

Oil palm plantations fail to support mammal diversity

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Abstract. Agricultural expansion is the largest threat to global biodiversity. In particular, the rapid spread of tree plantations is a primary driver of deforestation in hyperdiverse tropical regions. Plantations tend to support considerably lower biodiversity than native forest, but it remains unclear whether plantation traits affect their ability to sustain native wildlife populations, particularly for threatened taxa. If animal diversity varies across plantations with different characteristics, these traits could be manipulated to make plantations more “wildlife friendly.” The degree to which plantations create edge effects that degrade habitat quality in adjacent forest also remains unclear, limiting our ability to predict wildlife persistence in mixed-use landscapes. We used systematic camera trapping to investigate mammal occurrence and diversity in oil palm plantations and adjacent forest in Sabah, Malaysian Borneo. Mammals within plantations were largely constrained to locations near native forest; the occurrence of most species and overall species richness declined abruptly with decreasing forest proximity from an estimated 14 species at the forest ecotone to ~1 species 2 km into the plantation. Neither tree height nor canopy cover within plantations strongly affected mammal diversity or occurrence, suggesting that manipulating tree spacing or planting cycles might not make plantations more wildlife friendly. Plantations did not appear to generate strong edge effects; mammal richness within forest remained high and consistent up to the plantation ecotone. Our results suggest that land-sparing strategies, as opposed to efforts to make plantations more wildlife-friendly, are required for regional wildlife conservation in biodiverse tropical ecosystems.

Key words: agricultural expansion; camera trap; habitat connectivity; land sparing; oil palm plantations; species richness; tropical rainforest; wildlife-friendly farming.

INTRODUCTION

Agricultural expansion is arguably the greatest threat to global biodiversity by being the primary driver of habitat loss in tropical forests, Earth’s most biodiverse ecosystems (Tilman et al. 2001, Donald 2004, Kissinger and Herold 2012). Global demand for tropical agricultural commodities has increased dramatically in recent decades (Laurance et al. 2014). Resulting surges in crop production and expansion of agriculture into forested regions have led to wide-scale replacement of primary forests with biodiversity-deprived plantations (O’Brien and Kinnaird 2003, Fitzherbert et al. 2008).

Some of the most rapidly expanding crops are food and fiber tree plantations. Plantations generally support much less biodiversity than native forests (Barlow et al. 2007), but we have limited understanding of how plantation traits, such as canopy cover or tree height, affect their ability to sustain wildlife. This is important

because if plantation traits could be manipulated to increase habitat quality, proper management could reduce the impact of plantation expansion on wildlife (Luskin and Potts 2011).

Oil palm (*Elaeis guineensis*) is one of the most rapidly expanding commodity crops (Phalan et al. 2013). Fueled by increasing global demand for vegetable oils and biofuel, oil palm plantations have replaced large areas of primary forest and peatland in tropical Asia and Africa and now cover over 16 million hectares of tropical lowlands (Clay 2004, Koh et al. 2011, FAO 2012, Wilcove et al. 2013). Malaysia and Indonesia collectively produce over 80% of the world’s palm oil, but also hold 80% of the remaining primary rainforests in Southeast Asia, containing some of the highest levels of endemism and biodiversity in the world (Laurance 2007, FAO 2012).

Studies consistently show that oil palm plantations support lower animal diversity than native forest supports (reviewed by Fitzherbert et al. 2008 and Wilcove et al. 2013). Species richness in oil palm plantations averages less than half of that found in native forests for ants (Pfeiffer et al. 2008), frogs (Porter

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2010), bats (Danielsen and Heegaard 1995), beetles (Chung et al. 2000, Davis and Philips 2005), birds (Aratrakorn et al. 2006, Edwards et al. 2010, 2013), butterflies (Koh and Wilcove 2008), isopods (Hassall et al. 2006), moths (Chey 2006), non-volant small mammals (Bernard et al. 2009), and primates (Danielsen and Heegaard 1995).

While we know that oil palm plantations generally support less biodiversity than forests support, we have little understanding of the spatial variation of biodiversity within plantations. If diversity and species occurrence within plantations is high near forest and decreases away from the ecotone, this could provide insight about the maximum distance between forest patches that can maintain diversity within these patches. Indeed, the diversity of birds and butterflies within plantations is highest near adjacent forest (Koh 2008, Edwards et al. 2010). In contrast, ground-dwelling ant diversity does not appear to be affected by forest proximity (Bruhl and Eltz 2010).

We also need a better understanding of how plantation characteristics affect their ability to support native animals. This is critical because if plantation traits have measurable impacts on biodiversity, managers could alter factors such as tree spacing, cutting rotations, or removal of understory vegetation to reduce impacts on wildlife (Luskin and Potts 2011). For example, increasing ground vegetation cover can marginally increase bird and butterfly diversity in plantations (Koh 2008, Azhar et al. 2011).

Oil palm plantations might also affect biodiversity within adjacent forest. "Edge effects" from other land uses are known to reduce habitat quality for many forest animal taxa at relatively long distances from ecotone boundaries (O'Brien et al. 2003, Laurance 2004). Edge effects from open areas can extend up to 3 km into otherwise intact forest (Kinnaird et al. 2003), but there is a dearth of information on how proximity to oil palm plantations affects nearby forest animal diversity.

We assessed how occurrence patterns of individual mammal species and overall species richness within plantations varied in relation to forest proximity and plantation traits such as oil palm height and canopy cover. We also evaluated whether mammal richness and occurrence within native forest were affected by proximity to oil palm plantations. We focused on medium- and large-bodied mammal species amenable to detection and identification with camera traps. Mammals are of particular concern in Southeast Asia because the region contains the highest proportion of threatened mammal species of any tropical region (Sodhi et al. 2010).

METHODS

Study area

Field work was conducted in eastern Sabah, Malaysian Borneo, a region containing large oil palm plantations and substantial tracts of intact lowland

rainforest (Miettinen et al. 2012). Our intact forest sites were in the Danum Valley Conservation Area (DVCA) and the Ulu Segama Forest Reserve (USFR); our plantation sites were in two nearby oil palm estates, Danum Palm and Tingkayu Estates (Fig. 1).

The seasonality of rainfall and temperature in eastern Sabah is influenced by the Indo-Australian Monsoon System (Marsh and Greer 1992). Wet seasons occur from November to March and June to July. Two inter-monsoon periods with lower rainfall generally occur in April and August. Daily records from the Danum Valley Field Centre show a mean annual temperature of 26.9°C with a monthly range of 1.7°C, and a mean annual rainfall of 2881 mm from 1985 to 2011 (Hazebroek et al. 2012).

The Danum Valley Conservation Area consists of 438 km² of primary evergreen lowland dipterocarp rainforest, some of the last remaining in Southeast Asia (Marsh and Greer 1992). It is designated as a Class I Protected Forest Reserve by the Sabah Forestry Department, and no logging or disturbance is or has been allowed (Marsh and Greer 1992). The area supports some of the highest floral and faunal diversity in the world. The forests surrounding DVCA are part of the Ulu Segama Forest Reserve (2380 km²), a Class II Commercial Forest in which selective logging is permitted. The USFR contains lowland dipterocarp rainforest that was selectively logged (all dipterocarp trees >0.6 m diameter at breast height were harvested) from 1987 and 1991 (Fisher et al. 2011). These forests have a more open canopy and a denser understory of bamboos, gingers, and lianas, with skid trails and other signs of past logging activity.

Danum Palm Estate is northeast of the USFR and part of a large contiguous stretch of oil palm estates that dominate the landscape of northeastern Sabah. The plantation was cleared and replanted in 2000, and contains mostly mature palms ranging from 10 to 20 m in height. Tingkayu Estate is roughly 1 km west of the Madai-Baturong Reserve, a Class VI Virgin Jungle Reserve intended for research and conservation. The estate contains a mixture of young and mature palms ranging from 4 to 20 m in height and 3 to 18 years of age. A portion of the estate was cleared and replanted in 2009–2010.

Field sampling

We deployed infrared, motion-triggered, camera traps along transects in DVCA, USFR, and the two plantations from January to April 2013. Each transect had three to five camera traps. We placed camera trap points roughly 200 m apart along each transect. We chose camera locations by first going to each predetermined point, and then subjectively choosing a camera location within 10 m that we deemed would capture the most wildlife, such as along game trails and areas with the most open understory. We placed a single camera trap at each location, attached to a tree trunk

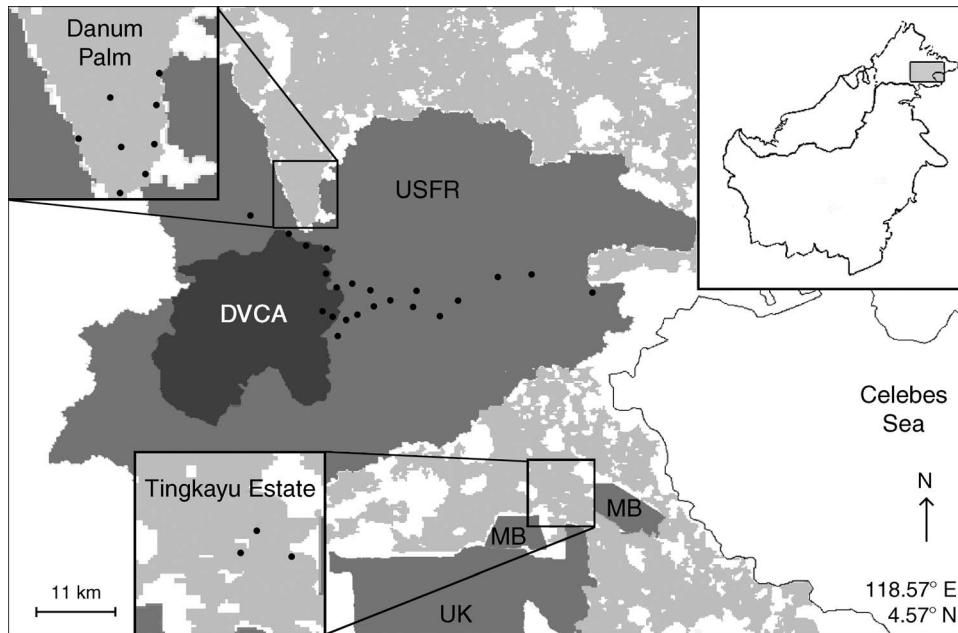


FIG. 1. Study area in eastern Sabah, Malaysia, showing the Danum Valley Conservation Area (DVCA), Ulu Segama forest reserve (USFR), Madai-Baturong (MB), and Ulu Kalumpang (UK) forest reserves, and two oil palm estates: Danum Palm and Tingkayu Estate. Dark and medium gray areas denote the boundaries of the reserves while light gray areas represent large-scale oil palm plantations. Each dot represents a line transect of two to five camera traps.

approximately 50 cm above the ground. The traps were placed facing the direction that provided the highest visibility. Each camera was set to high trigger sensitivity and programmed to record three photos when triggered. Cameras were taken down 4–5 weeks after deployment. We used Reconyx RM45, Reconyx HC500 Hyperfire, and Bushnell Trophycam camera traps (Reconyx, Holmen, Wisconsin, USA and Bushnell, Overland Park, Kansas, USA); trap model was incorporated as a covariate in the analysis to account for differences in detectability. We had 53 functional camera traps in native forest, yielding a total of 1574 trap-nights, and 38 camera traps in oil palm plantation, yielding 1191 trap-nights.

We measured several environmental covariates at each site. We calculated the approximate height of the forest canopy using a clinometer, and measured canopy cover by taking hemispherical photographs using a Nikon FC-E8 fisheye lens on a Nikon P5000 camera (Nikon, Melville, New York, USA) and analyzing the photographs in Gap Light Analyzer v.2 (Frazer et al. 1999). The understory of a rainforest can be very different from that of a plantation, which could affect both animal movement on the ground and their detectability with camera traps. To account for this in our analysis, we measured the visibility in front of each camera (how far the camera can see before being obstructed by undergrowth) and used this proxy for understory density as a covariate in our models.

Data analysis

We used multi-species occupancy models to estimate species occurrence probabilities and richness (Royle and Dorazio 2008). Wildlife surveys, including camera trapping, rarely capture all animals in an area. Overlooking differential detection rates among species and habitats can lead to biased comparisons. Occupancy models correct for imperfect detection by using temporally replicated data over a timeframe during which populations are assumed to be closed (MacKenzie et al. 2002). Using this approach, we can explicitly partition the data into separate state and observation processes and estimate the state variable, occupancy, which is of biological interest, separately from sampling noise. This is particularly important for our study because oil palm habitat has a more open understory, offering a much higher visibility and thus detectability of wildlife compared to rainforest.

A single-species occupancy model assumes that species occurrence z_{ij} is a Bernoulli process with occupancy probability ψ_{ij} for species i at site j

$$z_{ij} \sim \text{Bern}(\psi_{ij})$$

where $z_{ij} = 1$ when species i is present at site j and 0 when absent. It is not possible to observe the true occupancy state because camera traps do not detect species perfectly. Instead, we observe the trap data y_{ijk} , for species i at site j in the sampling period k . Species observation is conditional on both the true occurrence

(z_{ij}) and the detection probability, p_{ijk} , of species i at site j in the sampling period k . Thus, we can similarly specify the observation data according to a Bernoulli process

$$y_{ijk} \sim \text{Bern}(z_{ij} \times p_{ijk})$$

where $y_{ijk} = 1$ when the species has been detected and 0 when it is either present but not detected or absent. We modeled covariates into our estimates of occurrence and detection probabilities using logit link functions

$$\text{logit}(\psi_{ij}) = \alpha 0_i + \alpha_i \times \text{occupancy_covariate}_j$$

$$\text{logit}(p_{ij}) = \beta 0_i + \beta_i \times \text{detection_covariate}_j$$

where α_i and β_i are species-specific intercepts and α_i and β_i are vectors of species-specific parameter effects of occupancy and detection covariates, respectively.

To assess the influence of oil palm characteristics on mammal occurrence within plantations, we included forest proximity, tree height, canopy cover, and interactions between these factors as site covariates in our model of species occurrence probability:

$$\begin{aligned} \text{logit}(\psi_{ij}) = & \alpha 0_i + \alpha 1_j \times \text{forest_proximity}_j \\ & + \alpha 2_j \times \text{tree_height}_j + \alpha 3_j \times \text{canopy_cover}_j \\ & + \alpha 4_j \times \text{forest_proximity}_j \times \text{tree_height}_j \\ & + \alpha 5_j \times \text{forest_proximity}_j \times \text{canopy_cover}_j. \end{aligned}$$

Canopy cover and tree height were only weakly related ($R^2 = 0.22$), suggesting that both could be included in the same model without risk of significant collinearity.

To test the edge effects of oil palm on forest-dwelling species, we ran the following model on data collected within forest, and included oil palm proximity as a covariate. There was not enough variance in canopy cover and height for forest sites to be included in the model

$$\text{logit}(\psi_{ij}) = \alpha 0_i + \alpha 1_j \times \text{oil_palm_proximity}_j.$$

We similarly modeled the detection probability for species using the following covariates: camera trap model, visibility in front of the camera, number of days since deployment (animals may be less willing to approach a site immediately after a trap is deployed), and the number of hours each trap was active per day (to account for the shortened days when deploying and retrieving traps; the rest of the days had 24 hours of sampling). To account for spatial correlation among sites, camera traps within 3 km of each other were considered a single group, and “group” was incorporated as a random effect into estimates of detection. The 3-km threshold is arbitrary, but likely represents an approximate upper limit on the daily movements of most of the detected mammal species (Hazebroek et al. 2012). All continuous variables, in both occupancy and detection components of the model, were standardized to have a mean of 0 and variance of 1.

To estimate mammal species richness, we pooled the single-species occupancy models by drawing species-specific α and β parameters from community-level distributions (Royle and Dorazio 2008, Brodie et al. 2014). Each of the species-specific parameters was drawn from normally distributed, community-level “hyperparameters” (i.e., a mean and variance for each covariate effect across all mammal species in the community). To account for species that were present but never detected, we augmented the dataset with 20 “pseudospecies” with all-zero detection histories. Data augmentation is a mechanistic-based approach for estimating species richness by accounting for variability in detection and the influence of habitat covariates on the occurrence probabilities of unobserved mammal species (Royle and Dorazio 2008). We analyzed overall species richness as well as the richness of threatened species, those classified as vulnerable to critically endangered by the International Union for Conservation of Nature (IUCN) Red List. Studies have suggested that disturbance to tropical forests could have little impact on total species richness because common, generalist species persist in disturbed habitats (e.g., Dent and Wright 2009). Thus it is important to assess whether richness of threatened taxa differs between habitats.

We ran our models with WinBUGS through the R package R2WinBUGS (Sturtz et al. 2005). We used vague priors and ran three chains for 70 000 iterations after a burn-in of 30 000.

RESULTS

We had 688 detections (each detection being 1 h apart) of 19 species in forest and 889 detections of 17 species in plantations. Species only observed in forest were sambar, moonrat, elephant, long-tailed porcupine, banded linsang, and masked palm civet (Latin names shown in Table 1); species observed only in plantations were leopard cat, pangolin, thick-spined porcupine, and Malay badger, though all of these have also been observed in native forest either by us or the DVCA staff. This discrepancy exists because we only sampled for 4 months, which is by no means an exhaustive survey of the rainforest fauna. Sambar, moonrat, chevrotain, long-tailed porcupine, pig-tailed macaque, and muntjac had significantly higher occurrence probabilities in forest, whereas the common palm civet and leopard cat had significantly higher occurrence in oil palm (Table 1).

Within oil palm, distance from intact forest had a strong negative relationship with species in the overall community (the strength of correlation, $\beta = -3.16$; 95% CI $-5.27, -1.85$) as well as the community of threatened species ($\beta = -4.10$, 95% CI $-8.25, -1.46$; Fig. 2). We estimated large decreases in mean richness for all species (from 14.0 to 0.3) and threatened species (from 6.1 to 0.2) as distance from intact forest increased from 0 to 3 km (Fig. 3). Palm height also had a negative, although

TABLE 1. Species detected in our study sites in Malaysia (Danum Valley and the Ulu Segama Reserve, Tingkayu Estate, and Danum Palm) and their habitat preferences.

Common name	Scientific name	IUCN status	Detections per 100 trap nights		Occupancy		
			In forest	In oil palm	In forest	In oil palm	β habitat
Asian elephant	<i>Elephas maximus</i>	E	0.83	0	0.20 (0, 0.51)	†	-3.40 (-11.40, 4.56)
Banded civet	<i>Hemigalus derbyanus</i>	V	1.08	0.59	1.00 (0.87, 1.00)	0.16 (0, 0.37)	-1.70 (-4.70, 0.22)
Banded linsang	<i>Prionodon linsang</i>	LC	0.06	0	†	†	-3.49 (-11.34, 3.62)
Bearded pig	<i>Sus barbatus</i>	V	10.80	40.73	1.00 (0.99, 1.00)	0.84 (0.58, 1.00)	-0.40 (-1.56, 0.77)
Bornean orangutan	<i>Pongo pygmaeus</i>	E	0.19	0.08	0.99 (0.60, 1.00)	†	-1.10 (-7.58, 5.82)
Common palm civet	<i>Paradoxurus hermaphroditus</i>	LC	0.19	3.19	1.00 (0.75, 1.00)	1.00 (0.99, 1.00)	4.24 (1.69, 9.08)
Leopard cat	<i>Prionailurus bengalensis</i>	LC	0	3.61	†	0.85 (0.48, 1.00)	4.59 (2.07, 8.36)
Lesser and greater oriental chevrotain	<i>Tragulus kanchil</i> and <i>T. napu</i>	LC	8.58	0.59	1.00 (1.00, 1.00)	0.05 (0, 0.15)	-4.68 (-7.31, -2.81)
Long-tailed macaque	<i>Macaca fascicularis</i>	LC	0.06	1.60	1.00 (0.77, 1.00)	0.34 (0, 0.68)	1.08 (-1.72, 3.90)
Long-tailed porcupine	<i>Trichys fasciculata</i>	LC	0.76	0	0.12 (0, 0.23)	0.15 (0, 0.63)	-4.58 (-11.88, -0.39)
Malay badger	<i>Mydaus javanensis</i>	LC	0	0.34	†	1.00 (0.74, 1.00)	2.44 (-2.54, 9.15)
Malay civet	<i>Viverra zibetha</i>	LC	1.65	8.23	1.00 (0.98, 1.00)	0.94 (0.58, 1.00)	1.63 (-0.34, 5.24)
Malayan porcupine	<i>Hystrix brachyura</i>	LC	0.06	0.42	†	0.08 (0, 0.20)	0.04 (-4.50, 3.94)
Masked palm civet	<i>Paguma larvata</i>	LC	0.06	0	†	†	-3.38 (-11.36, 3.99)
Mongoose spp. (short-tailed and collared)	<i>Herpestes brachyurus</i> and <i>H. semitorquatus</i>	LC and DD	0.64	0.34	0.22 (0, 0.47)	0.23 (0, 0.63)	-1.11 (-4.96, 1.15)
Moonrat	<i>Echinosorex gymmura</i>	LC	0.95	0	0.17 (0.03, 0.30)	†	-4.68 (-11.7, -0.63)
Muntjac spp. (red and Bornean yellow)	<i>Muntiacus muntjak</i> and <i>M. atherodes</i>	LC	9.72	0.76	1.00 (0.98, 1.00)	0.23 (0, 0.50)	-2.80 (-4.52, -1.46)
Sambar	<i>Rusa unicorn</i>	V	2.67	0	1.00 (0.99, 1.00)	†	-6.99 (-13.81, -3.18)
Southern pig-tailed macaque	<i>Macaca nemestrina</i>	V	5.15	11.84	1.00 (0.99, 1.00)	0.29 (0.08, 0.51)	-3.83 (-8.50, -1.46)
Sun bear	<i>Helarctos malayanus</i>	V	0.13	0.08	0.08 (0, 0.19)	†	-0.51 (-6.62, 6.56)
Sunda pangolin	<i>Manis javanica</i>	E	0	0.17	†	†	1.56 (-5.05, 9.29)
Thick-spined porcupine	<i>Thecurus crassispinis</i>	LC	0	2.02	†	0.09 (0, 0.19)	1.94 (-0.78, 5.95)
Yellow-throated marten	<i>Martes flavigula</i>	LC	0.06	0.08	†	†	-0.09 (-6.55, 7.25)

Notes: We had 1574 trap nights and 688 independent detections in forest, and 1191 trap nights and 889 detections in oil palm. IUCN status is coded as follows: LC, least concern; V, vulnerable; E, endangered; and DD, data deficient. The β coefficient measures the relationship of habitat type (a binary of 0, forest; 1, oil palm) on species occurrence. A negative β implies preference to forest, a positive β implies preference to oil palm, and the amount represents the magnitude of the relationship. Values are means, with 95% CI in parentheses.

† Species-specific occupancy estimates are extremely imprecise due to the low number of detections.

weaker, correlation with average species occurrence probabilities in the community ($\beta = -1.29$, 95% CI $-2.52, -0.18$), but not with threatened species. Canopy cover, distance \times canopy interaction, and distance \times height interaction were not significant (Fig. 2). Within oil palm plantations, distance from intact forest had a strong negative effect on all species' occurrence probabilities except for the Malay badger. Canopy cover had a negative effect on only bearded pig occurrence ($\beta = -3.35$, 95% CI $-5.83, -1.71$), while tree height had a negative effect on leopard cat ($\beta = -1.66$, 95% CI =

$-3.73, -0.28$) and Malay civet occurrence probabilities ($\beta = -1.82$, 95% CI $-4.38, -0.26$).

Within forests, oil palm proximity had no significant effect on occupancy probabilities of all species and threatened species at the community level. Oil palm proximity had a negative relationship with only bearded pig occurrence ($\beta = -0.90$, 95% CI $-2.02, -0.86$) and Malay civet occurrence ($\beta = -1.36$, 95% CI $-3.00, -0.30$).

DISCUSSION

Our results show that caution must be applied when assessing wildlife abundance or diversity in oil palm

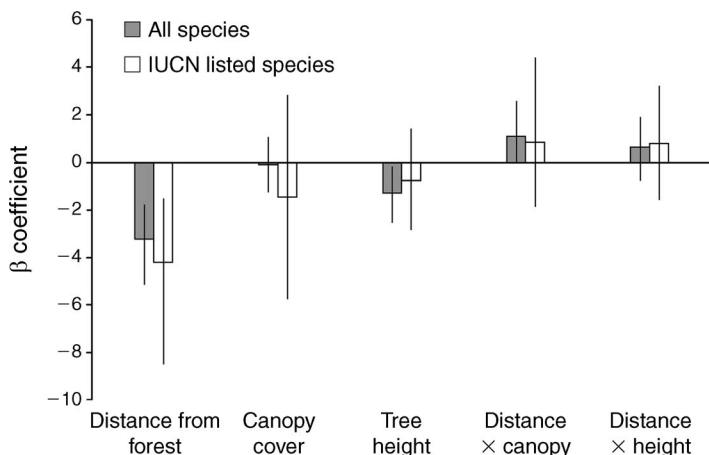


FIG. 2. Community-level effects (i.e., β coefficients) of oil palm characteristics on mammals. The β coefficient measures the average relationship of a habitat characteristic on mammal species. A negative β implies that the characteristic is negatively affecting species richness, and vice versa. Gray bars represent the effects on all species while white bars represent threatened species only. Error bars show 95% CI.

relative to forest; studies should account for where within oil palm the sampling occurred. If sampling locations within plantations are near adjacent forest, the impacts of plantations on biodiversity could be greatly underestimated. Moreover, our trap sites in oil palm were near some of the biggest and most well-protected forest reserves in Sabah, Danum Valley and the Ulu Segama and Madai Baturong reserves, all of which are known to have high mammalian diversity (Hazebroek et al. 2012). Assessments of mammal occurrence in plantations more distant from such reserves would likely be lower than what we estimated. Likewise, mammal richness could be lower in plantations that are near smaller reserves, unprotected forests, or forest fragments.

Our results show that oil palm is highly unfavorable for most species, and that animals may not permanently stay in oil palm, but only forage in and out from the forest edge. The limited mammal diversity in plantation interiors could result from few species being willing to forage far from forest. Species richness and the occurrence of individual species exhibited marked, in some cases precipitous, declines as forest proximity

decreased. These results are consistent with similar studies on other taxa, showing declines in bird and butterfly diversity with increasing distance from forest (Koh 2008, Edwards et al. 2010). This suggests that simple comparisons of species richness between oil palm and forest could underestimate true differences in diversity between these habitats if sampling within oil palm takes place near the forest edge.

We show that canopy cover and tree height had no significant influence on species richness and the occurrence of most species, suggesting that plantations cannot be made more wildlife-friendly by manipulating cutting rotation cycle (which determines tree height) or tree spacing (which partly determines canopy cover). Only the bearded pig, leopard cat, and Malay civet weakly benefited from lower canopy cover or shorter palms. This may be because fruits on younger, shorter palms are more accessible to frugivores and granivores such as bearded pigs and rodents. Rodents are in turn an attractive prey source for leopard cats and civets. The bearded pig, and the wild pig (*Sus scrofa*) in Peninsular Malaysia, can be abundant in oil palm and are

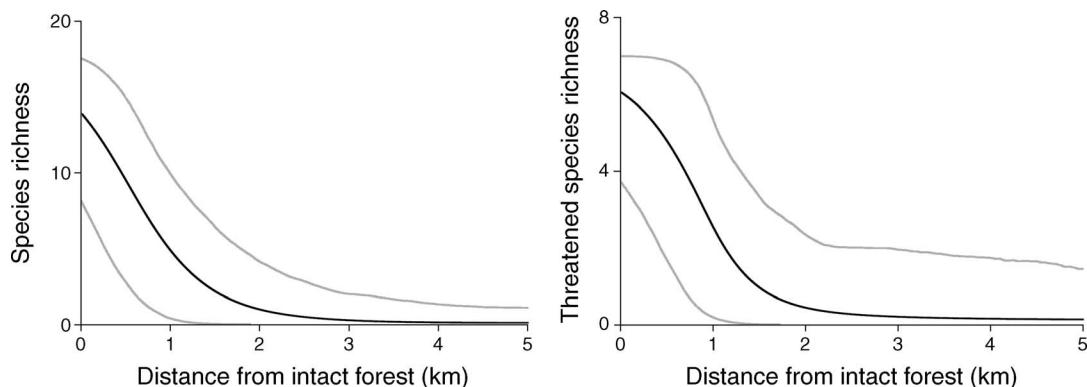


FIG. 3. Estimates of mammal richness (including unobserved species) in oil palm plantations relative to forest proximity. The black lines show the mean expected richness and gray lines show the 95% credible intervals.

sometimes considered pests because they feed on palm fruits (McShea et al. 2009).

Within forest, oil palm proximity had no significant effect on mammal richness or the occurrence of most species. Our results differ from those of a national park in Sumatra bordered by villages and croplands, where large mammals avoided forest edges for up to 3 km (Kinnaird et al. 2003); however, these edge effects became insignificant once nearby human density was taken into account (O'Brien et al. 2003). It may be that our plantation sites did not have a high enough human density to induce such strong avoidance. Further, some forest reserves in Borneo, such as Lambir Hills National Park, have experienced extensive illegal hunting and subsequently contain lower mammal abundances and diversity (Mohd-Azlan and Engkamat 2006). In contrast, our forest sites the DVCA and USFR have experienced relatively little hunting pressure, likely due to a strict entrance barrier and low accessibility. Therefore, the wildlife at our sites may be less sensitive to human activity compared to frequently hunted reserves.

Finally, the species captured in our study represent only a fraction of those known to occur in DVCA and USFR. Although our results show strong general avoidance of oil palm, we acknowledge that our survey is not exhaustive and is only a first step toward understanding the response of a diverse mammal community to oil palm expansion, especially for threatened species, for which had fewer detections. We also note that there are other management options for oil palm that may increase their habitat quality or permeability to dispersal, such as increasing the understory plant density and complexity, or increasing epiphyte abundance on palm trunks, though these do not significantly increase bird or butterfly diversity in plantations (Koh 2008).

Our study shows that very large forest patches are critical in sustaining mammal diversity, whereas little can be done within oil palm plantations to boost diversity or occurrence. We show that retaining corridors of palms with higher canopy cover or height within plantations will not promote diversity or occurrence, as suggested by some (Luskin and Potts 2011, RSPO 2013). Our findings concur with studies of other taxa (e.g., birds; Edwards et al. 2010) which conclude that little can be done to make plantations more wildlife-friendly. There is now extensive evidence suggesting that altering plantation design to enhance wildlife persistence may be ineffective, and that we should instead focus on land sparing strategies to ensure regional persistence of forest-dependent taxa.

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SUPPLEMENTAL MATERIAL

Data Availability

Data associated with this paper have been deposited in the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.363gs>