Effects of oil palm plantations on mammal communities in northeastern Borneo

by

Sam Yue

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Abstract

Agricultural expansion is considered the single largest threat to biodiversity. In Southeast Asia, the expansion of oil palm plantations is one of the leading causes of deforestation and habitat fragmentation. Studies have consistently shown that oil palm plantations support considerably lower biodiversity than native forest, yet little research has assessed how characteristics of the plantations influence diversity, or how edge effects of oil palm might impact species living in adjacent forest. I investigated whether 1) mammal diversity was different in oil palm plantations versus forest, 2) mammal diversity varied with characteristics of the plantations, such as tree height and proximity to forest, and 3) oil palm generated "edge effects" that reduced mammal diversity within nearby forest. Results were inconclusive as to whether the gamma diversity significantly differed between forest and oil palm at the $\alpha = 0.05$ level. However, diversity and occurrence declined abruptly with decreasing forest proximity, suggesting that mammals within oil palm are largely constrained to locations in close proximity to native forest. Canopy cover and tree height within plantations had minimal relationships with mammal diversity and occurrence. I suggest that the only effective way to connect mammal populations in forests fragmented by oil palm development would be to retain or create large strips of forest through plantations to act as corridors. My results also suggest that degraded forests not yet converted to agriculture still retain relatively high conservation value and should not be replaced by oil palm.

Preface

This dissertation is original, unpublished, independent work by the author Sam Yue.

Table of Contents

List of Tables

List of Figures

Acknowledgements

Chapter 1

Introduction

Agricultural expansion, driven by a skyrocketing human population and demand for food and biofuels, is the leading cause of deforestation in the tropics and the biggest threat to tropical biodiversity (Donald 2004; Norris 2008; Tilman et al. 2001). Agriculture has already altered the planet considerably, with cropland covering over 12% of Earth's ice-free land (Haberl et al. 2007). Agriculture continues to expand further with the human population projected to reach 11 billion by 2100 (United Nations 2013), and with increasing living standards and per-capita food consumption in many developing countries (Kastner et al. 2012). Moreover, even though the human population will eventually level out, stabilizing global food demand, the advent of the biofuel market may push agricultural expansion to even higher levels. As petroleum prices increase and non-renewable energy sources become depleted, the demand for biofuels may become virtually limitless (Fitzherbert et al. 2008; Laurance et al. 2014).

Agricultural expansion is most prevalent in tropical "hotspots", regions containing exceptional biodiversity and endemism (Fisher and Christopher 2007) for several reasons. First, agriculture is expected to expand the most in tropical regions because most human population growth is projected to occur there (United Nations 2013). Second, many human populations living in or near hotspots are currently impoverished but striving for higher living standards, further driving agricultural expansion (Fisher and Christopher 2007). Finally, many commodity crops with high global demand, such as cocoa, coffee, and soybean, grow best in tropical regions. These commodities provide quick ways for poor nations to earn money, by replacing biodiverse forests with agriculture.

Oil palm (*Elaeis guineensis*) is one of the fastest expanding crops in the world and conversion of natural habitat to oil palm plantations is one of the main drivers of deforestation and biodiversity loss in tropical Asia (Fitzherbert et al. 2008). Native to west Africa, oil palm now covers over 16 million hectares of tropical lowlands around the world (FAO 2012). Oil palm is especially prevalent in Southeast Asia – Malaysia and Indonesia together produce over 80% of the world's palm oil (Koh & Wilcove 2007).

Malaysia and Indonesia also contain most of the remaining primary forests in Southeast Asia, representing roughly 10% of the world's tropical forests, and hold numerous 'hotspots' of high biodiversity, endemism, and extinction risk (Myers et al. 2000; Sodhi et al. 2004). Oil palm expansion into these highly diverse habitats presents a critical conservation concern and balancing economic growth in developing countries with environmental destruction from agriculture is one of the biggest challenges of the 21st century (Laurance et al. 2014).

The rapid expansion of oil palm is due to its cheap production costs, high yields, and its many uses. The fruits of oil palm are processed to produce palm oil and palm kernel oil. Palm oil is the cheapest vegetable oil in the world and has the highest oil yield per hectare of any crop, making it the most widely used vegetable oil in processed foods (Sumathi et al. 2008). Palm kernel oil is used as an industrial lubricant and an edible oil, but it is less desirable in foods due to its high saturated fat content (Young 1983). Palm oil is also used in household products such as cosmetics, soaps, washing powders, and lotions. Although palm oil as of now is unsuitable as a biofuel, due to its high viscosity, palm oil can indirectly contribute to the biofuel industry be replacing suitable biofuel crops that would otherwise be used for vegetable oils, such as soybean and rapeseed (Carter et al. 2007). Further, there may very well be the possibility that technological advances in the future may allow production of cheap and suitable palm oil based biofuels, which would drive up the demand for oil palm considerably.

Oil palm contributes to deforestation and biodiversity loss in several ways. First, oil palm expansion can be a direct motive to replace forests, and it is easy to attribute oil palm as the 'cause' of deforestation and habitat destruction in this sense. However, there are also more indirect ways by which oil palm can lead to deforestation, making the quantification of the impacts of oil palm expansion difficult (Fitzherbert et al. 2008). For example, oil palm expansion may create road access into otherwise inaccessible forests, facilitating logging. Additionally, oil palm expansion may be used as an excuse to clear a patch of forest for timber, but in the end the area never gets developed into oil palm – this is especially widespread in Kalimantan, where corruption, lax regulations, and weak governance is prevalent (Laurance 2007; Sandker et al. 2007). Several recent initiatives are aimed at reducing oil palm's impacts on biodiversity. For example, the Roundtable on

Sustainable Palm Oil was established as a certification scheme for palm oil, and many large palm oil companies have adopted zero-net-deforestation policies, though this is not currently enforced (Butler 2014).

Oil palm plantations around the world follow roughly the same design with a structurally and ecologically simple arrangement that supporting few species. A typical oil palm plantation consists of rows of oil palm, usually of uniform age and height, grown on bare soil (Azhar et al.2013). Plantations generally have a lower canopy and more open understory than forest, and contain dense networks of unpaved roads for efficient harvest of palm fruits. The highest palms can reach around 20 m before the plantation is clearcut, usually every 25-30 years, and replanted. Studies have consistently found that oil palm supports much lower diversity for a variety of taxa, but may hold a hyperabundance of generalist species that thrive in the narrow niche of oil palm plantations (Fitzherbert et al. 2008).

The goal of my study was to compare the diversity and occurrence of medium- and large-sized mammals between forest and oil palm plantations. No study to my knowledge has investigated medium to large sized mammals collectively in oil palm. I looked at how site characteristics and spatial attributes of oil palm, such as canopy cover, tree height, and proximity to forest, influenced mammal occurrence and diversity. I also investigated the potential edge effects of oil palm on species dwelling within adjacent forest. Finally, I separated the responses of "all mammal species detected" from those species listed as vulnerable to endangered on the IUCN Red-list, because common species are sometimes generalists that can persist in altered habitats, whereas rarer species tend to do more poorly (Dent and Wright 2009). There is a critical need for better management practices in oil palm, and investigating the effects of plantation traits on wildlife can potentially provide insight into ways of making oil palm more wildlife-friendly. I used results from this study to suggest further research questions and management strategies to mitigate the adverse impacts of oil palm on biodiversity.

Chapter 2

Mammal diversity and occurrence in forest and oil palm landscapes of northeastern Borneo

2.1 Introduction

Agricultural expansion is the largest current threat to biodiversity (Tilman et al. 2001; Donald 2004), largely by virtue of being the primary driver of deforestation in the tropics (Kissinger & Herold 2012). The global demand for tropical crops such as cocoa, coffee, oil palm, and soybeans has increased dramatically in the past few decades, driven by the rapidly growing human population (Laurance et al. 2014). This has led to a surge of crop production and expansion of croplands in tropical regions (Donald 2004). These expanding croplands often replace primary forest, peatlands, and other areas of high conservation value or high carbon stock, leading to considerable biodiversity loss and environmental pollution (O'Brien and Kinnaird 2003; Fitzerbert et al. 2008).

Oil palm *Elaeis guineensis* (Koh & Wilcove 2007), one of the most rapidly expanding commodity crops in the world, has already replaced large areas of primary forest and peatland in tropical Asia and Africa (Fitzerbert et al. 2008). Fueled by increasing global demand for vegetable oils for food and biofuel (Clay 2004), oil palm now covers over 16 million ha of tropical lowlands, mostly in Southeast Asia (FAO 2012). In particular, Malaysia and Indonesia collectively produce over 80% of the world's palm oil (FAO 2012), and are covered by vast and expanding tracts of oil palm plantations. These two countries also hold 80% of the remaining primary rainforests in Southeast Asia, containing some of the highest levels of endemism and biodiversity in the world (Sodhi et al. 2004; Laurance 2007).

Studies have consistently shown that oil palm plantations support lower animal diversity than native forest. Diversity in oil palm plantations is on average less than half that found in forests for ants (Pfeiffer et al. 2008), frogs (Porter 2010), bats (Danielson and Heegaard 1995), beetles (Chung et al. 2000; Davis and Philips 2005), birds

(Aratrakorn et al. 2006; Edwards et al. 2013), butterflies (Koh and Wilcove 2008), isopods (Hassall et al. 2006), moths (Chey 2006), and primates (Danielson and Heegaard 1995). One study found more bee species in oil palm than in forest (Liow et al. 2001), but they may have under-sampled in the forest by ignoring the canopy.

Though our knowledge is increasing about biodiversity in oil palm relative to forest, we have much less understanding of how characteristics of oil palm plantations affect their ability to support native animals. This is critical because if traits of plantations did affect the biodiversity they could support, we could alter the management or design of plantations to generate more wildlife-friendly landscapes. Higher cover of ground vegetation in plantations has been shown to marginally increase diversity of butterflies (Koh 2008). Bird diversity in plantations may also marginally increase with higher ground vegetation cover (Azhar et al. 2011), lower tree canopy cover (Azhar et al. 2011), and higher epiphyte abundance (Koh 2008). Bird richness may be higher in small, independently-owned plantations that are intercropped with other tree species (e.g., banana, coffee, rambutan) than in larger plantation estates (Azhar et al. 2011), though such "small-holdings" may also be subject to increased levels of illegal hunting and other anthropogenic threats (Azhar et al. 2013). We still have little information, however, on how plantation characteristics affect diversity in taxa other than birds and butterflies.

Likewise, we lack a general understanding of how spatial factors might affect how animal diversity varies within plantations. For example, the proximity of oil palms to forest may critically determine the amount of biodiversity they contain. If diversity in oil palm is higher near forest and decreases away from the ecotone, this could provide insight on the maximum distance between forest patches that could maintain connectivity and biodiversity. The diversity of birds and butterflies within plantations is highest near adjacent forest (Koh 2008; Edwards et al. 2010), though these responses vary strongly among species (Edwards et al. 2010). In contrast, ground-dwelling ant diversity does not appear to be affected by forest proximity (Bruhl and Eltz 2010).

Having oil palm plantations adjacent to forest may also affect animal diversity within the forest itself. Indeed, "edge effects" can reduce habitat quality for many forest taxa at relatively long distances from ecotone boundaries. Edge effects alter forest microclimate, structure, and tree species composition, as well as the survival, abundance,

and species composition of animals and understory plants (Broadbent et al. 2010; Laurance et al. 2011). Numerous animal groups, including small mammals (Goosem 2000), insects (Carvalho and Vasconcelos 1999; Didham et al. 1998), birds (Laurance 2004), and medium to large mammals (O'Brien et al. 2003; Kinnaird et al. 2003) show decreased abundances near the forest edge. The negative impacts on large tropical mammals of edges bordering open habitat can extend for up to 3 km from the ecotone (Kinnaird et al. 2003). Edge effects from tree plantations could in theory be lower than those caused by proximity to open areas, though to date no studies of which I am aware have examined how proximity to oil palm plantations affects diversity within adjacent forest.

My objectives were to assess mammal occurrence and diversity in a landscape of oil palm plantations and native forest reserves. Specifically, I sought to ask:

1) Do mammal diversity and occurrence differ between plantations and forest?

2) Within plantations, are mammal diversity and occurrence related to tree height, canopy cover, or proximity to forest?

3) Within forest, are mammal diversity and occurrence related to proximity to plantations?

I used non-invasive camera trap surveys and hierarchical Bayesian modeling to measure occurrence and species richness while accounting for the fact that individual species are detected imperfectly. I focused my analysis on medium- and large-bodied, mostly terrestrial, mammal species that are amenable to detection and identification with camera traps. Mammals are of particular conservation concern in Southeast Asia because the region contains the highest proportion of threatened mammal species of any tropical region (Sodhi et al. 2010), and 20-50% of these species could face extinction over the next century (Sodhi et al. 2004). I analyze overall species richness as well as the richness of IUCN Red-listed species (those classified as vulnerable, endangered, or critically endangered). Other studies have suggested that disturbance to tropical forests could have little impact on total species richness because common, generalist species persist in disturbed habitat (e.g., Dent and Wright 2009). Thus it is important to assess whether richness of threatened taxa differs between the habitats.

2.2 Methods

2.2.1 Study area

I worked in eastern Sabah, Malaysian Borneo, a region containing large oil palm plantations and substantial tracts of intact lowland rainforest. The landscape is a mosaic of oil palm plantations, intact rainforest, regrowth forest, other croplands, and open areas, as defined by the 2010 land cover map of Southeast Asia by Miettinen et al. (2012). For the intact forest habitat I worked in the Danum Valley Conservation Area (DVCA) and the Ulu Segama Forest Reserve (USFR). For the plantation habitat I worked in two oil palm plantations, Danum Palm and Tingkayu Estate. Nearby regrowth habitat included natural regrowth and young secondary forest.

The climate of eastern Sabah is considered aseasonal but is influenced by the Indo-Australian Monsoon System (Marsh and Greer 1992). Weather is affected by two monsoons every year, with wet seasons 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 2881mm from 1985 to 2011 (Hazebroek et al. 2012). Eastern Sabah is also subject to occasional droughts caused by El Niño Southern Oscillation (ENSO) events during which rainfall, cloudiness, and wind are generally reduced. Record high temperatures and record low rainfall and humidity have been recorded during ENSO events. Extensive canopy defoliation, but little tree mortality, was observed in DVCA during the ENSO event of 1997-98 (Hazebroek et al. 2012). There was no ENSO event during this study.

The Danum Valley Conservation Area consists of 438 km^2 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 (Hazebroek et al. 2012). The area also contains all of Borneo's large terrestrial mammals including the banteng (*Bos javanicus*), Bornean elephant (*Elephas maximus borneensis*), orangutan (*Pongo pygmaeus*), sun bear (*Helarctos malayanus*), Sunda clouded leopard (*Neofelis diardi*), and Sumatran rhinoceros (*Dicerorhinus sumatrensis*;

7

Marsh and Greer 1992). The forests surrounding DVCA are part of the Ulu Segama Forest Reserve (2380 km^2), a "Class II Commercial Forest" in which selective logging is permitted. The USFR also contains lowland dipterocarp rainforest and has been selectively logged since 1987 (Fisher et al. 2011). These forests have a more open canopy and a denser mid- and understory of bamboos, gingers, and lianas (Berry et al. 2008). Past logging activity and skid trails were often observed.

Just northeast of the USFR lies Danum Palm Estate. The north side of Danum Palm is connected to a large stretch of other contiguous oil palm estates that dominate the landscape of northeastern Sabah. The rest of Danum Palm is bordered by the USFR, with the Segama River separating the two on the eastern side. The plantation contains mostly mature palms ranging from 10 - 20 m in height (personal observation). Tingkayu Estate is a smaller plantation surrounded by large plantations. It is roughly 1 km west of the Madai-Baturong Reserve (MBR), a "Class VI Virgin Jungle Reserve" intended for research and conservation. The estate contains a mixture of young and mature palms ranging from 4 - 20 m in height (personal observation).

2.2.2 Field sampling

I deployed infrared, motion-triggered cameras ("camera traps") in line transects in DVCA, USFR, and the two plantations from January to April 2013. I selected the location of each transect in relatively flat areas with high visibility to optimally detect wildlife, and predetermined the camera trap locations to be spaced roughly 200 m apart along each transect. Within 10 m of the predetermined point, trap locations were subjectively chosen to capture the most wildlife (e.g., along wildlife trails).

I placed a single camera trap at each location, attached to a tree trunk approximately 50 cm above the ground. I selected trees that were large and robust enough to remain stable throughout the duration the trap was employed. The traps were placed facing the direction that provided the highest visibility. Different camera trap models were used for the study – Reconyx RM45, Reconyx HC500 Hyperfire, and Bushnell Trophycam - so camera model was included as a covariate in the analysis. Each camera was set to high trigger sensitivity and programmed to record three photos when triggered. The cameras were powered by rechargeable AA batteries (or C cell batteries for the

Reconynx RM45) and could last for several months without recharging. An SD card (varying from 1 to 16 GB), capable of storing thousands of photos, was inserted into every camera. None of my cameras completely used up the SD card space. Each camera was taken down 4 to 5 weeks after deployment.

I measured several environmental covariates at each site. I recorded the approximate average height of the forest canopy with a clinometer and meter tape. I measured canopy cover by taking hemispherical photographs of the canopy at each site using a Nikon FC-E8 fisheye lens mounted on a Nikon P5000 camera, and analyzing the photographs in Gap Light Analyzer v.2 (Fraser 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 the maximum distance from the camera at which detections could be obtained. To account for this, I estimated the visibility range in front of each camera as a proxy for understory density and incorporated this as a covariate in my models.

2.2.3 Assessing habitat preferences

To determine how habitat type influenced individual mammal species and overall species richness, I first calculated simple estimates of relative abundance and diversity in the different habitats. As a crude metric of relative abundance commonly used in camera trapping studies (e.g., O'Brien et al. 2003), I calculated the number of separate detections per 100 trap nights for each species in forest and oil palm. Detections more than 1 hour apart were considered separate; this threshold is arbitrary but is more conservative than the 0.5 hour threshold used by O'Brien et al. (2003). For estimates of richness, I calculated the cumulative species count and the Chao1 estimator (Chao 1984) for all detected species and, separately, for IUCN Red-listed species in each habitat. The Chao1 estimator corrects for false absences by extrapolating from the proportion of rare species detected (Chao 1984).

The problem with the above estimates of relative abundance is that they do not account for the fact that species are detected imperfectly; overlooking differential detectability among habitats can lead to biased comparisons (Mackenzie et al. 2002). In order to incorporate imperfect detection, I used hierarchical occupancy models to assess

habitat effects on species occurrence and richness (Royle and Dorazio 2008). These models partition the data into a state component and an observation component (Royle and Dorazio 2008). The state component represents the variable of interest (e.g., species occurrence), which cannot be measured directly and must be inferred. The observation component describes variation in the observed data as being governed by the state variable plus 'nuisance' parameters. The nuisance parameters do not affect the state variable, but rather the power of the sampling. With sampling replication, the model can estimate detectability, and from that, infer the state variable. The advantage of these hierarchical models is that they can calculate the state variable, which is ultimately relevant to the question of biological interest, after correcting for nuisance parameters (i.e., imperfect detection) which are of less biological importance.

The state variable (in my case, species occurrence) may be influenced by site covariates, while detectability may be affected by both site (temporally static) and observation (temporally dynamic) covariates. To investigate habitat preferences, I used *habitat* as the site covariate. *Habitat* was a binary measure with forest = 0 and plantation = 1. Detection covariates included *visb* - the visibility in front of the camera; *cam* - the camera trap model; *camdays* - the number of days since employment (since animals may be less willing to approach the trap site right after the trap has been employed); and *camhours* - the number of hours the trap was active per day (this is to account for the shortened days when deploying and retrieving the traps; the rest of the days had the full 24 hours). For *cam*, the Reconyx HC500 was grouped with the Bushnell Trophycam, as they had similar detection rates, whereas the Reconyx RM45 produced more blurry and empty photos. To account for spatial autocorrelation among sites, camera traps that were within 3 km of each other were considered a single group, and *group* was incorporated as a random effect. 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).

The model assumes that species occurrence z_{ij} is a Bernoulli process of the occupancy ψ_{ij} of species i at site j:

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

where z is 1 when the species is present and 0 when absent. However, the camera traps may not detect species perfectly, so the trap data y_{ijk} is conditional on both the occurrence z_{ij} and the detectability p_{ijk} of species i at site j in the sampling period k. The model assumes that the trap data is also the outcome of a Bernoulli trial:

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

where y is 1 when the species has been detected and 0 when not or when it is absent. Both occupancy and detectability can be governed by covariates in the logit link functions:

$$\text{logit}(\psi_{ij}) = \alpha_i + \alpha_j$$
$$\text{logit}(p_{ij}) = \beta_i + \beta_j$$

where α_i and β_i are the species-specific effects (i.e., the intercepts), and α_j and β_j are the site and detection covariate effects respectively. Thus, to investigate effects of habitat type, the occupancy of species i at site j was modeled as

$$\text{logit}(\psi_{ij}) = \alpha_i + \alpha 1_i habitat_j$$

where $\alpha 1_i$ is the effect of *habitat*. Similarly, the detection probability of species i at site j was modeled as

$$\text{logit}(p_{ij}) = \beta_i + \beta 1_i visb_j + \beta 2_i cam_j + \beta 3_i camdays_j + \beta 4_i camhours_j$$

where $\beta 1_i$ to $\beta 4_i$ are the effects of the corresponding covariates.

To estimate effects on species richness, the model pools the single-species models together and assumes that species-specific parameters are drawn from a community-level "hyperparameter" with a normal distribution (Royle and Dorazio 2008). To account for species that were present but never detected, I augmented the dataset with 20 "pseudospecies" with all-zero detection histories. The model regards this augmented dataset as a zero-inflated logistic regression of the species-specific detectability p_i in order to predict the true number of species present. Data augmentation requires that the number of psuedospecies exceeds the number of detected species (Royle and Dorazio 2008) – in my case, 19 in forest and 17 in oil palm – so the choice of 20 pseudospecies is adequate. Data augmentation is a recognized method for estimating species richness while accounting for the likely fact that not all species in the area were detected during the study (Royle and Dorazio 2008). The model was run with WinBUGS through the R package R2WinBUGS. I used vague priors and ran 3 chains for 70,000 iterations after a burn-in of 30,000.

11

2.2.4 Assessing preferences within oil palm

To assess how species occurrence and diversity in oil palm plantations vary with select site covariates, I first plotted the number of species observed at each trap site against distance from the nearest forest patch, percentage of nearby forest cover, canopy cover, or tree height. I assessed the influence of these covariates using linear regression analysis.

To incorporate imperfect detection and spatial autocorrelation, I ran a hierarchical model similar to the one described above but with different site covariates and a dataset restricted to camera locations in oil palm plantations. I chose tree height (*tree*), canopy cover (*canopy*), and six spatial attributes -distance from the nearest intact forest (*distintact*) or from regrowth forest (*distregrowth*), percentage cover of intact forest (*intact1*) or intact plus regrowth forest (*intactreg1*) within a 1 km radius, or within a 2 km radius (*intact2* and *intactreg2*) – as site covariates. Distance to nearest forest and percentage forest cover were measured in ArcMap 10 (ESRI 2010) for every trap site. Because the spatial covariates were correlated I ran six separate models, each with only one of the spatial covariates. Thus, the occupancy of species i at site j was modeled as:

$$\text{logit}(\psi_{ij}) = \alpha_i + \alpha 1_i S_j + \alpha 2_i canopy_j + \alpha 3_i height_j + \alpha 4_i canopy_j * S_j + \alpha 5_i height_j * S_j$$

where $\alpha 1_i$ to $\alpha 5_i$ are the effects of the corresponding covariates and S_j represents one of the six spatial covariates. The detection covariates were only *camdays* and *camhours* as there was not enough variance to include *visb* and *cam*. Therefore the detection probability of species i at site j was modeled as:

$$\text{logit}(p_{ij}) = \beta_i + \beta 1_i camdays_j + \beta 2_i camhours_j$$

For diversity estimates, I augmented the dataset with 20 pseudospecies and used vague priors. I ran 3 chains for 70,000 iterations after a burn-in of 30,000.

To compare the six different models, I calculated the deviance information criterion (DIC) for each model using the R package AICcmodavg. DIC is an analog of the Akaike information criterion (AIC) and is useful in determining the fit of hierarchical models that have been run with MCMC sampling in a Bayesian framework (Spiegelhalter et al. 2002). As with AIC, models with lower DIC values fit the data more parsimoniously. For the spatial metrics with the lowest DIC values, I ran a model fit to data to predict how diversity would vary with these metrics.

2.2.5 Assessing edge effects of oil palm

To assess edge effects on forest species, I determined how occurrence of particular species and overall species richness in intact forest varied with distance from oil palm or regrowth forest. I compared the number of species detected at each trap site against distance from the edge of the oil palm plantation or regrowth forest using linear regression analysis. I then ran hierarchical models using a dataset restricted to camera locations in forest only. I chose distance from oil palm (*distOP*) or *distregrowth* as the site covariates, and *visb*, *cam*, *camdays*, and *camhours* as the detection covariates. Thus, occupancy was modeled as

$$\text{logit}(\psi_{ij}) = \alpha_i + \alpha 1_i distOP_j \ \text{ or}$$
$$\text{logit}(\psi_{ij}) = \alpha_i + \alpha 1_i distregrowth_j$$

and detection probability as

$$\text{logit}(p_{ij}) = \beta_i + \beta 1_i visb_j + \beta 2_i cam_j + \beta 3_i camdays_j + \beta 4_i camhours_j$$

Again, I used vague priors, added 20 pseudospecies, and ran 3 chains for 70,000 iterations after a burn-in of 30,000. To compare the fit of the two models, I calculated the DIC of each model.

2.3 Results

I had 53 functional camera traps in native forest, yielding a total of 1574 trap days, and 38 camera traps in oil palm plantation, yielding 1191 trap days. There were 688 detections, one hour apart, of 19 species in forest, and 889 detections of 17 species in oil palm.

2.3.1 Habitat preferences

The Chao1 diversity estimates did not significantly differ between forest and oil palm for IUCN listed species (Fig. 2A); however, it is inconclusive as to whether the Chao1 estimates for all species differed significantly between habitats at the $\alpha = 0.05$ level, as the 95% confidence intervals slightly overlap (MacGregor-Fors and Payton 2013). The raw cumulative diversity for all species or only IUCN listed species did not differ significantly (Fig. 2B). The habitat coefficients in the hierarchical models were also

not considerable for richness of all species and IUCN Red-listed species, in that the 95% credibility intervals included zero (Fig. 2C).

The species that were only found in forest in this study were sambar, moonrat, elephant, long-tailed porcupine, banded linsang, and masked palm civet (latin names shown in Table 1). The species found only in plantations were the leopard cat, pangolin, thick-spined porcupine, and Malay badger, though all of these have been observed before in DVCA either by myself or others (personal communication with the DVCA staff). Detection rates were highest for bearded pig in forest (10.8 detections / 100 trap nights) and in oil palm (40.7 / 100 nights; Fig. 3).

Occurrence rates of several species, estimated from the Bayesian hierarchical models, were lower in plantations than in forest: sambar (habitat coefficient, ß = -6.99, 95% credibility interval, CI = -13.81 : -3.18), moonrat (ß = -4.68, CI = -11.7 : -0.63), mousedeer (ß = -4.68, CI = -7.31 : -2.81), long-tailed porcupine (ß = -4.58, CI = -11.88 : -0.39), pig-tailed macaque (ß = -3.83, CI = -8.50 : -1.46), and muntjac (ß = -2.8, CI = -4.52 : -1.46; Fig. 3). The common palm civet (ß = 4.24, CI = 1.69 : 9.08) and leopard cat (ß = 4.59, CI = 2.065 : 8.36) had significantly positive coefficients, meaning they prefer oil palm.

2.3.2 Habitat preferences within oil palm

There was a significant negative relationship between the number of species detected at each camera location and distance from intact forest (linear regression: ß = -1.88 $\pm$ 0.54 SE, p = 0.0014, R^2 = 0.25) but not regrowth forest (Fig. 4). The slope was significantly negative for IUCN Red-listed species richness with both distance from intact forest (ß = -0.84$\pm$0.21, p = 0.0003, R^2 = 0.31) and regrowth forest (ß = -0.79$\pm$0.33, p = 0.0209, R^2 = 0.16). There was a significant positive relationship between IUCN Red-listed species richness and oil palm tree height (ß = 0.039$\pm$0.012, p = 0.0017, R^2 = 0.11) and canopy cover (ß = 4.17$\pm$1.47, p = 0.0055, R^2 = 0.08), but the regressions for richness of all species were non-significant. All regressions with percentage of nearby forest cover were significant and positive. Overall species richness was positively associated with the percentage of intact forest cover within 1 km (ß = 10.71$\pm$2.67, p = 0.0003, R^2 = 0.31) and 2 km (ß = 7.63$\pm$1.84, p = 0.0002, R^2 = 0.32), and with the percentage of intact plus

14

regrowth forest within 1 km ($ß = 5.26\pm1.50$, $p = 0.0012$, $R^2 = 0.26$) and 2 km ($ß = 5.98\pm1.58$, $p = 0.0006$, $R^2 = 0.29$). Similarly, IUCN Red-listed species richness was positively related to the percentage of intact forest cover within 1 km ($ß = 4.27\pm1.07$, $p = 0.0003$, $R^2 = 0.31$) and 2 km ($ß = 3.23\pm0.71$, $p = 0.0001$, $R^2 = 0.36$) and to the percentage of intact plus regrowth forest within 1 km ($ß = 2.58\pm0.55$, $p = 0.0000$, $R^2 = 0.38$) and 2 km ($ß = 2.56\pm0.61$, $p = 0.0002$, $R^2 = 0.33$).

Results from the hierarchical models showed that distance from intact forest had a negative relationship with total species richness ($ß = -3.16$, 95% CI $= -5.27 : -1.85$), while the relationships of percent intact forest within 1 km ($ß = 2.76$, CI $= 1.39 : 4.55$), percent intact forest within 2 km ($ß = 3.34$, CI $= 1.87 : 5.53$), percent intact plus regrowth forest within 1 km ($ß = 2.20$, CI $= 1.24 : 3.58$), and percent intact plus regrowth forest within 2 km ($ß = 4.66$, CI $= 2.33 : 8.58$) were all positive (Fig. 5). For IUCN Red-listed species richness, the relationship with distance from intact forest ($ß = -4.10$, CI $= -8.25 : -1.46$) was negative, while the relationships with percent intact forest within 2 km ($ß = 3.92$, CI$= 1.08 : 7.59$), percent intact plus regrowth forest within 1 km ($ß = 3.82$, CI $= 1.13 : 10.57$), and percent intact plus regrowth forest within 2 km ($ß = 3.92$, CI $= 1.08 : 7.59$) were positive. Percentage of intact forest within 1k m had the lowest DIC (1516) for total species richness, whereas percent intact plus regrowth forest within 2 km had the lowest DIC (450) for IUCN listed species richness.

Total species richness increased from 3 species to 18 species as the proportion of intact forest within 1 km increased from 0 to 100%, and decreased from 14 species to 0 species as the distance from intact forest changed from 0 to 3 km (Fig. 6). Similarly, IUCN Red-listed species richness increased from 0 to 7 species as the proportion of intact plus regrowth forest within 2 km changed from 0 to 100%, and decreased from 6 species to 0 species as the distance from intact forest changed from 0 to 3 km.

For species-specific occurrence, I compared three models: the *intact1* model, having the lowest DIC for total species richness, the *intactreg2* model, having the lowest DIC for IUCN Red-listed species richness, and the *distintact* model, being the better of the two distance models. For the *intact1* model, *intact1* had a positive relationship with occurrence for all species except for the orangutan, Malay badger, mongooses, and pangolin (Fig. 7 A). *Canopy* had a negative relationship with only the bearded pig and

15

height had a negative relationship with the leopard cat, Malay civet, and pig-tailed macaque. *Intact1*canopy* had a negative relationship with the common porcupine, leopard cat, long-tailed macaque, Malay badger, Malayan sun bear, mousedeer (two species combined), muntjac (two species combined), pig-tailed macaque, and thick-spined porcupine. *Intact1*height* had no significant influence for any of the species. For the *distintact* model, *distintact* had a negative relationship with the occurrence for all species except for the Malay badger (Fig. 7 B). *Canopy* had a negative relationship with only the bearded pig and *height* had a negative effect on the leopard cat and Malay civet. *Distintact*canopy* had a positive relationship with the leopard cat only, while *distintact*height* had a postive relationship with the long-tailed macaque. For the *intactreg2* model for only IUCN Red-listed species (Fig. 7 C), *intactreg2* had a positive relationship with all species except for the pangolin. *Canopy* had a negative relationship with only the bearded pig and *height* had a marginally negative relationship with the pig-tailed macaque. *Intactreg2*height* had a negative relationship with the bearded pig, but the rest of the covariate effects were non-significant for all IUCN Red-listed species.

2.3.3 Edge effects of oil palm

There was a significant negative relationship between the number of species detected at each camera location and distance from oil palm (linear regression: ß = -0.10 $\pm$ 0.05, p = 0.0500, R^2 = 0.07) but not regrowth forest (Fig. 8 A). None of the distance metrics had a significant correlation with IUCN Red-listed species richness. Results from the hierarchical models showed that the distance metrics had no considerable relationship with total or only IUCN Red-listed species richness (Fig. 8 B). Distance from oil palm had the lower DIC of 2599 for total species richness, but distance from regrowth forest had the lower DIC of 1313 for IUCN listed species richness.

Distance from oil palm had a significant negative relationship with the occurrence of only the bearded pig and Malay civet, and distance from regrowth forest had a significant relationship with only the bearded pig (Fig. 9).

16

2.4 Discussion

Habitat type had a strong influence on mammal diversity, with oil palm plantations exhibiting a considerable decline in diversity as forest proximity decreases, though this effect was hidden when only comparing the cumulative species richness (i.e., gamma diversity) between habitats. Although comparisons of gamma diversity in oil palm versus native forest were inconclusive at the $\alpha = 0.05$ level , my simulations of how richness within oil palm varies with forest proximity showed a very abrupt drop in diversity further from forest. Estimated species richness dropped from 14 to 0 species at 3 km from the forest, or from 18 to 3 species as forest cover within a 1 km radius changed from 100% to 0% (Fig. 6). This suggests that simply comparing the gamma diversity between oil palm and forest can mask true differences between the habitats, especially if sampling within oil palm takes place near the forest edge. Future studies should account for where in oil palm sampling took place, and ideally ensure that sampling sites in oil palm span a wide range of proximities from forest. My simulations suggest 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 animals captured by my camera traps may therefore only reflect the random scattering of animals from the forest; further into oil palm there is likely limited mammal diversity because few species will forage that far.

Within oil palm, proximity to forest, measured either as the nearest distance to forest or the percentage cover of nearby forest, had by far the strongest relation to mammal diversity. This result is congruent with the few studies that have looked at proximity to forest on diversity in oil palm for other taxa; for example bird and butterfly diversity was higher near forest (Koh 2008; Edwards et al. 2010). Compared to forest proximity, canopy cover and tree height had very weak or no effects. After comparing the fit of the six spatial measures using DIC, the percentage of intact forest within 1 km (*intact1*) was the best predictor for total species richness, while the percentage of intact plus regrowth forest within 2 km (*intactreg2*) was best for IUCN Red-listed species richness. All of the percent forest cover measures had a better fit than the nearest distance measures, suggesting that the amount of surrounding forest is more important than simply distance from the nearest forest. Interestingly, *intact1* showed no strong relationship with

IUCN listed species richness, but *intactreg2* (the best measure for IUCN species) had a positive relationship. This discrepancy suggests that threatened species as a whole respond differently than all species combined. Therefore, it is recommended that when investigating threatened species, one should look at only the responses of these species, instead of combining all species found, to ensure that their responses are not masked by commoner species of less conservation concern. Finally, the result that *intactreg2* had a strong positive relationship suggests that regrowth forest is indeed important in maintaining diversity of threatened species. Oil palm companies often expand into regrowth or secondary forests arguing that they are of low conservation value (Koh and Wilcove 2008), but here I show the contrary – regrowth forest has a strong positive influence on the diversity of threatened species. Oil palm should therefore not expand into regrowth forest, let alone intact forest.

Differences in occurrence between forest and oil palm were highly species specific. The leopard cat and common palm civet had much higher detection rates in oil palm than in forest, and the hierarchical models also showed that both of these species preferred oil palm. These preferences may be due to a higher rodent prey base in oil palm plantations (Rajaratnam et al. 2007). The bearded pig, Malay civet, and pig-tailed macaque had higher detection rates in oil palm, but the hierarchical models showed no strong preferences for these species. Conversely, the long-tailed porcupine, moonrat, mousedeer, muntjac, and sambar had many more detections in forest, and the hierarchical models also showed strong preferences for forest. For these species, there may be little food in oil palm, or else the understory may be too open, increasing their vulnerability to hunting or predation.

Proximity to forest had a strong positive correlation with the occurrence of most species detected, further suggesting that oil palm is unfavorable overall. *Intact1* had a strong positive relation with the occurrence of all species except for the orangutan, Malay badger, mongoose, and pangolin. Moreover, *intactreg2* had a positive relation with all species except the pangolin. The relationship may not be strong for the above species because of insufficient power: there were only three detections of Malay badger in oil palm, one of orangutan, four of mongoose, and two of pangolin. On the whole, however,

18

there is a clear strong trend for species to stay near forest, in support of my deduction that most mammals prefer to only forage in and out of oil palm from the forest edge.

Canopy cover and tree height had relatively weaker correlations with species occurrence overall, and with fewer species. Canopy cover was only strongly negative for bearded pig occurrence, while height was strongly negative for the leopard cat, Malay civet, and pig-tailed macaque. There does seem to be a general negative trend for canopy and height on species occurrence, though the correlations were not considerable for most species. These patterns suggest that lower tree canopy cover and palm height, and thus denser understory cover, would be more favorable for mammals. Perhaps for lower palms, the fruits are quite low, which means easier access for fruit and seed predators like rodents. This provides a more abundant prey source for the leopard cat and Malay civet. The bearded pig and pig-tailed macaque, as omnivores, may have easier access to fruits of lower palms, or may feed on invertebrates that are found on oil palms. Alternatively, these results could suggest that understory cover may be more important than tree canopy cover in terms of determining mammal usage of oil palm plantations. Future research on understory cover or density, perhaps investigating whether maintaining a dense shrub understory in tall plantations increases mammal occurrence, would be valuable.

Although proximity to forest influenced most species occurring in oil palm, the edge effects of oil palm on species within the adjacent forest were unsubstantial. Raw counts of total species richness increased significantly with distance from oil palm, but when accounting for imperfect detectability of each species using hierarchical models, these effects disappeared and distance from oil palm had no major effect on diversity. The hierarchical models also showed that distance from regrowth forest did not strongly relate to diversity. On average, distance to oil palm and regrowth was negatively associated with occurrence for all species, though for most the relationship was not statistically important. Only the bearded pig and Malay civet showed considerable negative relationship with distance to oil palm, suggesting that they prefer forest-oil palm edges. Indeed, both of these species were frequently detected in oil palm. Additionally, the bearded pig had a strong negative beta for distance from regrowth forest, suggesting that they prefer ecotones between intact and regrowth forest as well. My result differs from those of another camera trap study in Bukit Barisan Selatanin in Sumatra, a national

park bordered by villages and croplands, which found significant avoidance of forest edges by tigers (*Panthera tigris*), Sumatran rhinoceroses (*Dicerorhinus sumatrensis*), and elephants for up to 3 km (Kinnaird et al. 2003). However, another study at that same park found no significant edge effects for medium and large mammals, including tigers, ungulates, and macaques, after accounting for nearby human density (O'Brien et al. 2003). I did not have access to any human population density data in my study area and so could not assess whether human density had an influence on species occurrence.

There are several caveats to my study. First, my trap sites in oil palm were near some of the biggest and most well-protected forest reserves in Sabah, the Ulu Segama and the Madai Baturong reserves, both of which are known to hold high mammalian diversity (Hazebroek et al. 2012). Assessments of mammal occurrence in plantations not adjacent to such reserves may be lower than what I present. There could very well be much lower mammal diversity in oil palm plantations that are near smaller reserves, unprotected forests, or forest fragments. Furthermore, I sampled for only 4 to 6 weeks at each camera trap location in only one field season, which is relatively short compared to other camera trap studies (e.g., Kinnaird et al. 2003). There are many threatened species in Danum Valley and the Ulu Segama reserve that have been previously documented but have not been detected in my study, for example the banteng (*Bos javanicus*), binturong (*Arctictis binturong*), otter civet (*Cynogale bennettii*), clouded leopard (*Neofelis diardi*), marbled cat (*Pardofelis marmorata*), and bay cat (*Catopuma badia*; Hazebroek et al. 2012). Finally, all of my trap sites in oil palm were quite close to the forest (range = 0.07 to 2.56 km from the forest), so animals captured in my traps may only reflect the random dispersal of animals from the forest edge. My mean estimates of diversity in oil palm may therefore be inflated, as I did not have any traps deep in oil palm. This may explain why my comparisons of diversity in forest and oil palm were non-significant. Therefore, future studies should use caution when assessing wildlife in oil palm compared to forest. Researchers should not simply compare the diversity in oil palm with forest, as is done in many previous studies (Fitzherbert et al. 2008), but must also account for where in oil palm the sampling took place relative to forest. Moreover, although my data do show a steep decline in richness as one goes further into oil palm and away from forest, future studies should survey areas deeper in oil palm to verify if any species do actually persist

or inhabit oil palm. Alternatively, future studies could track individual animals to see if they only forage in and out of oil palm from the forest edge, or if they actually inhabit oil palm plantations long-term.

As oil palm expansion continues, habitat connectivity is becoming an increasing priority for threatened taxa, yet there do not seem to be any management plans on how to connect populations in forests fragmented by oil palm. Here I show that having 'corridors' of palms with higher canopy cover or height within plantations will not work in maintaining diversity or providing connectivity between forests, for it is ultimately forest proximity that determines diversity within oil palm. My results show that the only effective 'corridor' design is to have a strip of forest, or very closely linked forest fragments, within oil palm that connects to large forest patches.

There are many small forest fragments within large oil palm estates in Borneo (Miettinen et al. 2012), but whether these can support any diversity or act as stepping stones for wildlife remains unknown. Future studies should focus on these forest fragments, looking at their size, age, and isolation to see if they hold any value in maintaining connectivity. One notable example is the Stability of Altered Forest Ecosystems (SAFE) project also located in Sabah, Borneo. The project focuses on a region containing mostly selectively logged forest and some old growth forest set to be cleared into oil palm, but with a portion of it to remain as forest fragments (Ewers et al. 2011). The SAFE project aims to measure the diversity, composition, and ecological processes of different spatial scales at different locations relative to these forest fragments (Ewers et al. 2011). Because the data collection spans the entire process of forest clearance to oil palm conversion, the project is a strong before-after-control-impact (BACI) experiment that can effectively isolate habitat, landscape, and temporal effects. Researchers should seize opportunities to perform similar BACI experiments in other forests, especially of other regions or countries, designated for oil palm conversion. Although we are gaining increasing insight on how animals respond to oil palm in Southeast Asia, there is a dearth of data on how wildlife respond to oil palm in other regions of the world. Especially as oil palm is now starting to expand in Africa and the Neotropics, these BACI experiments are a crucial first step in determining how animal communities specific to those regions will be affected, and how these impacts can be

21

mitigated. Finally, it is important to note that although these BACI experiments are strong in assessing short-term community changes in response to oil palm conversion, animals may respond very differently to oil palm over the long term. Therefore, observational space-for-time experiments that compare plantations of different age since establishment are as important and highly recommended. Furthermore, the SAFE project only compares diversity and composition between fragments, but does not directly assess whether fragments are useful for connectivity. Future studies should seek to measure the degree of connectivity of different sized fragments (e.g., via DNA sampling, tracking, or mark-recapture) to verify if these fragments do provide connectivity for wildlife, which is of ultimate concern in these increasingly fragmented landscapes.

Several conclusions regarding the management and design of oil palm plantations can be drawn from my study. I show that although canopy cover and palm height have weak or no relationships with mammal diversity, proximity to forest has a strong influence on most, if not all, species. I show that diversity in oil palm declines sharply as forest proximity decreases, and the only way to maintain adequate levels of diversity in oil palm is to have a small patch of oil palm surrounded by forest, though this is far from practical in reality. This sharp decline in richness suggests that large continuous patches of oil palm are essentially 'dead zones' for mammal diversity, and the only effective way to connect forest populations is to have large corridors of forest through oil palm that connect fragmented forest tracts. Investigating the effects of plantation age since establishment, the value of forest fragments within oil palm, and the importance of nearby forest reserves are important next-steps to understanding how to mitigate the effects of oil palm expansion and habitat fragmentation on forest animal diversity.

Chapter 3

Conclusions

Habitat preferences of all animals vary by species. In this study, I found that many species preferred forest while a few preferred oil palm. However, I showed that all of the species that preferred oil palm were only found near the forest edge and did not venture deep into the plantations. This provides strong evidence that oil palm plantations are unfavorable for most larger mammals, and can only support relatively diverse mammalian communities if they are near (i.e., within about 1 km) large tracts of forest. Within plantations, I showed that forest proximity was the main determinant of mammal richness and occurrence, whereas canopy cover and palm height had almost no effect. Diversity and occurrence of almost all species dropped abruptly as the distance from nearest forest increased, or as the percent nearby forest cover decreased.

I looked at how covariates influenced total species richness, as well as only IUCN Red-listed species richness, and found discrepancies in their responses. The amount of nearby intact forest cover was the best predictor for total richness, but the amount of intact *and* regrowth forest was the best for threatened species. This finding suggests that regrowth forest is important for threatened species and should not be replaced by oil palm, contrary to what oil palm companies propose. Further, this suggests that in addition to looking at total species richness, future studies should also investigate richness of threatened species only to ensure that commoner species do not obscure the response of threatened species.

In terms of maintaining or restoring connectivity among forests fragmented by oil palm, I showed that there is little use in having strips of taller palms, or palms with more canopy cover, linking forests. Corridors of oil palms with increased height or cover have little to no effect on mammalian diversity. However, forest proximity (both distance and area) does have a huge positive influence. I suggest that the only effective corridor design is to have large strips of forest within oil palm, through which animals can travel.

Because my sampling duration and study areas were limited, further thorough research on how oil palm plantations influence various taxa are required. First, I recommend that future studies include spatial factors in their analyses, such as where in

oil palm the sampling occurred, as proximity to forest or other habitat types may play a big role in determining diversity. Future studies can also sample deeper in oil palm, for longer durations, to see if any species do inhabit oil palm. Finally, as habitat connectivity is becoming a critical issue when dealing with oil palm expansion, studying how forest fragments within oil palm – their size, shape, and proximity – affect wildlife is strongly recommended.

Table 1 – List of all the species detected, including their common and scientific names,
IUCN status, and approximate size (Payne and Francis 2007).

| Common name	Scientific name	IUCN status	Head and body length (cm)	Tail length (cm)
Banded civet	*Hemigalus derbyanus*	Vulnerable	50-57	30-37
Banded linsang	*Prionodon linsang*	Least concern	35-41	30-36
Bearded pig	*Sus barbatus*	Vulnerable	122-152	17-26
Bornean elephant	*Elephas maximus*	Endangered	150-260 tall	-
Bornean orangutan	*Pongo pygmaeus*	Endangered	140 tall	-
Common palm civet	*Paradoxurus hermaphrodites*	Least concern	42-50	33-42
Common porcupine	*Hystrix brachyura*	Least concern	59-63	10-13
Leopard cat	*Felis bengalensis*	Least concern	40-44	18-22
Long-tailed macaque	*Macaca fascicularis*	Least concern	40-47	50-60
Long-tailed porcupine	*Trichys fasciculata*	Least concern	38-44	15-24
Malay badger	*Mydaus javanensis*	Least concern	37-52	3-4
Malay civet	*Viverra tangalunga*	Least concern	62-67	29-36
Malayan sun bear	*Helarctos malyanus*	Vulnerable	113-126	3-9
Masked palm civet	*Paguma larvata*	Least concern	58-61	57-60
Mongoose spp. (short-tailed & collared)	*Herpestes brachyurus & H. semitorquatus*	Least concern & Data deficient, respectively	38-46	21-30
Moonrat	*Echinosorex gymnurus*	Least concern	32-40	21-29
Mousedeer spp. (lesser & greater)	*Tragulus kanchil & T. napu*	Least concern	43-57	6-10
Muntjac spp. (red & Bornean yellow)	*Muntiacus muntjak & M. atherodes*	Least concern	86-111	14-20
Pig-tailed macaque	*Macaca nemestrina*	Vulnerable	50	18
Sambar	*Rusa unicolor*	Vulnerable	154-204	21-27
Sunda pangolin	*Manis javanica*	Endangered	40-65	35-57
Thick-spined porcupine	*Thecurus crassispinis*	Least concern	55-67	9-14
Yellow-throated marten	*Martes flavigula*	Least concern	40-46	31-38
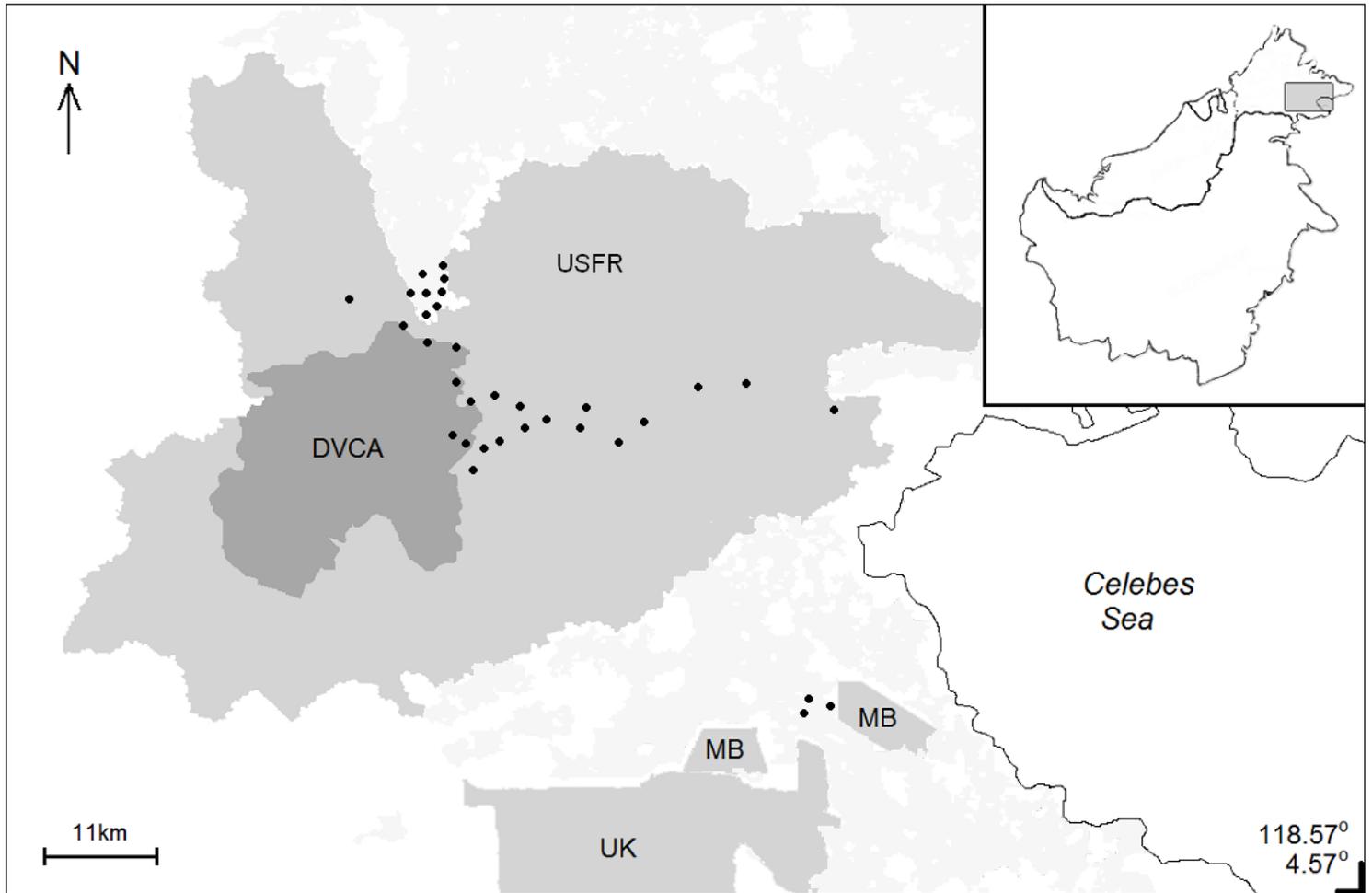
Fig. 1 – Map of eastern Sabah, showing the Danum Valley Conservation Area (DVCA), Ulu Segama forest reserve (USFR), Madai-Baturong (MD) and Ulu Kalumpang (UK) forest reserves, as denoted by the medium- and dark-grey areas. Light-grey areas represent large scale oil palm plantations. Each dot represents a transect of 3 to 5 camera traps.
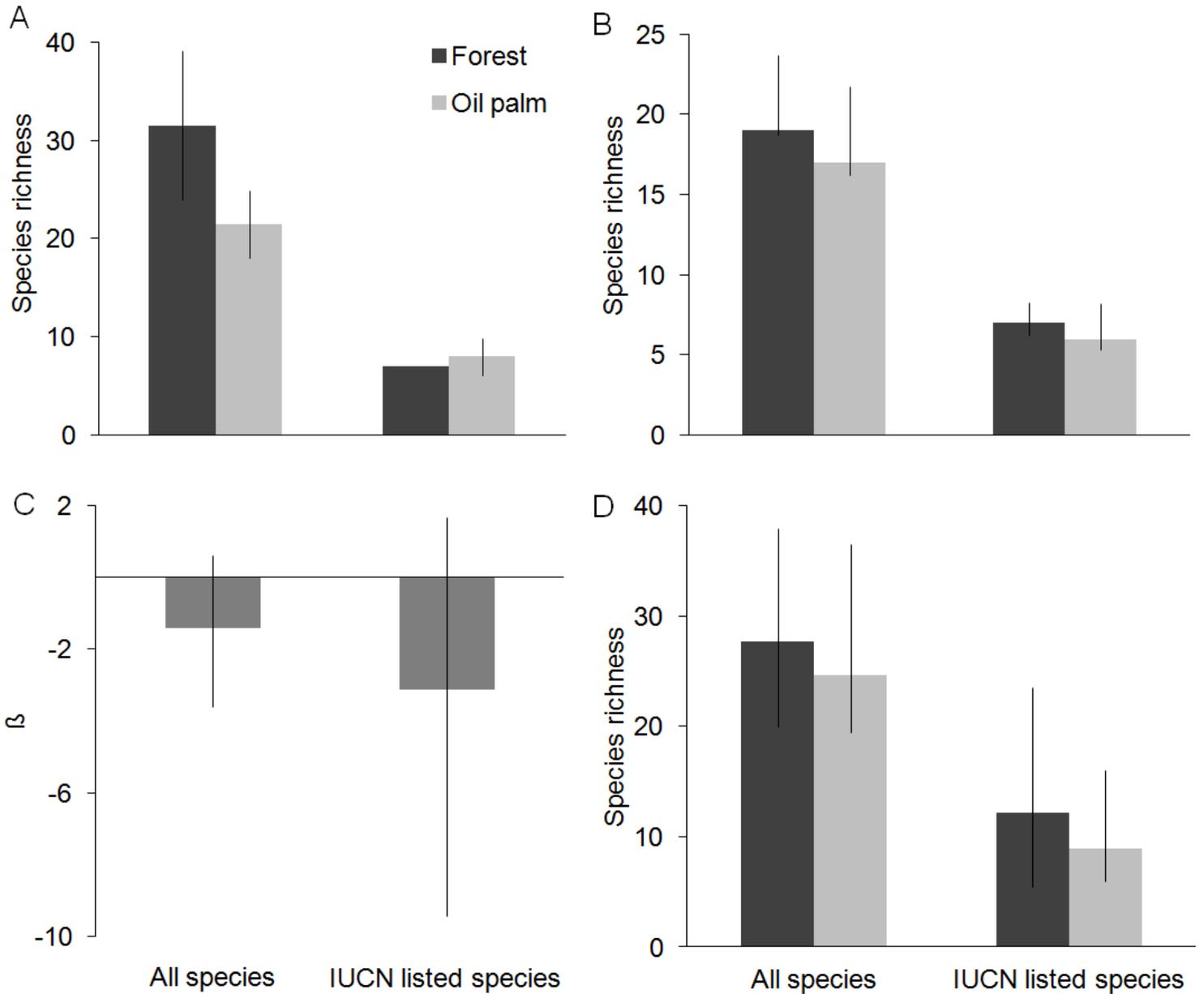
Fig. 2 – A) Cumulative species richness as calculated using the Chao1 estimator, in forest and oil palm. B) Raw cumulative species richness in forest and oil palm. C) The relationship (i.e., the ß coefficient) of habitat, as a binary of forest=0 and oil palm=1, on species richness. A negative ß means preference to forest, whereas a positive ß means preference to oil palm. D) Cumulative species richness in forest and oil palm, as estimated with Bayesian hierarchical models. Error bars represent 95% confidence intervals in A and B, or credibility intervals in C and D.
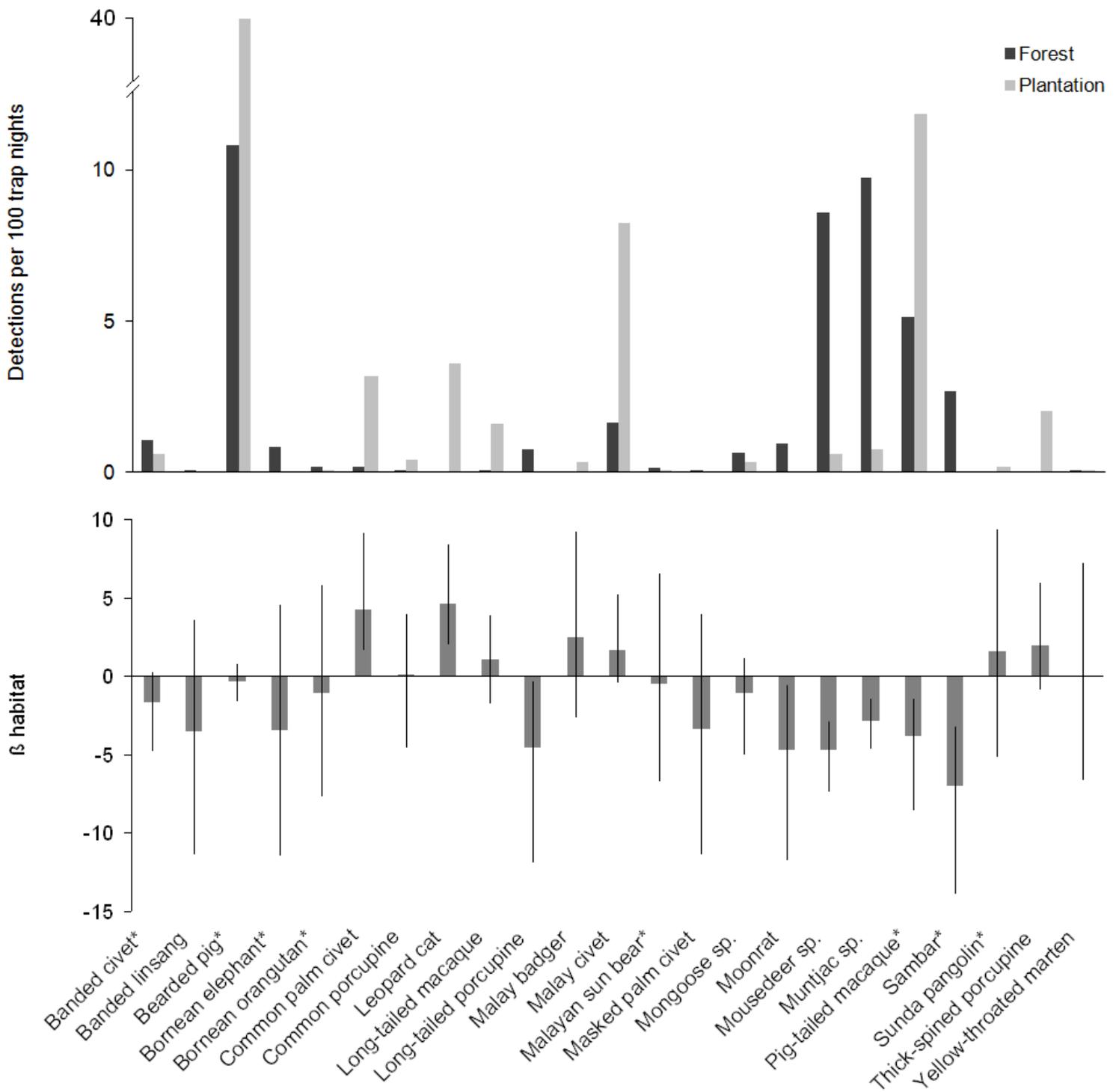
Fig. 3 – Detection rates for each species in each habitat, and the relationship i.e., the ß coefficient) of habitat, as a binary of forest=0 and oil palm=1, on species specific occurence. A negative ß means preference to forest, whereas a positive ß means preference to oil palm. Error bars represent 95% credibility intervals, and * denotes an IUCN Red-listed species.
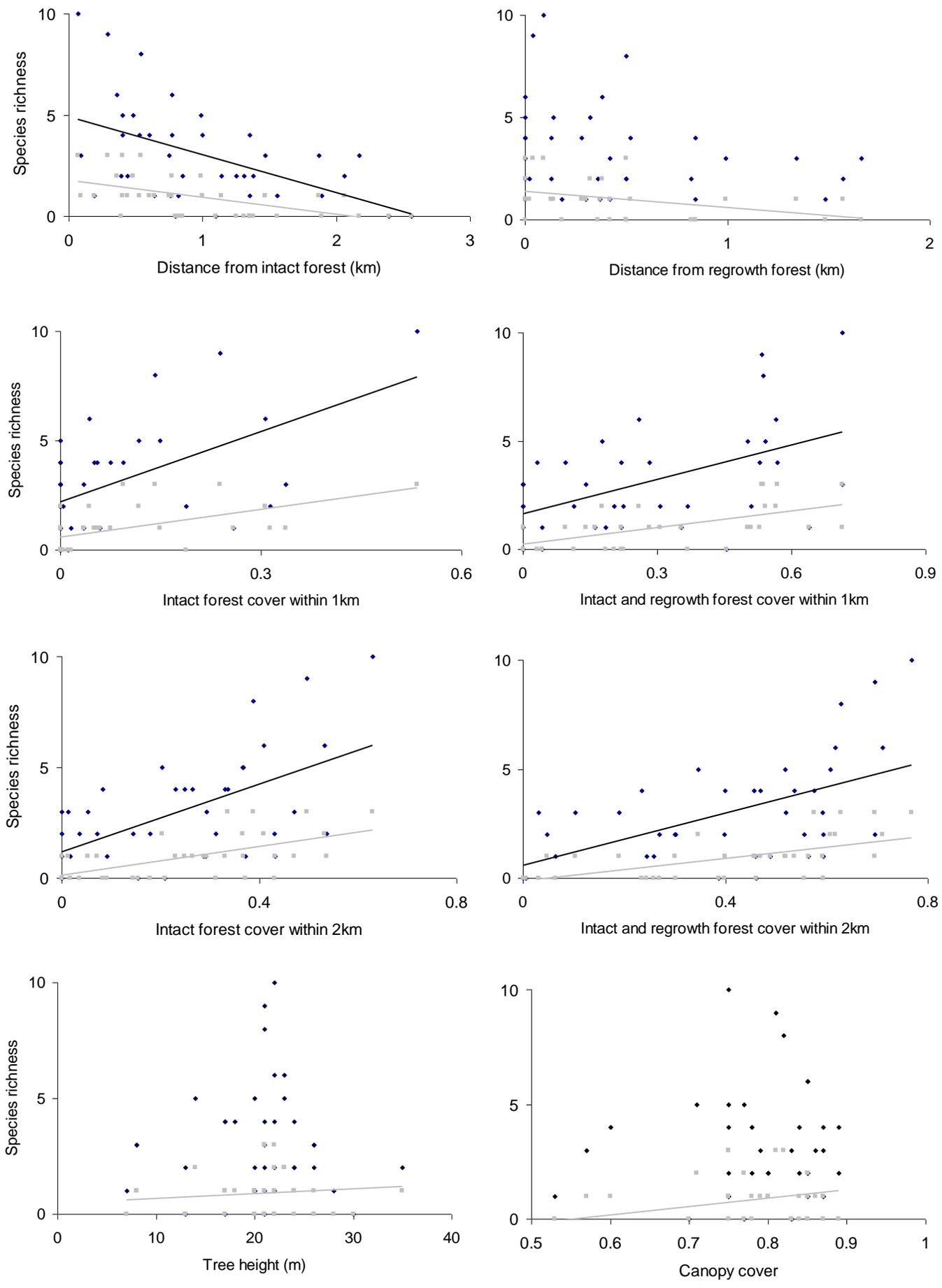
Fig. 4 – Relationship between habitat covariates and species counts across camera trap sites in oil palm, where black dots represent all species and grey dots represent IUCN Red-listed species. Trend-lines are shown if the linear regression was significant at $\alpha = 0.05$.
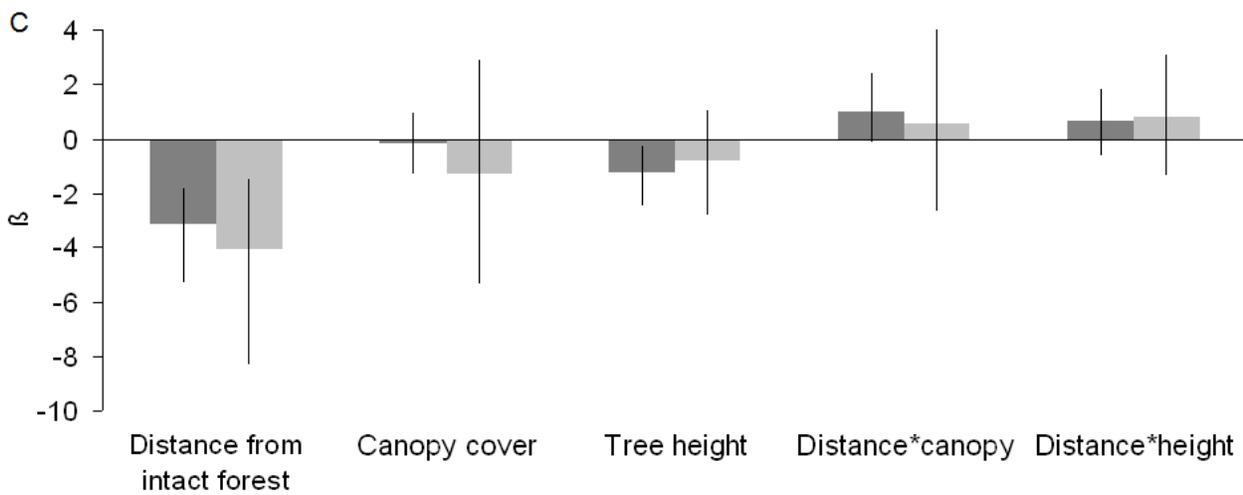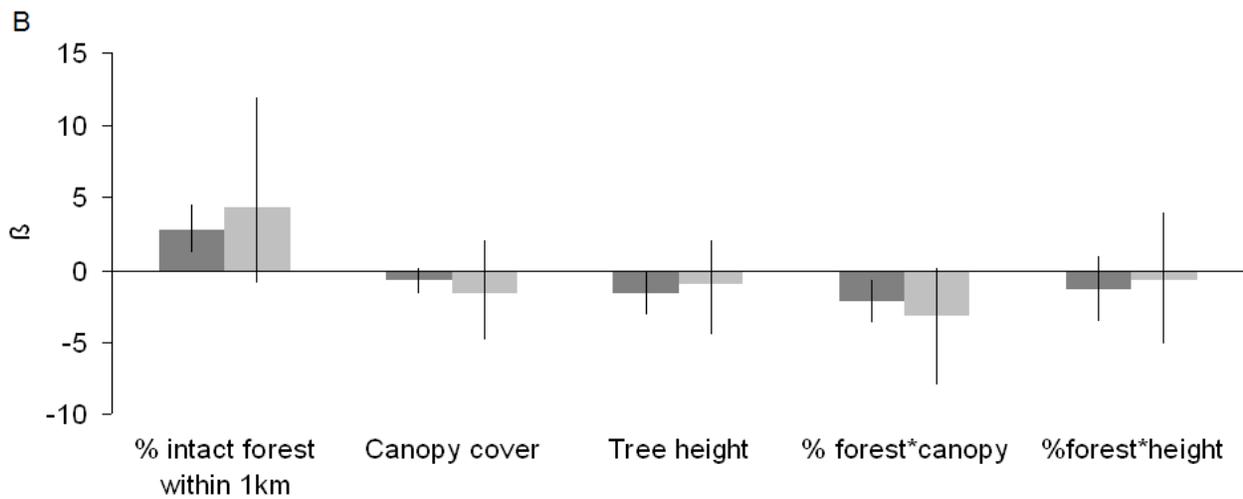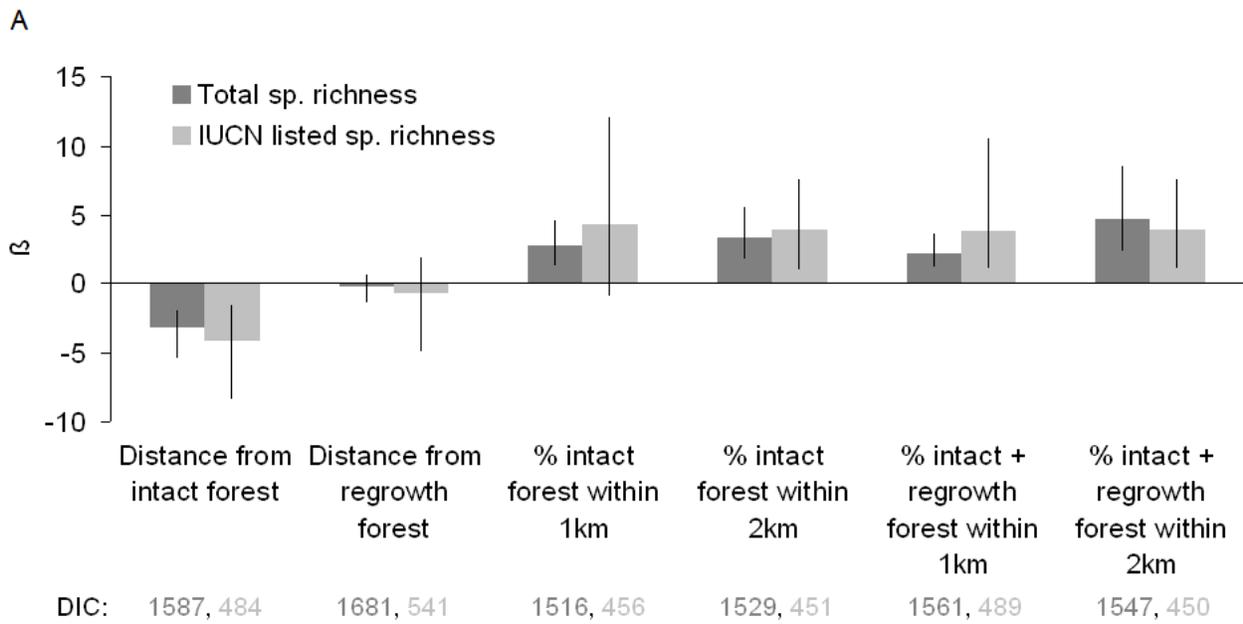
Fig. 5 – A) Comparison of the fit of six models, each with a different spatial covariate, and their relationship (i.e., the ß coefficient) with species richness. A negative ß means the covariate has a negative relation with species richness, and vice versa. B) Relationships of site covariates on species richness for the model with "Percent intact forest within 1km", being the model with the lowest DIC for total species richness. C) Relationships of site covariates on richness for the model with "distance from intact forest", having the lower DIC of the two distance metrics.
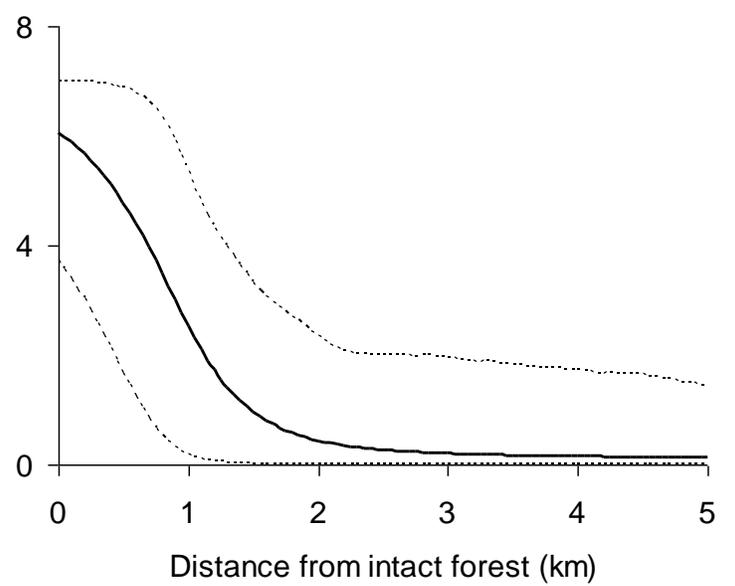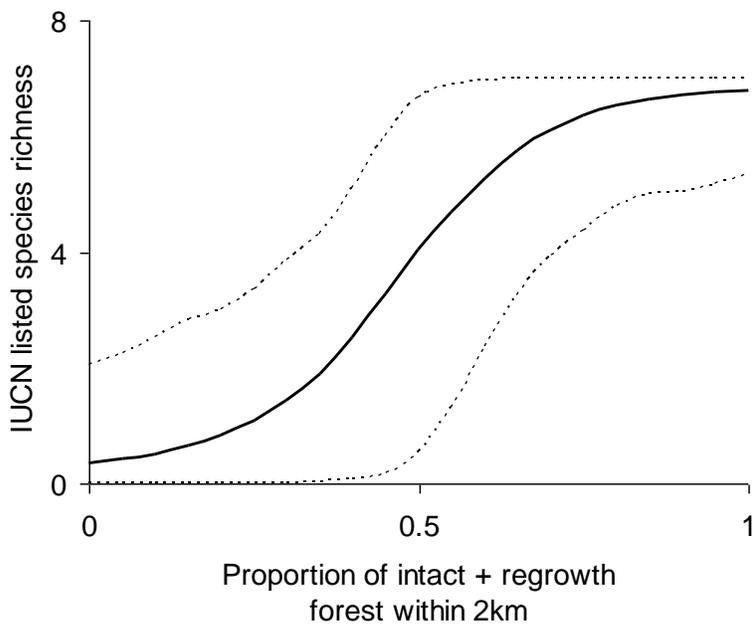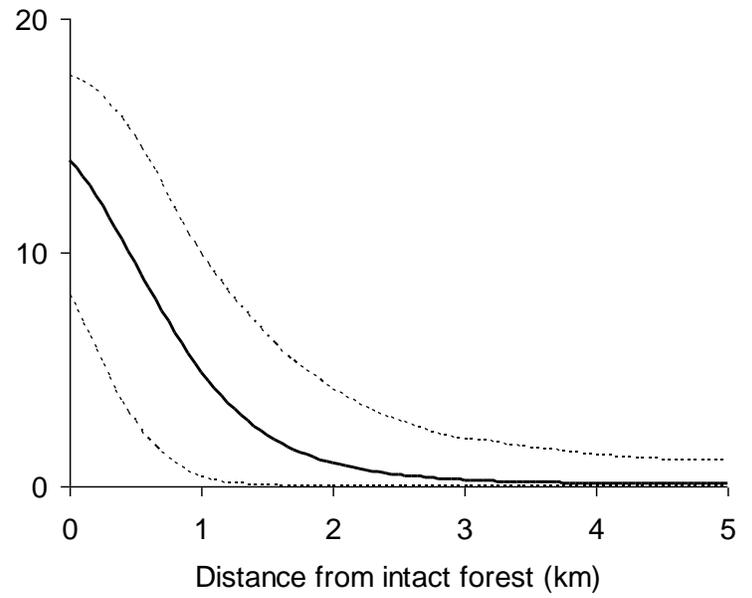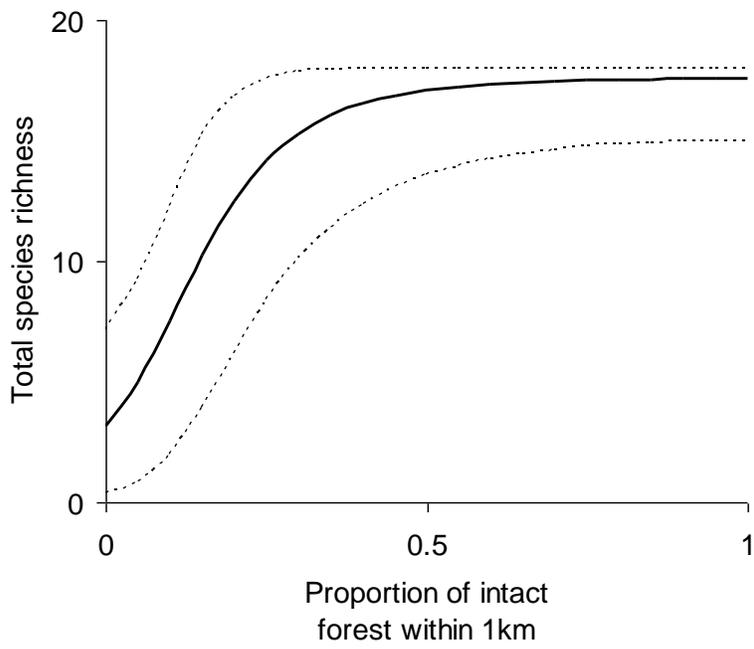
Fig. 6 – Predictions of how species richness varies with spatial metrics, based on models fit to data. Dotted lines show 95% credibility intervals.
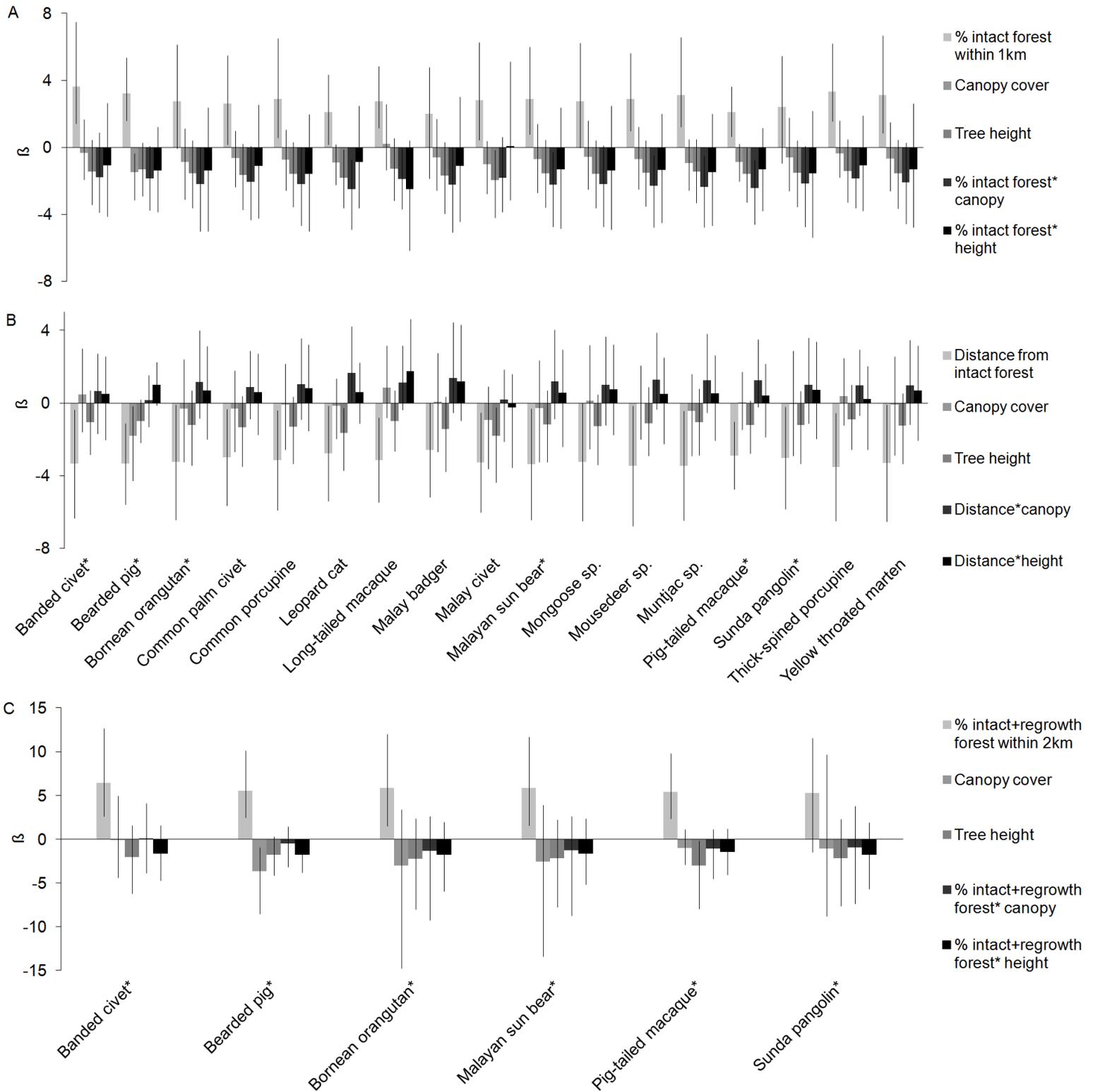
Fig. 7 – Relationship (i.e., the ß coefficient) of covariates on species occurrence for A) the "percent intact forest within 1km" model, having the lowest overall DIC; B) the "distance from intact forest" model, having the lower DIC of the distance metrics; and C) the "percent intact plus regrowth forest within 2km" model, having the lowest DIC for richness of IUCN Red-listed species. Error bars show 95% credibility intervals, and * denotes an IUCN Red-listed species.
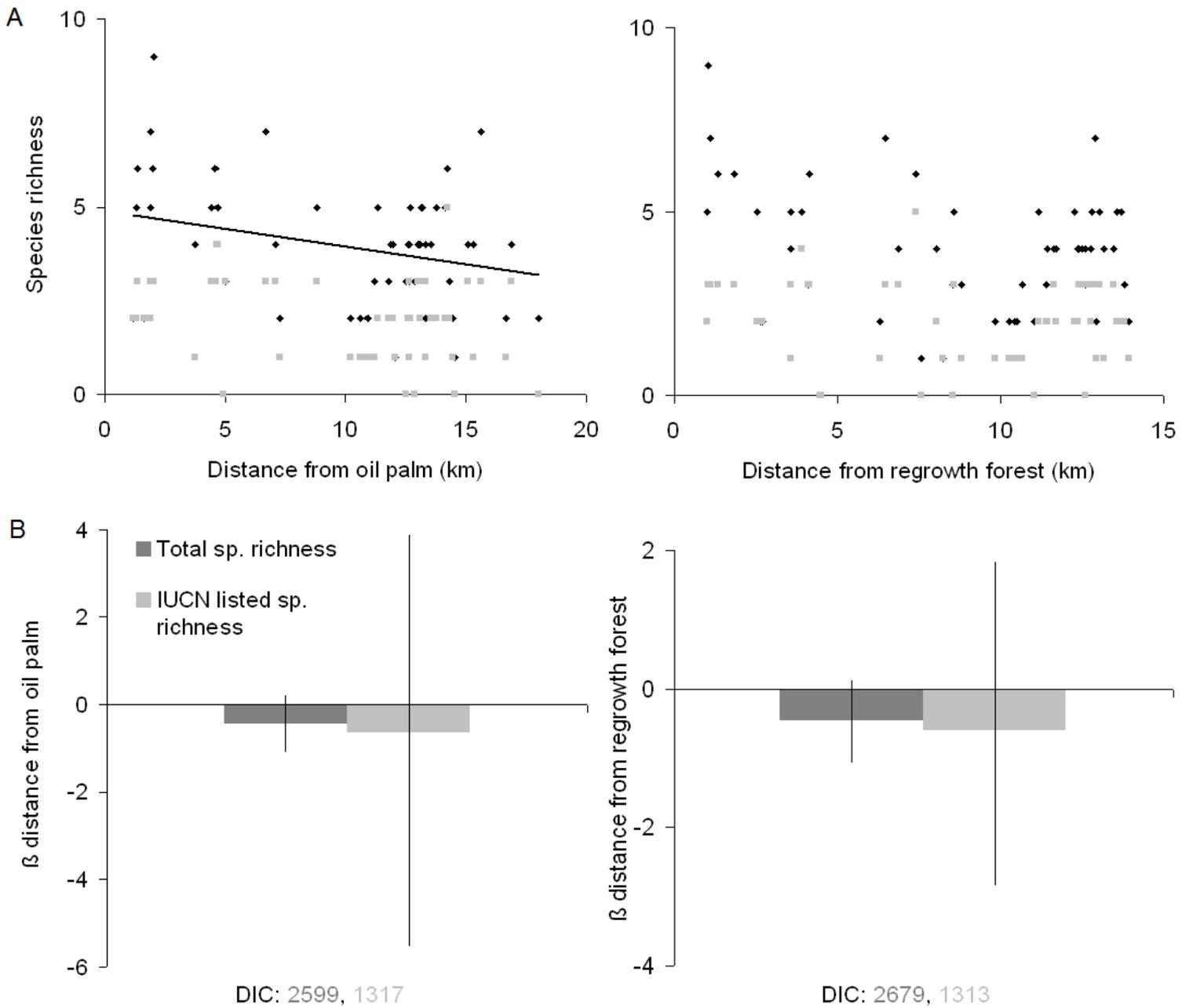
Fig. 8 – A) Relationship between site covariates and species counts across camera trap sites in forest, where black dots represent all species and grey dots represent IUCN Red-listed species; trend-lines are shown if the linear regression was significant at $\alpha = 0.05$. B) Relationship (i.e., the ß coefficient) of distance to the nearest oil palm or regrowth forest on mammal species richness in forest.

Fig. 9 – A) Relationship (i.e., the ß coefficient) of "distance to nearest oil palm" with the occurrence of all species detected (this spatial metric had the lowest DIC for all species). B) Relationship of "distance to nearest regrowth forest" on IUCN Red- listed species occurrence (this metric had the lowest DIC for IUCN Red-listed species).

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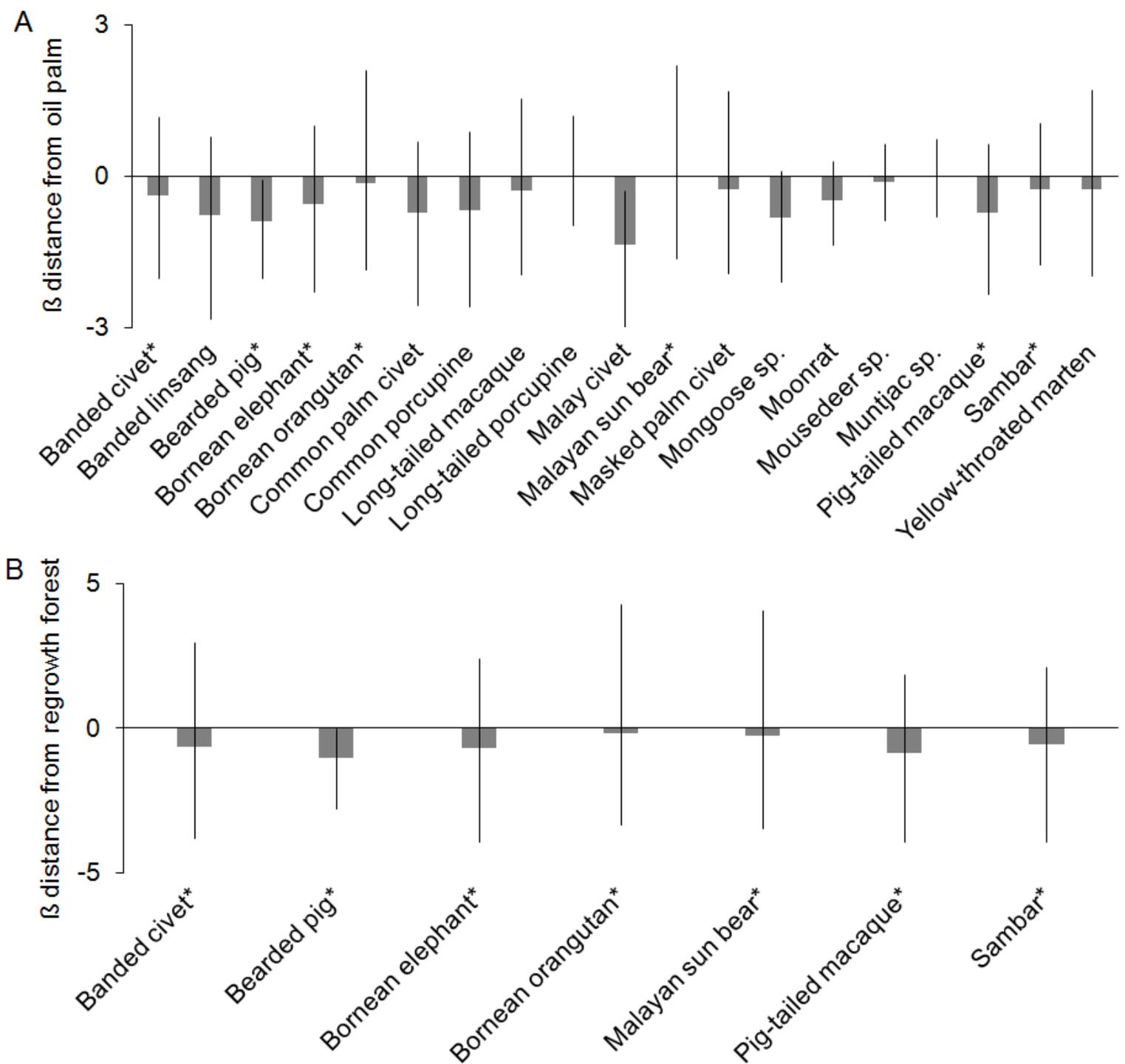Altieri, M. A. 1999. The ecological role of biodiversity in agroecosystems. Agriculture, Ecosystems and Environment **74:**19-31.

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