0	3	2	0	7
<i>Macaca fascicularis</i>	2	1	0	0	1	0	1	0	1	0	6
<i>Nasalis larvatus</i>	0	0	0	0	0	0	0	0	1	0	1
<i>Presbytis hosei</i>	1	0	0	0	0	0	0	0	0	0	1
Total	22	14	26	22	27	35	25	59	27	2	259
No. of primate species detected	6	5	2	5	4	3	5	6	6	2	–
No. of monthly survey	6	6	9	11	11	11	12	12	11	9	98
Trail length at each site (km)	2.9	1.4	3.3	2.5	3.9	2.5	1.9	2.8	2.8	5.4	29.4
Total cumulative length (km) of trails walked (day and night)	34.8	16.8	59.4	55.0	85.8	55.0	45.6	67.2	61.6	97.2	578.4

Note. Cumulative number of monthly independent detections (via direct and indirect observations) of nine species of nonhuman primates at 10 different sampling sites in and around the Stability of Altered Forest Ecosystems (SAFE) project area in south central Sabah, Malaysian Borneo, between November 2011 to November 2012. Habitat types: old growth forest (OGF = site OG2, VJR), twice logged forest (TLF = site LF2), repeatedly logged forest (RLF = Site A-F), and oil palm plantation (OP = site OP3).

detections), although mainly through indirect detections. Pig-tailed macaque and western tarsier together accounted for 10% of the total detections. The least number of detections were for proboscis monkey and gray leaf monkey, with only one detection recorded for both species (Table 1).

Primate species detected in the most number of sampling sites were orangutan (nine sites), Bornean gibbon (eight sites), and red leaf monkey (six sites). Three species, the long-tailed macaque, pig-tailed macaque, and western tarsier, were detected in five sites, while the slow loris was detected in four sites. Two species, the proboscis monkey and gray leaf monkey, were detected in only one site, representing the least widespread species in this study.

Factors Affecting Primate Species Richness

Descriptive comparisons of the relative primate species richness across all sampling sites (Figure 2(a)) and between habitat types (Figure 2(b)) generally indicated significantly higher species richness in old growth forest sites than in oil palm plantation (Kruskal–Wallis test between sampling sites: $\chi^2 = 26.112$, $df = 9$, $p < .01$; Kruskal–Wallis test between habitat types: $\chi^2 = 23.798$, $df = 3$, $p < .001$). However, the response within the logged forest sites showed some variations, with some sites, in repeatedly logged forest, indicating comparable primate species richness to those of the old growth forest sites.

The monthly detected number of primate species, while statistically controlling for differences in survey

trail length (random variable), survey frequency, and understory density, appeared to be influenced by habitat type with a negative effect suggesting generally that more primate species were found in old growth forest (as reference) compared with in disturbed habitats and oil palm plantation (negative coefficient values range: -1.135 to -2.093 , Table 2). However, there were significant differences only between old growth forest versus twice logged forest and between old growth forest versus oil palm plantation (Table 2). The difference between old growth forest and repeatedly logged forest was not significant (Table 2). The top-ranked model, evaluated using the AICc criterion, in the initial GLMM analysis predicting the monthly number of primate species detected included habitat type (Table 3). Although another model was also selected ($\Delta AICc = 1.99$), this model also included habitat type in addition to survey frequency (Table 3).

The second GLMM analysis conducted to predict the effects of specific habitat characteristics (i.e., tree density, tree dbh, and tree diversity) on the monthly number of primate species detected in the forest sampling sites, while controlling statistically for differences in survey trail length (random variable), survey frequency, and understory density, indicated that only tree density was a significant factor with a positive effect (Table 4). The top-ranked model, evaluated using the AICc criterion, in the second GLMM analysis included tree density (Table 5). Although four other models were also selected based on $\Delta AICc < 2$, all these models included tree density with large positive coefficient values (range: 14.68 – 20.17) compared with other variables (tree diversity: -0.118 to -0.172 ; tree dbh: 0.275 – 0.387 ; and survey frequency: -0.029 ; Table 5). Hence, our results suggest that with increasing tree density, the number of detected primate

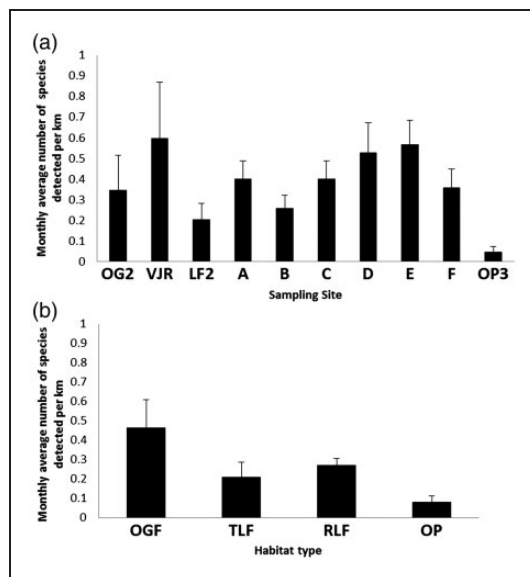


Figure 2. Relative primate species richness calculated as monthly average number of primate species detected weighted by trail length (\pm SD) at all 10 sampling sites (a) and grouped according to habitat type (b).

Table 2. Generalized Linear Mixed-Effects Model (GLMM, $n = 98$) for the Effect of Habitat Type.

	Estimate	SE	Z	p
(Intercept)	0.081	0.811	0.038	0.970
Forest type				
Old growth forest	reference			
Twice logged forest	-2.093	0.781	-2.680	0.007**
Repeatedly logged forest	-1.135	0.877	-1.294	0.195
Oil palm plantation	-2.092	0.780	-2.681	0.007**
Survey frequency	0.114	0.145	0.788	0.431
Understory density	-0.188	0.302	-0.621	0.535

Note. Generalized linear mixed-effects model (GLMM, $n = 98$) for the effect of habitat type (categorical variable: old growth forest, twice logged forest, repeatedly logged forest, and oil palm plantation) on the monthly number of primate species detected controlling for differences in survey frequency and understory density (logit transformed) at each sampling site as covariates and differences in trail length as a random variable.

** $p < .01$.

Table 3. Summary of Model Selection by Generalized Linear Mixed-Effects Model (GLMM) used to Model the Effect of Habitat Type.

Intercept	Habitat type	Understory density	Survey frequency	df	Log-likelihood	AICc	Δ AICc	AICcwt
0.606	+			5	-116.491	243.6	0.00	0.450
0.239	+		0.061	6	-116.349	245.6	1.99	0.200

Note. Summary of model selection by generalized linear mixed-effects model (GLMM) used to model the effect of habitat type on monthly number of primate species detected with survey frequency and understory density as covariates and trail length as a random variable (only models with Δ AICc score of ≤ 2 are shown).

Table 4. Generalized Linear Mixed-Effects Model (GLMM, n = 89) for the Effects of Forest Characteristics.

	Estimate	SE	Z	p
(Intercept)	-0.861	1.240	-0.694	0.488
Tree diversity	-0.184	0.136	-1.349	0.177
Tree density	21.554	8.091	2.664	0.008**
Tree dbh	0.530	0.445	1.190	0.234
Survey frequency	0.011	0.062	0.179	0.858
Understory density	-0.157	0.265	-0.593	0.553

Note. Generalized linear mixed-effects model (GLMM, n = 89) for the effects of forest characteristics (i.e., tree diversity, tree density, and tree dbh) on the monthly number of primate species detected controlling for differences in survey frequency and understory density as covariates and trail length as a random variable.

**p < .01.

Table 5. Summary of Model Selection by Generalized Linear Mixed-Effects Model (GLMM) Used to Model the Effect of Forest Characteristics.

Intercept	Tree div	Tree den	Tree dbh	Undstr den	Surveyfreq	df	Log-likelihood	AICc	Δ AICc	AICcwt
-0.305		15.20				3	-113.349	233.0	0.00	0.184
-0.026	-0.118	18.51				4	-112.887	234.2	1.27	0.097
-0.766		15.50	0.275			4	-112.934	234.3	1.36	0.093
0.002		14.68			-0.029	4	-113.153	234.8	1.80	0.075
-0.540	-0.172	20.17	0.387			5	-112.108	234.9	1.96	0.069

Note. Summary of model selection by generalized linear mixed model (GLMM) used to model the effect of forest characteristics (i.e., tree diversity, tree density, and tree dbh) on the monthly number of primate species detected while controlling for differences in survey frequency and understory density as covariates and trail length as a random variable (only models with Δ AICc score of ≤ 2 are shown).

species also increases. There was a general trend that with decreasing disturbance level of forests, the tree density increased in general, that is, old growth forests were denser than the logged forests habitat, although tree density was similarly high in one of the repeatedly logged forest sites (Figure 3).

Discussion

Using both direct and indirect methods for detecting primate species with considerable sampling effort, we confirmed the existence of 9 out of the total 10 primate

species found in Sabah, within the surveyed areas. The only primate species that was not detected in our study was the silvered leaf monkey, *Trachypithecus cristatus*, a species known to be mainly associated with coastal, riverine, and swamp forest (Payne et al., 1985). Since these forest types are not typical habitats in the inland areas of Sabah, the absence of the silvered leaf monkey in our study sites was not unexpected. Our study has also successfully added new distribution records of primates in the central part of Sabah. The number of species found at individual sampling sites (range: 2–6 species in each site) in our survey was relatively low compared with

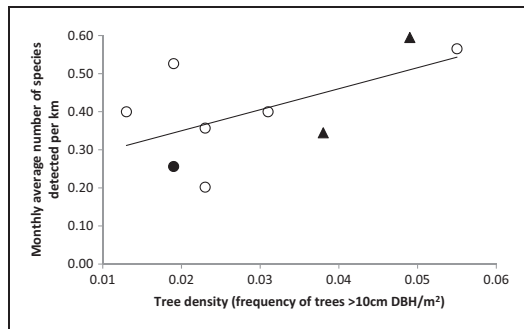


Figure 3. Relationship between tree density and mean monthly number of primate species weighted by trail length at all 10 sampling sites. Note. ▲ = old growth forest sites; ● = twice logged forest site; ○ = repeatedly logged forest sites.

that in other sites of Borneo such as Barito Ulu, Kutai, Gunung Palung, and Tanjung Puting (range: 7–8 species; Gupta & Chivers, 1999). Furthermore, the encounter rate of a primate species in each sampling site in our study was low throughout the study period. This was the case not only in the disturbed forest sites but also in less disturbed sites, in areas of old growth forest at MBCA and VJR where the tree family Dipterocarpaceae is dominant (Hazebroek, Adlin, & Sinun, 2004). This observation, however, is in agreement with the suggestion that primate biomass in forests dominated by trees from the Dipterocarpaceae family in Southeast Asia is low (Gupta & Chivers, 1999). Indeed, fruit fall, which is an important positive indicator of frugivorous primate biomass, was relatively low in the large undisturbed forest of Danum Valley in the north of the SAFE project area compared with those in other tropical regions (Hanya et al., 2011). In addition, leaf quality (protein-to-fiber ratio; Chapman & Chapman, 2002), which affects folivorous primate biomass positively, was significantly lower in this area than in riverine forests in the lower Kinabatangan region in the east of Sabah (Matsuda, Tuuga, Bernard, Sugau, & Hanya, 2013). Confirmation of fruit availability and leaf nutritional quality, as well as their overall abundance, would be necessary to further test hypotheses regarding the detailed primate community in our study sites. In fact, differences in dietary nutritional quality, even within similar habitat types, have been found to affect density of primates elsewhere (e.g., Vogel et al., 2015) and may also influence primate species richness.

The most widespread species detected in our study were the orangutan and Bornean gibbon, partly because both species are also detectable through indirect means, such as nests (orangutan) or vocalizations (Bornean gibbon). Orangutan nests were encountered in all of the repeatedly logged forest sites in our study, although occasionally adult males and adult females, along with their

dependent infants, were also observed at some of these sites. An individual orangutan was even encountered in an oil palm plantation near a riparian forest. This single sighting was likely of a transient individual moving through the agricultural landscape, as observed elsewhere for this species, for example, in the lower Kinabatangan Wildlife Sanctuary in proximity to oil palm plantations (Ancrenaz et al., 2015). Adult male orangutan, in particular, being the dispersing sex, have been demonstrated by genetic study to travel widely (Arora et al., 2012; Goossens et al., 2006). Thus, those orangutans seen in heavily degraded or converted habitats are likely to be dispersing animals en route to more diverse natural forests (Ancrenaz et al., 2015). However, orangutans have been documented to exhibit great dietary flexibility even in degraded habitat (Campbell-Smith, Campbell-Smith, Singleton, & Linkie, 2011). While primarily frugivorous, orangutans change their diet seasonally depending on the availability of food sources (e.g., leaves, flowers, cambium, and insects; MacKinnon, 1971; Morrogh-Bernard et al., 2008; Singleton & van Schaik, 2001; Wartmann, Purves, & van Schaik, 2010). There are also an increasing number of studies supporting the resilience of this species to habitat disturbance particularly in extensively logged but not clear felled forests (e.g., the lower Kinabatangan Wildlife Sanctuary) and even ongoing selectively logged forests (e.g., Deramakot Forest Reserve) on Borneo, most notably in Sabah (Ancrenaz et al., 2010; Ancrenaz et al., 2015; Campbell-Smith et al., 2011; Johns, 1985; Meijaard et al., 2010; Payne & Davies, 1987; Russon, Kuncoro, & Ferisa, 2015; Samejima, Ong, Lagan, & Kitayama, 2012).

In contrast, the Bornean gibbon occupies exclusive and well-defined home ranges and is usually reluctant to move outside of their territories (Hazebroek, Adlin, & Sinun, 2012; Wilson & Johns, 1982), which may mean that the species is negatively affected directly by the logging process. Thus, the resilience of Bornean gibbon to habitat disturbance in the present study was unexpected. A study on the Lar gibbon (*Hylobates lar*) in Peninsular Malaysia found that this species adapted to the changed conditions of their habitat, following selective logging, by changing their behavior to reduce their energetic costs, by reducing the time spending traveling, and altering their diet, by preferentially feeding on less nutritious but more ubiquitous leaf material (Johns, 1982). The Bornean gibbon may also be able to adopt this strategy to survive in disturbed habitats such as in our study sites, although the shift towards folivory may lower their reproductive potential. Studies of gibbons (*Hylobates* spp.) elsewhere in Sumatra and Kalimantan generally showed that logging has negatively affected the abundance of these primates principally because of a decrease in food availability (Cheyne et al., 2016; Johns, 1985; Johns, 1988; Lee, Powell, & Lindsell, 2014; O'Brien, Kinnaird,

Nurcahyo, Iqbal, & Rusmanto, 2004). Further studies are needed to test our hypothesis regarding the persistence of Bornean gibbon in our study.

The present study showed that the primate community in and around the SAFE Project area was generally negatively affected by habitat disturbance and conversion. We found that tree density was the most important factor in predicting the richness of primate community. As tree density is an equally important factor to predict the primate community biomass in southern Asia in general (Gupta & Chivers, 1999), this may be a key indicator for evaluating primate communities. In addition, we have to note that oil palm plantation habitat evidently had the most detrimental effect on the primate community as a whole. Therefore, further logging and expansion of areas planted with oil palm is clearly expected to have adverse effects on the primate community.

Higher tree density has been hypothesized to be associated with higher food availability, leading to a more diverse primate community in habitats with higher tree density (Gupta & Chivers, 1999). However, as described above, food availability (quality and abundance) in the higher tree density forests in our study sites, dominated by the trees of the Dipterocarpaceae family, is likely to be lower than in the lower tree density sites. We do not, therefore, propose this explanation for our study sites. Another hypothesis is that forests with higher tree density may facilitate efficient arboreal locomotion, possibly giving primates easy access to food sources with relatively low energetic costs (Bernard, Matsuda, Hanya, & Ahmad, 2011). Arboreal living is also part of an anti-predation strategy, that is, predation pressure on arboreal primates is reported to be lower than that on terrestrial primates (Cheney & Wrangham, 1987), and there would be more choices for better sleeping sites and sites for building nests (for orangutans) in forests with higher tree density (Ancrenaz, Goossens, Gimenez, Sawang, & Lackman-Ancrenaz, 2004; Prasetyo et al., 2008).

Implications for Conservation

Clearly more studies are required in the future to clarify the processes and factors influencing primate species presence and persistence not just in primary forests but also in a complex mosaic of variously degraded habitats such as those in the present study. Assessing fruit availability and leaf nutritional quality, as well as their overall abundance, and studying the roles of the surrounding forest habitats and relevance of certain aspects of habitat characteristics, such as tree density, will also be important in elucidating species distributions and persistence, and monitoring of species in heavily disturbed forests. It is interesting to note that the heavily degraded forest sites, that have been repeatedly logged, in our study collectively recorded the highest primate species number (eight species),

although with a higher sampling effort. The species recorded here included endemic species and species that are of high conservation concern such as the orangutan and Bornean gibbon. Furthermore, in terms of feeding habit, they included the folivorous, frugivorous, and insectivorous species that vary in body size from the biggest >50 kg (orangutan) to the smallest 80 g (western tarsier; Payne et al., 1985). Thus, it seems that almost the full spectrum of life history characters present in the regional primate species pool are retained in these heavily degraded forests.

Large continuous areas of undisturbed forests are undoubtedly irreplaceable and important for sustaining tropical biodiversity (Gibson et al., 2011), including the primate community, and wherever such forest still exist, they should be given priorities to be conserved. However, given the predicted effects of land-use and climate change (Struebig et al., 2015), and the fact that logged and disturbed forests are now covering a much larger area than the so-called primary forest, we contend that the role of disturbed habitat for primate conservation should not be ignored.

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References

- Ancrenaz, M., Ambu, L., Sunjoto, I., Ahmad, E., Manokaran, K., Meijaard, E., . . . Lackman, I. (2010). Recent surveys in the forests of Ulu Segama Malua, Sabah, Malaysia, show that

- orang-utans (*P. p. morio*) can be maintained in slightly logged forests. *PLoS ONE*, 5(7), e11510. doi:10.1371/journal.pone.0011510.
- Ancrenaz, M., Calaque, R., & Lackman-Ancrenaz, I. (2004). Orangutan nesting behavior in disturbed forest of Sabah, Malaysia: Implications for nest census. *International Journal of Primatology*, 25, 983–1000.
- 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 orang-utans in lower Kinabatangan, Sabah, Malaysia. *Animal Conservation*, 7, 375–385.
- Ancrenaz, M., Oram, F., Ambu, L., Lackman, I., Ahmad, E., Elahan, H., . . . Meijaard, E. (2015). Of Pongo, palms and perceptions: A multidisciplinary assessment of Bornean orang-utans *Pongo pygmaeus* in an oil palm context. *Oryx*, 49, 465–472.
- Arora, N., Van Noordwijk, M. A., Ackermann, C., Willems, E. P., Nater, A., Greminger, M., . . . Krutzen, M. (2012). Parentage-based pedigree reconstruction reveals female matrilineal clusters and male-biased dispersal in nongregarious Asian great apes, the Bornean orang-utans (*Pongo pygmaeus*). *Molecular Ecology*, 21(13), 3352–3362.
- Bates, D., Maechler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, 67, 1–48.
- Bartoń, K. (2012). *MuMIn: Multi-model Inference*.
- Bernard, H., Matsuda, I., Hanya, G., & Ahmad, A. H. (2011). Characteristics of night sleeping trees of proboscis monkeys (*Nasalis larvatus*) in Sabah, Malaysia. *International Journal of Primatology*, 32, 259–267.
- Berry, N., Phillips, O., Lewis, S., Hill, J., Edwards, D., Tawatao, N., . . . Hamer, K. (2010). The high value of logged tropical forests: Lessons from northern Borneo. *Biodiversity and Conservation*, 19, 985–997.
- Burnham, K. P., & Anderson, D. R. (2002). *Model selection and multimodel inference: A practical information-theoretic approach* (2nd ed.). Verlag, Germany: Springer.
- Campbell-Smith, G., Campbell-Smith, M., Singleton, I., & Linkie, M. (2011). Raiders of the lost bark: Orangutan foraging strategies in a degraded landscape. *PLoS ONE*, 6(6), e20962. doi:10.1371/journal.pone.0020962.
- Chapman, C. A., & Chapman, L. J. (2002). Foraging challenges of red colobus monkeys: Influence of nutrients and secondary compounds. *Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology*, 133, 861–875.
- Cheney, D. L., & Wrangham, R. W. (1987). Predation. In B. B. Smuts, D. L. Cheney, R. M. Seyfarth, R. W. Wrangham, & T. T. Struhsaker (Eds.). *Primate societies* (pp. 227–239). Chicago, IL: University of Chicago Press.
- Cheyne, S. M., Gilhooly, L. J., Hamard, M. C., Höing, A., Houlihan, P. R., Kursani, . . . Zrust, M. (2016). Population mapping of gibbons in Kalimantan, Indonesia: Correlates of gibbon density and vegetation across the species' range. *Endangered Species Research*, 30, 133–143.
- Cheyne, S. M., Thompson, C. J. H., & Chivers, D. J. (2013). Travel adaptations of Bornean Agile Gibbons *Hylobates albibarbis* (Primates: Hylobatidae) in a degraded secondary forest, Indonesia. *Journal of Threatened Taxa*, 5, 3963–3968.
- Corlett, R. T. (2009). *The ecology of Tropical East Asia*. New York, NY: Oxford University Press.
- Eeley, H., & Lawes, M. J. (1999). Large-scale patterns of species richness and species range size in anthropoid primates. In J. G. Fleagle, C. H. Janson, & K. Reed (Eds.). *Primate communities* (pp. 191–219). Cambridge, England: Cambridge University Press.
- Eisenberg, J. F., & Lockhart, M. (1972). *An ecological reconnaissance of Wilpattu National Park, Ceylon*. Washington, DC: Smithsonian Institution Press.
- Ewers, R. M., Didham, R. K., Fahrig, L., Ferraz, G., Hector, A., Holt, R. D., . . . Turner, E. C. (2011). A large-scale forest fragmentation experiment: The stability of altered forest ecosystems project. *Philosophical Transactions of the Royal Society of London B*, 366, 3292–3302.
- Fleagle, J. G., Janson, C., & Reed, K. E. (1999). *Primates communities*. Cambridge, England: Cambridge University Press.
- Gibson, L., Lee, T. M., Koh, L. P., Brook, B. W., Gardner, T. A., Barlow, J., . . . Sodhi, N. S. (2011). Primary forests are irreplaceable for sustaining tropical biodiversity. *Nature*, 478, 378–383.
- Goossens, B., Setchell, J. M., James, S. S., Funk, S. M., Chikhi, L., Abulani, A., . . . Bruford, M. W. (2006). Philopatry and reproductive success in Bornean orang-utans (*Pongo pygmaeus*). *Molecular Ecology*, 15, 2577–2588.
- Gupta, A. K., & Chivers, D. J. (1999). Biomass and use of resources in south and south-east Asian primate communities. In J. G. Fleagle, C. H. Janson, & K. Reed (Eds.). *Primate communities* (pp. 38–54). Cambridge, England: Cambridge University Press.
- Hamard, M., Cheyne, S. M., & Nijman, V. (2010). Vegetation correlates of gibbon density in the peat-swamp forest of the Sabangau catchment, Central Kalimantan, Indonesia. *American Journal of Primatology*, 72, 607–616.
- Hanya, G., & Aiba, S. I. (2010). Fruit fall in tropical and temperate forests: Implications for frugivore diversity. *Ecological Research*, 25, 1081–1090.
- Hanya, G., Stevenson, P., van Noordwijk, M., Wong, S. T., Kanamori, T., Kuze, N., . . . van Schaik, C. (2011). Seasonality in fruit availability affects frugivorous primate biomass and species richness. *Ecography*, 34, 1009–1017.
- Hazebroek, H. P., Adlin, T. Z., & Sinun, W. (2004). *Maliau Basin Sabah's Lost World*. Kota Kinabalu, Malaysia: Natural History Publication (Borneo).
- Hazebroek, H. P., Adlin, T. Z., & Sinun, W. (2012). *Danum Valley the rain forest*. Kota Kinabalu, Malaysia: Natural History Publication (Borneo).
- Hillebrand, H. (2004). On the generality of the latitudinal diversity gradient. *American Naturalist*, 163, 192–211.
- Inoue, Y., Sinun, W., & Okanoya, K. (2016). Activity budget, travel distance, sleeping time, height of activity and travel order of wild East Bornean Grey gibbons (*Hylobates funereus*) in Danum Valley Conservation Area. *Raffles Bulletin of Zoology*, 64, 127–138.
- IUCN. (2015). IUCN red list of threatened species. Version 2015.2. Retrieved from <http://www.iucnredlist.org>.
- Johns, A. D. (1982). *Ecological effects of selective logging in a West Malaysian Rain-Forest* (PhD thesis). University of Cambridge, Cambridge, England.
- Johns, A. D. (1985). Selective logging and wildlife conservation in tropical rain-forest: Problems and recommendations. *Biological Conservation*, 31, 355–375.

- Johns, A. D. (1988). Effects of 'selective' timber extraction on rain forest structure and composition and some consequences for frugivores and folivores. *Biotropica*, *20*, 31–37.
- Kay, R. F., Madden, R. H., VanSchaik, C., & Higdon, D. (1997). Primate species richness is determined by plant productivity: Implications for conservation. *Proceedings of the National Academy of Sciences of the United State of America*, *94*, 13023–13027.
- Konopik, O., Steffan-Dewenter, I., & Grafe, T. U. (2015). Effects of logging and oil palm expansion on stream frog communities on Borneo, Southeast Asia. *Biotropica*, *47*, 636–643.
- Lee, D. C., Powell, V. J., & Lindsell, J. A. (2014). The conservation value of degraded forests for Agile Gibbons *Hylobates agilis*. *American Journal of Primatology*, *77*, 76–85.
- Leighton, D. (1987). Gibbons: Territoriality and monogamy. In B. Smuts, D. Cheney, R. Seyfarth, R. Wrangham, & T. Struhsaker (Eds.). *Primate societies* (pp. 135–145). Chicago, IL: University of Chicago Press.
- MacKinnon, J. (1971). The orang-utan in Sabah today. *Oryx*, *11*, 141–191.
- Matsuda, I., Tuuga, A., Bernard, H., Sugau, J., & Hanya, G. (2013). Leaf selection by two Bornean colobine monkeys in relation to plant chemistry and abundance. *Scientific Reports*, *3*, 1873.
- Meijaard, E., Albar, G., Nardiyono, Rayadin, Y., Ancrenaz, M., & Spehar, S. (2010). Unexpected ecological resilience in Bornean orangutans and implications for pulp and paper plantation management. *PLoS ONE*, *5*(9), e12813. doi:10.1371/journal.pone.0012813.
- Meijaard, E., & Nijman, V. (2003). Primate hotspots on Borneo: Predictive value for general biodiversity and the effects of taxonomy. *Conservation Biology*, *17*, 725–732.
- Morrogh-Bernard, H. C., Husson, S. J., Knott, C. D., Wich, S. A., van Schaik, C. P., van Noordwijk, M. A., ... Sakong, R. B. (2008). Orangutan activity budgets and diet. In S. A. Wich, S. S. Utami, M. Setia, & C. P. van Schaik (Eds.). *Orangutans: Geographic variation in behavioral ecology and conservation* (pp. 119–134). Oxford, England: Oxford University Press.
- O'Brien, T. G., Kinnaird, M. E., Nurcahyo, A., Iqbal, M., & Rusmanto, M. (2004). Abundance and distribution of sympatric gibbons in a threatened Sumatran rain forest. *International Journal of Primatology*, *25*, 267–284.
- Payne, J., & Davies, G. (1987). *A faunal survey of Sabah (No. 1692)*. Kuala Lumpur, Malaysia: IUCN/WWF Malaysia.
- Payne, J., Francis, C. M., & Phillips, K. (1985). *A field guide to the mammals of Borneo*. Kota Kinabalu, Malaysia: The Sabah Society & World Wildlife Fund Malaysia.
- Pielou, E. C. (1966). Shannon's formula as a measure of specific diversity: Its use and misuses. *American Naturalist*, *104*, 463–465.
- Prasetyo, D., Ancrenaz, M., Morrogh-Bernard, H. C., Utami Atmoko, S. S., Wich, S. A., & van Schaik, C. P. (2008). Nest building in orangutans. In S. A. Wich, S. S. Utami, M. Setia, & C. P. van Schaik (Eds.). *Orangutans: Geographic variation in behavioral ecology and conservation* (pp. 269–278). Oxford, England: Oxford University Press.
- R Development Core Team. (2015). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.
- Reynolds, G., Payne, J., Sinun, W., Mosigil, G., & Walsh, R. P. (2011). Changes in forest land use and management in Sabah, Malaysian Borneo, 1990–2010, with a focus on the Danum Valley region. *Philosophical Transactions of the Royal Society of London B*, *366*, 3168–3176.
- Russon, A. E., Kuncoro, P., & Ferisa, A. (2015). Orangutan behavior in Kutai National Park after drought and fire damage: Adjustments to short- and long-term natural forest regeneration. *American Journal of Primatology*, *77*, 1276–1289.
- Samejima, H., Ong, R., Lagan, P., & Kitayama, K. (2012). Camera-trapping rates of mammals and birds in a Bornean tropical rainforest under sustainable forest management. *Forest Ecology and Management*, *270*, 248–256.
- Singleton, I., & van Schaik, C. P. (2001). Orangutan home range size and its determinants in a Sumatran swamp forest. *International Journal of Primatology*, *22*(6), 877–911.
- Sodhi, N. S., Koh, L. P., Brook, B. W., & Ng, P. K. (2004). Southeast Asian biodiversity: An impending disaster. *Trends in Ecology & Evolution*, *19*, 654–660.
- Struebig, M. J., Fischer, M., Gaveau, D. L., Meijaard, E., Wich, S. A., Gonner, ... Kramer-Schadt, S. (2015). Anticipated climate and land-cover changes reveal refuge areas for Borneo's orangutans. *Global Change Biology*, *21*(8), 2891–2904.
- Struebig, M. J., Turner, A., Giles, E., Lasmana, F., Tollington, S., Bernard, H., ... Bell, D. (2013). Quantifying the biodiversity value of repeatedly logged rainforests. *Advances in Ecological Research*, *48*, 183–224.
- Takyu, M., Kubota, Y., Aiba, S., Seino, T., & Nishimura, T. (2005). Pattern of changes in species diversity, structure and dynamics of forest ecosystems along latitudinal gradients in East Asia. *Ecological Research*, *20*, 287–296.
- Tashiro, Y. (2001). *Ecological factors influencing primate abundance and feeding activity in the Kalinzu Forest, Uganda*. Kyoto, Japan: Kyoto University.
- Vogel, E. R., Harrison, M. E., Zulfa, A., Bransford, T. D., Alavi, S. E., Husson, S., ... Farida, W. R. (2015). Nutritional differences between two orangutan habitats: Implications for population density. *PLoS ONE*, *10*(10), e0138612. doi:10.1371/journal.pone.0138612.
- Wartmann, F. M., Purves, R. S., & van Schaik, C. P. (2010). Modelling ranging behaviour of female orang-utans: A case study in Tuanan, Central Kalimantan, Indonesia. *Primates*, *51*, 119–130.
- Wearn, O. R., Rowcliffe, J. M., Carbone, C., Bernard, H., & Ewers, R. M. (2013). Assessing the status of wild felids in a highly-disturbed commercial forest reserve in Borneo and the implications for camera trap survey design. *PLoS ONE*, *8*(11), e77598. doi:10.1371/journal.pone.0077598.
- Wilson, W. L., & Johns, A. D. (1982). Diversity and abundance of selected animal species in undisturbed forest, selectively logged forest and plantations in East Kalimantan, Indonesia. *Biological Conservation*, *24*, 205–218.
- Woodruff, D. S. (2010). Biogeography and conservation in Southeast Asia: How 2.7 million years of repeated environmental fluctuations affect today's patterns and the future of the remaining refugial-phase biodiversity. *Biodiversity and Conservation*, *19*, 919–941.
- Yue, S., Brodie, J. F., Zipkin, E. F., & Bernard, H. (2015). Oil palm plantation fails to support mammal diversity. *Ecological Applications*, *25*(8), 2285–2292.