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Primate responses to habitat fragmentation in the Lower Kinabatangan Floodplain, Sabah, Malaysia.

ABSTRACT:

1. Tropical biodiversity loss due to oil palm cultivation is one of the most significant human-mediated threats to the natural world. Primates are particularly sensitive to anthropogenic disturbance, and have suffered extensive habitat loss and population declines due to agricultural plantation expansion and timber production; those species which are primarily arboreal are especially affected, since plantations show reduced canopy cover and diversity of food resources.

2. The present study aims to document primate responses to habitat fragmentation and oil palm plantations, in the Lower Kinabatangan Wildlife Sanctuary, Sabah. It investigates whether primate densities are affected by edge effects, such as modifications to forest canopy integrity. It also documents which species are the most prevalent crop-raiders, and whether plantations are used as 'corridors' to travel between fragments of secondary forest, as a strategy to minimise demographic and reproductive isolation. Hypotheses to be tested are: (1) At habitat edges, primate densities will be higher in forest margins relative to plantation margins, or to the edge itself. (2) Encounter frequencies will be higher in forest fragments relative to habitat edges and plantation. (3) Encounter frequencies decrease as distance from edge into plantation increases. (4) Encounter frequencies will decrease with canopy density, limiting the potential for use of plantations as 'corridors'.

3. 12 500m line transects were placed across the floodplain: four in fragmented secondary forest; four in oil palm plantation and four at habitat edges. Each transect was surveyed five times to obtain primate encounter frequencies.

4. A negative binomial generalized linear model (GLM) showed significantly lower in encounter frequencies in plantation compared to forest; encounters also decreased as proximity to the habitat edge increased. A further GLM suggested that encounter frequencies were higher closer to the river. However due to a small size, residuals for the models could not be normalised, and so these results must be interpreted conservatively.

5. The study highlighted some interesting trends with regards to the responses of primates in human-modified landscapes, suggesting further research is necessary to push for legislation changes to riparian buffer widths and to facilitate development of habitat corridors within the LKWS.

Keywords: Anthropogenic disturbance; Habitat fragmentation; Lower Kinabatangan Wildlife Sanctuary; Oil Palm; Riparian buffer zones; Sabah; Species extinctions; Sustainable agriculture; Wildlife corridors.

INTRODUCTION

GLOBAL DEFORESTATION TRENDS

Tropical forests are the most ancient, biologically diverse and ecologically complex of terrestrial communities, but are disappearing faster than any other biome (Laurance, 1999; Marsh, 2003; Rudel *et al*., 2009). The vital ecosystem goods which they provide make rainforests particularly vulnerable to anthropogenic exploitation, providing nutritional- and economic security for millions of people (IUCN, 2011a). As such, tropical forests have been felled at ever-increasing rates since the 1960s (Rudel et al., 2009), which has had devastating repercussions for biodiversity. As we endure the 6th mass extinction crisis, species are being lost between 1000 and 10,000 times higher than the natural rate (IUCN Red List, 2007); this, in light of the failure of the Convention on Biodiversity to meet its 2010 target in full (COP 10 Outcomes, 2010), calls for urgent attention to be paid to the specific drivers of population declines following deforestation.

Recent estimates for global rainforest losses are ~10-15 million hectares (Mha); this is most acute in the tropical lowlands, since they are most accessible by road (Bruhl and Eltz, 2010; Koh *et al*., 2010). ~5.8Mha were lost annually between 1990 and 1997, with a further ~2.3Mha degraded (Achard *et al*., 2002). Small-scale farming, fuelwood extraction and commercial logging were the key agents of tropical deforestation during this period (Rudel et al., 2009). Deforestation trends have been most pronounced in Southeast Asia, Africa and Latin America - particularly since the 1970s (Laurance, 1999). With most extinctions occurring in the tropics (IUCN Red List, 2007), Southeast Asia is of particular concern, due to considerably higher rates of deforestation and degradation, and has less surviving forest than either Africa or Latin America (Achard *et al*., 2002). Much of this forest loss has occurred unsustainably through the international timber trade (Meyer and Turner, 1992; Laurance, 1999). Deforestation rates for Southeast Asia remain the highest in the tropics, posing a serious threat to its high biodiversity– many of which are already threatened, and/or endemic to the area (Bruhl and Eltz, 2010; Sodhi *et al*., 2010). For example the proboscis monkey (*Nasalis larvatus*), endemic to Borneo, has suffered extensive reductions in range and population sizes over the last 40 years due to hunting and habitat destruction (Meijaard *et al*., 2008).

Exponential increases in the global population have contributed towards a paradigm shift in the nature and scale of tropical deforestation and land usage patterns (Geist and Lambin, 2002; Cotter *et al*., 2009). From 1980-2000, tree plantation coverage in the tropics increased from ~17.8-70Mha (Barlow *et al*., 2007a). With the total population projected to reach 9 billion by 2050 and the global food demand expected to more than double during this period, increased global economic and nutritional pressures will exacerbate current threats facing tropical rainforests (Green *et al.* 2005; Population Reference Bureau, 2009).

IMPACTS OF DEFORESTATION AND LAND CONVERSION

Large-scale tropical forest conversion to plantations is one of the greatest threats facing tropical biodiversity- particularly in Southeast Asia - due to impacts of habitat loss and fragmentation (Wilcove and Koh, 2010; Pozo-Montuy *et al*., 2011; Fig. 1). Primates are one of the most sensitive taxa to anthropogenic disturbance, and have suffered extensive habitat loss and population declines due to agricultural plantation expansion and timber production (Crooks and Sanjayan, 2006; Pozo-Montuy *et al*., 2011). For example the greater bamboo lemur *Prolemur simus*, the most abundant lemur in northern sub-fossorial sites of Madagascar, is now critically endangered due to deforestation during the 1970s/80s, after which it was believed to be extinct. However arecent census estimates 60 individuals in an area over 500km^2, calling for urgent conservation action in order to save this once abundant species from extinction (Wright *et al*., 2008). With 90% of primate species occurring in the tropics, (Marsh, 2003), research into their specific responses to habitat fragmentation, is vital to develop the most appropriate conservation strategies and agricultural management policies.

a) *Formation of metapopulations*

Demographic isolation of individuals within fragmented landscapes is one of the most deleterious impacts of deforestation, making species considerably more vulnerable to local extinction (Bruford *et al*., 2010; Fig. 1). Sub-population isolation within forest fragments increases population densities, driving resource competition (Fig. 1); this is exacerbated due to the heterogeneous spatiotemporal distribution of food resources on which many primates depend (Meijaard *et al*., 2005). Arboreal primates are particularly sensitive to fragmentation, due to their reliance on dense canopy cover for food, refuge and reproduction (Pliosungnoen *et al*., 2010; Campbell-Smith, 2011). Limitations in migratory potential inhibit genetic dispersal, causing reproductive isolation and inbreeding. This is particularly detrimental to primates, many species of which occur at low densities, and demonstrate slow life histories and long inter-birth intervals (Laurance, 1991); limiting their capacity to recover from population declines resulting from habitat disturbance, predisposing them to extinction.

Conservation planning must assess potential for populations to persist in fragmented landscapes, and estimate the importance of different ecological parameters in determining extinction risk (Goossens *et al*., 2005). Species that can manipulate certain aspects of their life histories to exploit modified habitats- to compensate for reduction in food availability and/or facilitate genetic dispersal- may be able to maintain stable, viable population sizes, and recolonize fragmented sub-populations (Goossens *etal*., 2005). Investigating responses to habitat modification therefore has important primate conservation implications, since it can be used to develop species-specific conservation strategies, to reduce the frequency of local extinctions.

b) *Edge effects*

Landscape fragmentation causes increased frequencies of habitat edges, which can prove hostile environments for many species, as resource availability is modified, and travel becomes limited (Laurance and Yensen, 1991; Fig. 1). Characteristics of the resulting fragments, which can impact on biodiversity interactions, are determined by edge effects (changes in physical and biological conditions at boundaries of habitat fragments (Laurance, 2008). Microclimatic changes (eg changes in temperature, humidity, water fluxes and wind exposure) have been shown to cause elevated rates of tree mortality, damage, and canopy-gap formation in the Amazon (Laurance, 1991; Mesquita *et al*., 1999). The magnitude and penetration distance of these effects, varies in relation to the habitat type and species in question (Mesquita *et al*., 1999). According to Laurance and Yensen (1991), edge effects can penetrate between 15m and 5 km, with most significant changes occurring within 200m (Laurance, 1991).

Although not well studied, edge effects can have deleterious impacts on primates, since their capacity to find food and mates is directly affected by forest structure. Lianas are among the most successful colonisers of gaps, and although these can facilitate canopy travel in continuous forest, they have been shown to reduce rates of forest regeneration by inhibiting tree growth rates (Meijaard *et al*., 2005). Furthermore, changing resource conditions associated with edge effects, eg reduced seedling abundance and growth, directly impacts primates through reduced food availability (Laurance, 2008).

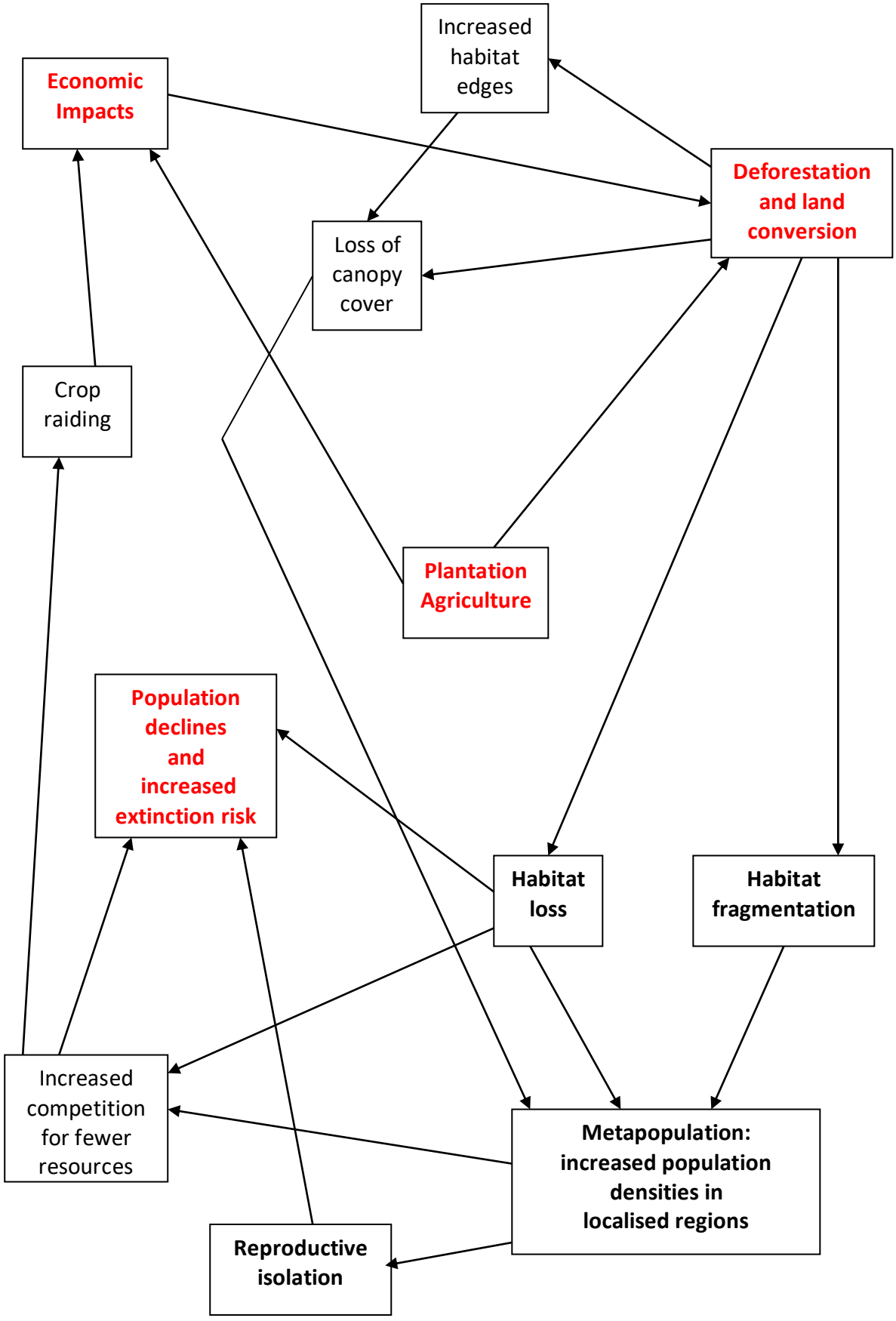

Fig. 1. Conceptual model showing the interactions between plantation agriculture and species declines

EXPLOITATION OF HUMAN-MODIFIED HABITATS

Southeast Asia, Africa and Latin America are the most vulnerable regions to land conversion, particularly for rubber, *Eucalyptus*, coffee and oil palm plantations (Hartemink, 2005; Barlow *et al*., 2007a; Cotter *et al*., 2009). Although some forest plantations such as *Eucalyptus* may, to some extent, offset some of the biodiversity losses from deforestation, little is known about the true conservation value of such homogeneous environments - especially since organism responses are taxon specific (Barlow *et al*., 2007a,b). Furthermore, primary, secondary and plantation forests show distinct community structure and composition (Barlow *et al*., 2007b); for example, oil palm plantations have been shown to support lower species diversity (Fitzherbert *et al*., 2008). These changes plantations are primarily due to lack of structural complexity, reduced canopy integrity, uniform tree age and height, and less stable microclimatic conditions (Fitzherbert *et al*., 2008).

One of the most significant repercussions is increased heterogeneity in the spatiotemporal distribution of food resources; this is particularly problematic for species with highly specialised diets eg frugivores. However some of the more disturbance-tolerant primate species exhibit dietary plasticity, manipulating their feeding strategies (eg from frugivory to folivory, or exploitation of agricultural crops) to compensate for changes in resource availability and abundance; this has been identified as a key factor in determining the potential for primates to persist following logging activities and subsequent expansions in agriculture (Meijaard et al., 2005). However crop raiding by primates has increased human-wildlife conflict (Brown and Jacob-son 2005; Nahallage *et al*., 2008); tolerance of crop raiding is limited, particularly where important cash crops are concerned, since they are a key driver of local economic growth in developing tropical countries. For example raiding of cocoa plantations by a fragmented chimpanzee subspecies (*Pan troglodytes schweinfurthii*) in the Hoima District of Uganda, resulted in deliberate catching and killing of chimpanzees (McLennan, 2008). Therefore investigating primate responses to agricultural expansion also carries implications for habitat management strategies, to mitigate human-wildlife conflicts (Fig. 1).

OIL PALM

The African oil palm plant (*Elaeis guineensis*) is one of the most rapidly expanding plantation crops in the tropics, and represents the most significant threat to it's biodiversity (Wilcove and Koh, 2010). Cultivated since the 1960s for use in food products and, to a less extent, as a biofuel to replace diesel, (Kalam and Masjuki, 2002; Murphy, 2007), oil palm has grown rapidly in production and economic importance. On a global scale, oil palm agriculture has increased from 3.6-13.2 Mha between 1961 and 2006, and is now cultivated in approximately 43 countries (Koh and Wilcove, 2008; Fig. 2).

Indonesia and Malaysia account for 85% of the global output, with plantations occupying 4.1 million hectares and 3.6 million hectares respectively (Carter et al., 2007; Koh and Wilcove,

2008). As the biggest single export earner in Malaysia, palm oil is a significant driver of both local and national economic growth (Kalam and Masjuki, 2002; Fig. 1. However Malaysia not only experiences the highest levels of oil palm production per unit area compared to Indonesia, but also the highest relative number of endangered species, making it of particular concern to conservationists (Bruhl and Eltz, 2010).

The tropical rainforests of Borneo are some of the most species-rich in the world, supporting many endemics as well as populations which have become extinct in other parts of their ranges - for example the Malayan Sun Bear and the Clouded Leopard (Crooks and Sanjayan, 2006). The island supports a high primate diversity, all of which are becoming increasingly threatened due to deforestation and habitat fragmentation. Despite its high conservation value, Borneo currently experiences ~3,122km^2 forest losses annually - much of this occurring in primary tropical peatswamp forest (Meijaard and Wich, 2007; Bruhl and Eltz, 2010; Koh *et al*., 2010). Understanding species' responses to habitat conversion to agriculture is vital to develop effective conservation and land management policies required to prevent local extinctions and minimise human-wildlife conflict in expanding agricultural landscapes. This is particularly important in Sabah, the leading state in Malaysia for total oil palm plantation coverage.

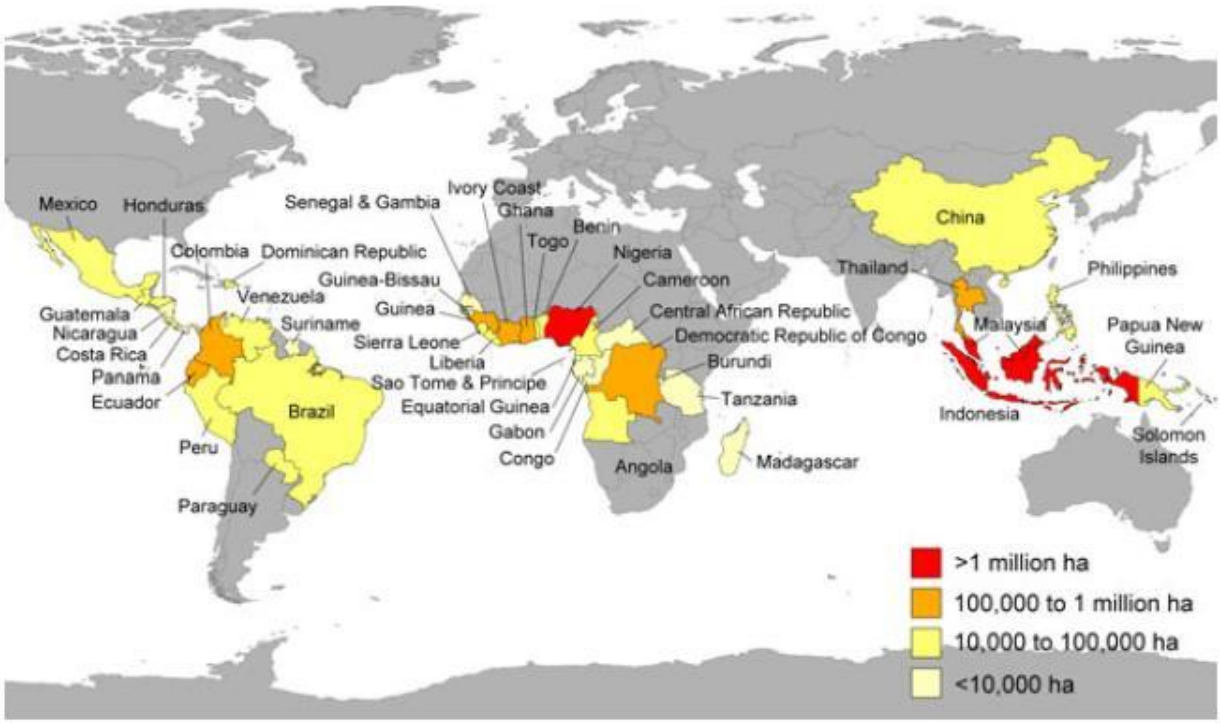

Fig. 2. World oil palm cultivation map (FAO, 2007; cited in Koh and Wilcove, 2008)

This expansion has mainly occurred in Sandakan – particularly in the Kinabatangan District, where total oil palm cultivation reached 265,111 ha in 1999 (31.4% of the total area cultivated with oil palm in Sabah) (Environmental Conservation Department], Sabah, 2002). This region supports many species which are particularly sensitive to habitat transformation: arboreal primates, and Asia's only great ape, the orang-utan (Pliosungnoen *et al*., 2010; Pozo-Montuy *et al*., 2011; Campbell-Smith *et al*., 2011). Despite this, oil palm coverage in Sabah continue to expand; in 2001, it was estimated that between one third and one half of the original forest area had disappeared (Goossens *et al*., 2005).

The present study aims to document primate responses to habitat fragmentation and oil palm plantations, in the Lower Kinabatangan Wildlife Sanctuary, Sabah. More specifically, this study will investigate whether primate densities are affected by edge effects, such as modifications to forest canopy integrity. It also documents which species are the most prevalent crop-raiders, and whether plantations are used as 'corridors' to travel between fragments of secondary forest, as a strategy to minimise demographic and reproductive isolation. Hypotheses to be tested are: (1) At habitat edges, primate densities will be higher in forest margins relative to plantation margins, or to the edge itself. (2) Encounter frequencies will be higher in forest fragments relative to habitat edges and plantation. (3) Encounter frequencies decrease as distance from edge into plantation increases. (4) Encounter frequencies will decrease with canopy density, limiting the potential for use of plantations as 'corridors'.

METHODS

STUDY AREA

The Lower Kinabatangan Wildlife Sanctuary (LKWS) is a mosaic of protected secondary forest, interspersed with oil palm plantations and Virgin Jungle Forest Reserves (VJFR), in the Lower Kinabatangan floodplain of eastern Sabah, Malaysia (Fig. 3). Gazetted in 2005 by the State Government of Sabah, the 26,000 ha Sanctuary is divided into ten forest blocks ('lots'); the aim of Sabah State Government is to link LKWS with VJFR (managed by Sabah Forest Department) as well as state- and private forest land, to create a network of continuous protected forest totalling approximately 51,000 ha (Bruford et al., 2010). Successful co-management between Sabah Wildlife Department, Sabah Forest Department and state- and private land owners, could carry huge conservation implications for the biodiversity of the Lower Kinabatangan floodplain. With habitats ranging from riverine forest, seasonally-flooded forest, swamp forest, dry dipterocarp forest and mangrove swamps, the Kinabatangan floodplain carries high biodiversity value, and is one of the most important wetland areas in Malaysia (Goossens et al., 2005; Bruford et al., 2010). Despite this, the forests are highly degraded and fragmented due to deforestation for timber and, more recently, extensive land conversion to oil palm plantations, and so also represent an important conservation priority for Sabah (McMorrow and Talip, 2001).

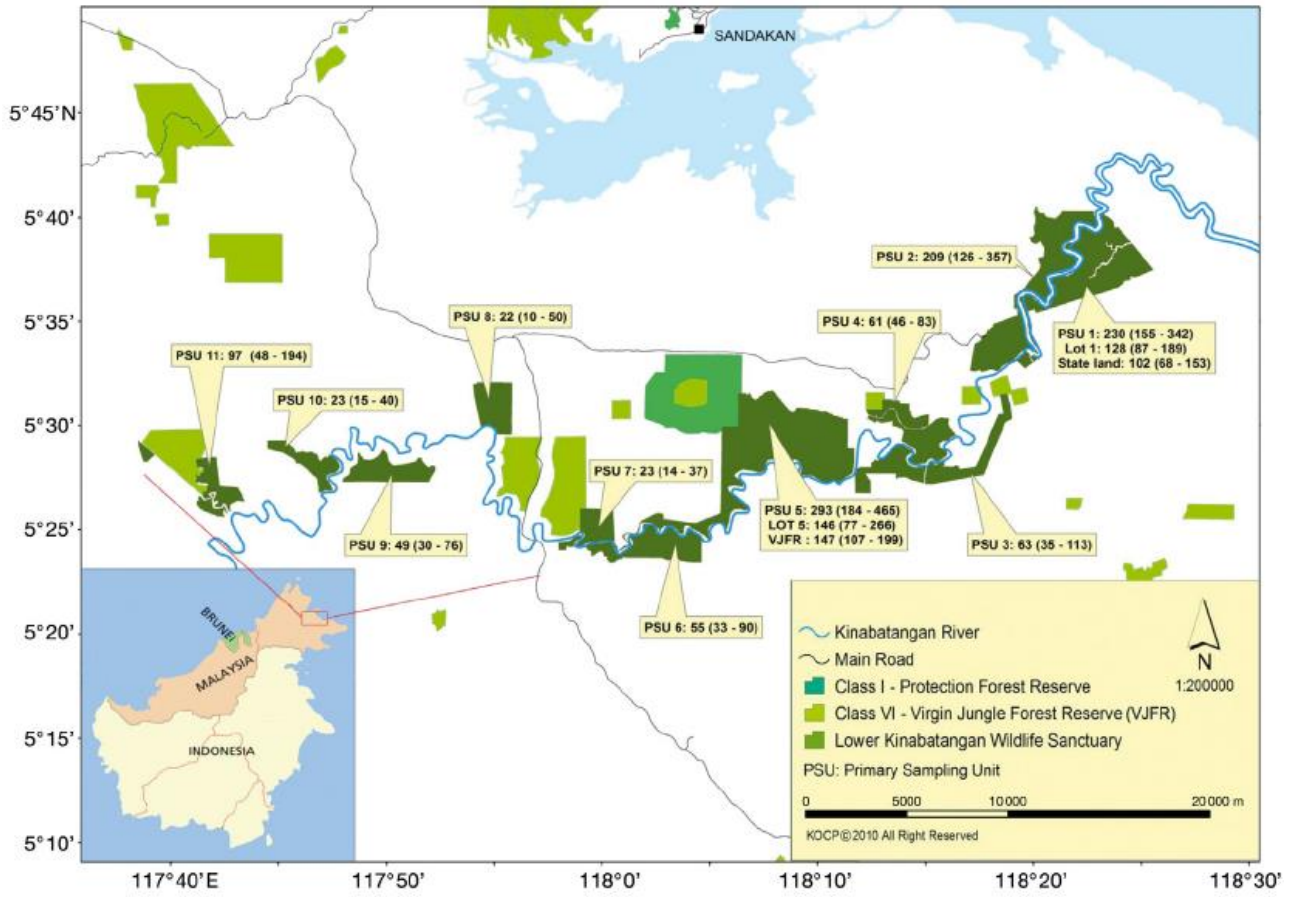

Fig. 3. Map of the Lower Kinabatangan Wildlife floodplain, showing the lots (Primary Sampling Units) of the Lower Kinabatangan Wildlife Sanctuary (LKWS), Virgin Jungle Forest Reserves (VJFR) and oil palm plantations. (Values refer to orang-utan populations and ranges). From Bruford *et* al., 2010.

The Lower Kinabatangan floodplain supports a high diversity of primates, all of which are decreasing due to deforestation and habitat fragmentation (IUCN, 2011b). One of the largest remaining populations of endangered proboscis monkeys exists here (Meijaard *et al*., 2008; Stark *et al.,* in press), as well as a metapopulation of 1125 Northeast Bornean orang-utans (*P. p. morio*) - a subspecies restricted to Sabah and East Kalimantan (Indonesian Borneo) (Ancrenaz *et al*., 2008; Bruford et al., 2010). Other species include: the maroon leaf monkey (Least Concern; IUCN, 2011b); and Hoses langur (*Presbytis hosei;* Vulnerable); silvered langur (*Trachypithecus cristatus;* Near Threatened; IUCN, 2011b); long-tailed macaque (*Macaca fascicularis* Least Concern; IUCN, 2011b); pig-tailed macaque (*Macaca nemestrina;* Vulnerable; IUCN, 2011b); the Bornean gibbon (*Hylobates albibarbis*); and two species of nocturnal primates, both classified by the IUCN (2011b) as Vulnerable with populations decreasing: the Bornean slow loris (*Nycticebus menagensis*) and the Western tarsier (*Tarsius bancanus*).

EXPERIMENTAL DESIGN

Four 500m line transects were randomly positioned in each of the three habitat types (forest, plantation and edge; Fig. 4); where possible, transects were situated perpendicular to- and a minimum of 150m away from the Kinabatangan river. Inkeeping with similar experimental protocol adopted by Delgado *et al*. (2001), transects were placed 200m apart at each site, to minimise spatial dependence of encounters.

For logistical reasons, plantation transects used roads already created in within the plantation itself (with the exception of one transect for which 150m meandered between the oil palm trees); this was to ensure transects were straight, and to avoid irrigation ditches. Forest transects were cut using a perang over two days prior to the start of the study, and left for a minimum of three days before surveying began to allow the effects of the disturbance to settle.

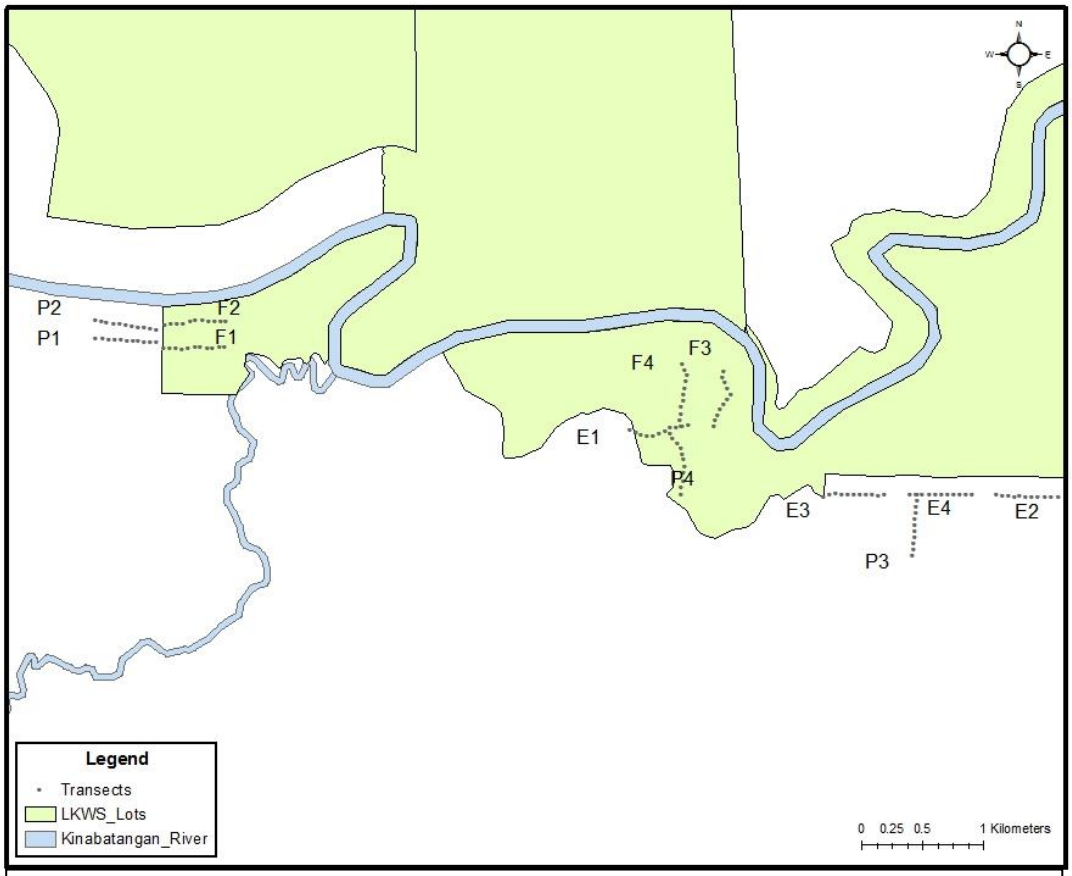

Fig. 4. Transect positions (grey dots) within the Lower Kinabatangan floodplain. White areas indicate oil palm plantation. (Projection: WGS 1984 UTM Zone 50N).

Two transects were walked each morning between 8am and 11am (and labelled as either 'AM1' or 'AM2'), with five repeats taken of each transect. GPS waypoints were taken at each primate encounter, together with species identification, observation type (visual or audio) and time, group size range and number observed, as well as perpendicular distance of the centre of the group from the transect (to within 50m, as in a study by Salter *et al*., 1985) and the side of the transect on which the group was located. Visual sightings were assumed to involve audio

encounters also. Where possible, additional notes on behavioural observations were recorded. GPS waypoints were then uploaded into MapSource®, in order to calculate the distance of each encounter to the habitat edge; since each forest and plantation transect began at the habitat margin, distance to habitat edge was calculated as the distance of each encounter waypoint to the transect start. These distances were then used to calculate encounter frequencies per 50 m, in forest and plantation habitat. Encounter waypoints were also used to calculate the shortest distance of each observed group to the Kinabatangan river. In order to catalogue general mammalian usage of each habitat type, waypoints were taken of footprints observed on transects, including taxa identification, and perpendicular distance from the transect.

HABITAT ANALYSIS

Habitat analysis was conducted for trees situated within 3m either side of the transects. Tree height was calculated by recording distance to the tree, from where a clinometer measurement was taken. This was done all the way down each transect (for trees with diameter at breast height (DBH) >10cm in forest), to calculate an average tree height for every 50m stretch of transect. Tree canopy density was calculated every 50m on all transects using a densiometer. To classify forest habitat type, understorey vegetation density was recorded every 50m along forest transects. A vegetation pole was used, marked with 50 black lines; the percentage of visible black lines was taken, and this value subtracted from 100 to ascertain the percentage of lines covered with vegetation. Trees with a DBH >10cm were identified to family level.

STATISTICAL ANALYSES

All statistical analyses were carried out in R (R Development Core Team, 2009) and P-values were significant at the 0.05 critical level.

Initially, the dataset was 'refined' by checking for collinearity between covariates using the 'car' library (Zuur *et al*., 2010). Highly correlated covariates were removed from analysis up to a threshold variance inflation factor (VIF) of 10 (Zuur *et al*., 2010). Remaining variables were used in a negative binomial Generalized Linear Model (GLM) to investigate which were the most significant predictors of primate encounter frequencies. This model type is an appropriate regression model for count data (Zeileis *et al*., 2007). Initially, a simple model was run using the model fitting function glm.nb() in the MASS package, consisting of the response variable (encounter frequency) and a single explanatory variable. The model was gradually made more complex by adding one variable at a time, and dropping any which proved to be non-significant, to produce a model which best described the data.

RESULTS

Six species of primate in five genera were recorded along 12 transects in the Lower Kinabatangan floodplain (Figs. 5-7): Eastern Bornean orang-utan, proboscis monkey, long-tailed macaque, pig-tailed macaque, silver langur and maroon leaf monkey. Just two of these species (long-tailed macaques and pig-tailed macaques) were encountered within oil palm plantations. Sampling took place over 30 days, totalling 90 hours of survey work, with a further 12 hours field work for habitat analysis.

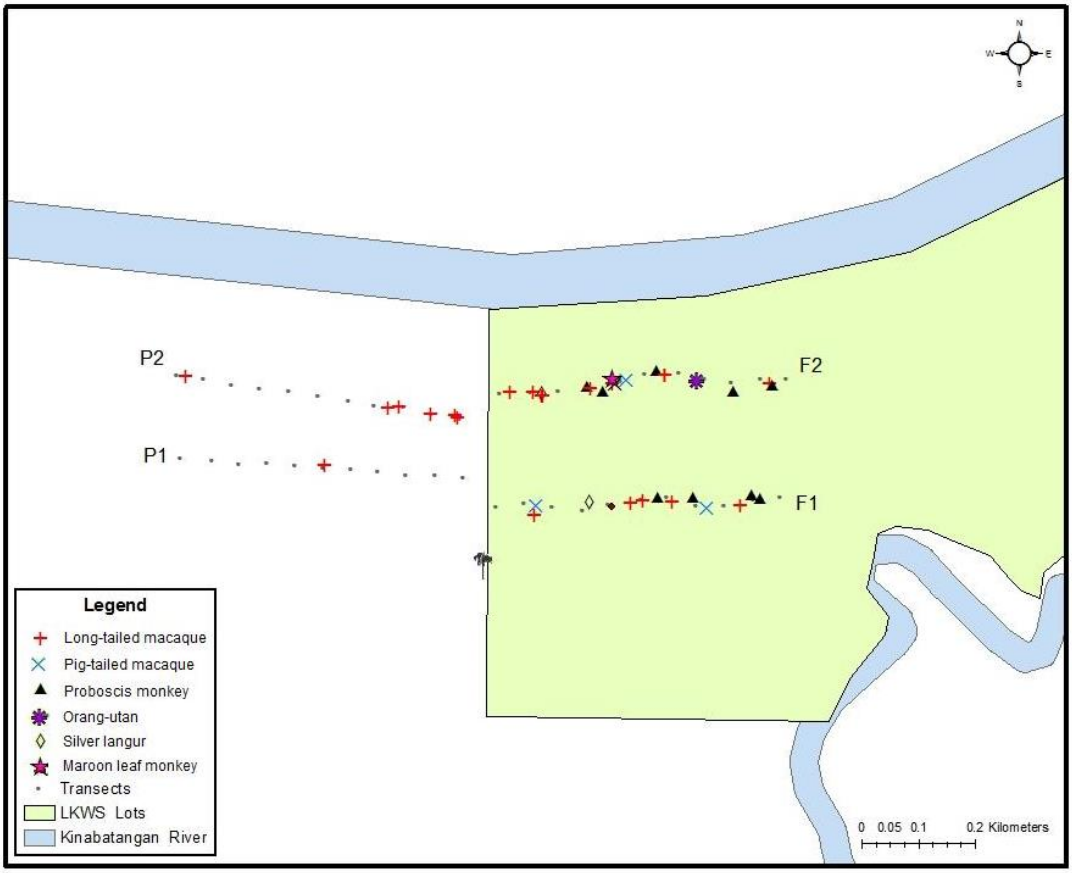

Fig. 5. Primate encounters in lot 7b of the Lower Kinabatangan floodplain. White areas indicate oil palm plantation. (Projection: WGS 1984 UTM Zone 50N).

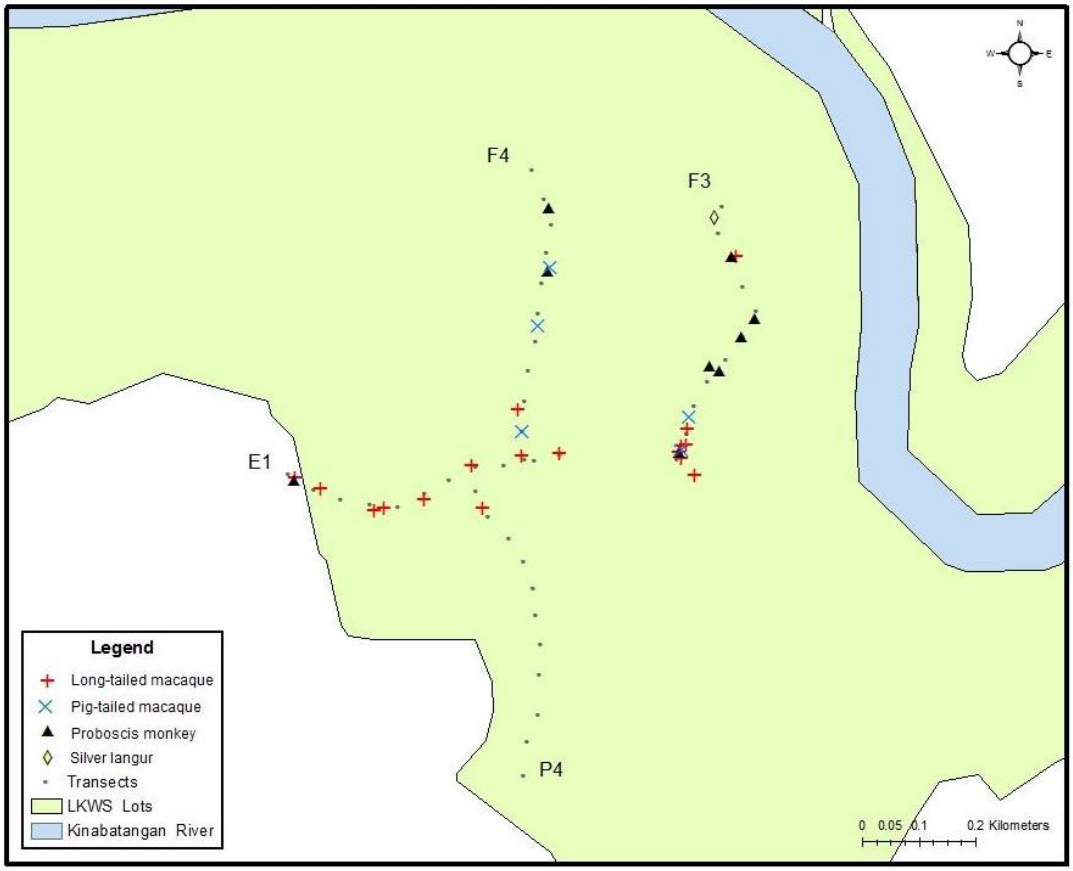

Fig. 6. Primate encounters in lot 6 of the Lower Kinabatangan floodplain. White areas indicate oil palm plantation. (Projection: WGS 1984 UTM Zone 50N).

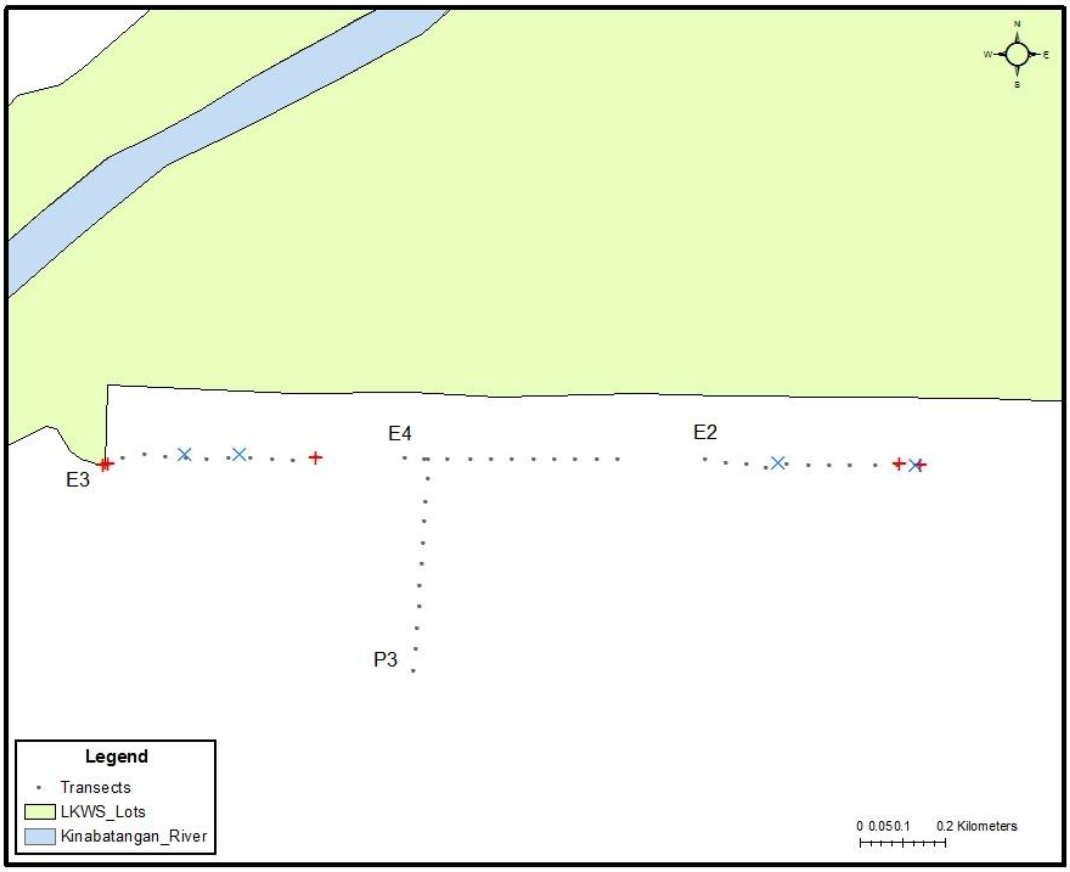

Fig. 7. Primate encounters in lot 6 of the Lower Kinabatangan floodplain. White areas indicate oil palm plantation. (Projection: WGS 1984 UTM Zone 50N).

A total of 78 encounters were recorded during sampling; of these, 53 were in forest, 17 at habitat edges, and only 8 in plantation. Long-tailed macaques were encountered most frequently (42 observations), followed by proboscis monkeys (21), pig-tailed macaques (10) and silver langurs (3); the orang-utan and maroon leaf monkey and orang-utan were encountered just once. Only long-tailed macaques and pig-tailed macaques were found to be present in plantations.

Primates were encountered along the entire length of forest transects with the exception of between 100-150m; however the frequency was highest in the first 250 m (Fig. 8). In plantation only one encounter occurred after 250 m (Fig. 9). All forest transects were situated in riparian secondary forests, since there was no significant difference in understorey vegetation density between transects (Anova; P=0.73). This result was also supported by tree species identification, where individuals of the *Lauraceae* family were dominant along each transect.

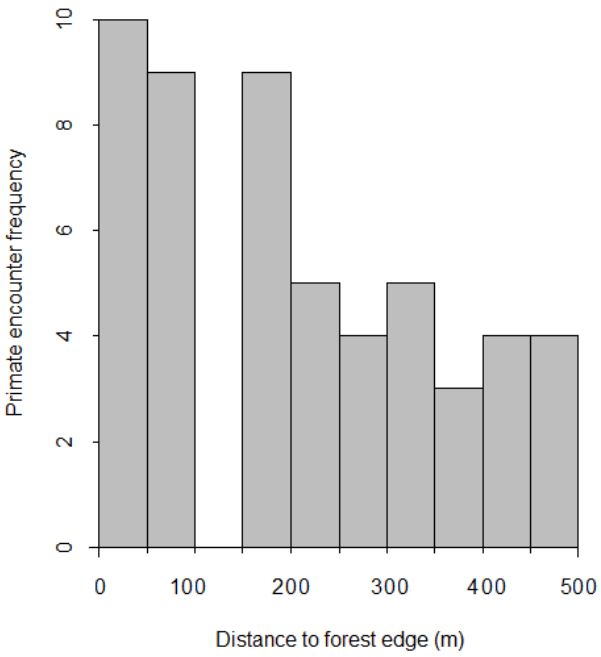

Fig. 8. Total number of primate encounters in disturbed secondary forests in the Lower Kinabatangan Wildlife Sanctuary (part of the Lower Kinabatangan floodplain), Sabah, as distance to the habitat edge (metres) increases.

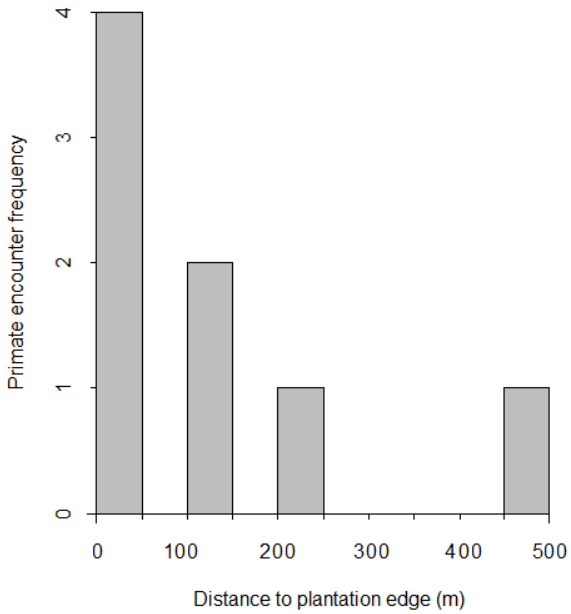

Fig. 9. Total number of primate encounters in oil palm, plantation in the Lower Kinabatangan floodplain, Sabah, as distance to the habitat edge (metres) increases.

Encounter frequencies were calculated every 50m along transects. Since the 'distance to edge' value would always be zero for edge transects, these were analysed separately; for these transects, perpendicular distance of each encounter to the edge transect was analysed, to get an overall impression of primate densities. At habitat edges, significantly higher densities of primates were observed in forest than plantation (Chi squared x_2 = 7.88, 3df, p=0.04; Fig. 10); suggesting that primate densities observed on either side of the transect were not random. All primates observed in forest margins (1-10m into forest) were further than 10m into the habitat, and all primates observed in plantation margins (1-10m into plantation) were observed no further than 10 m into the habitat.

NEGATIVE BINOMIAL REGRESSION

Encounter frequency was significantly lower in plantation relative to forest (P<0.0001; coefficient= -1.91; Fig. 10). Furthermore, distance from the habitat edge also had a significant affect on primate encounter frequency, and decreased as proximity to edge increased (P=0.001; -0.15). Canopy density was weakly non-significant (P=0.09; coefficient=0.02). Sampling day was not significant (P=0.918), therefore experience in detecting groups should not have introduced bias into the results. Because the overall sample size was too small (n=61) residuals couldn't be normalised (even following an arc sine transformation and run in a further GLM); therefore these results must be interpreted conservatively.

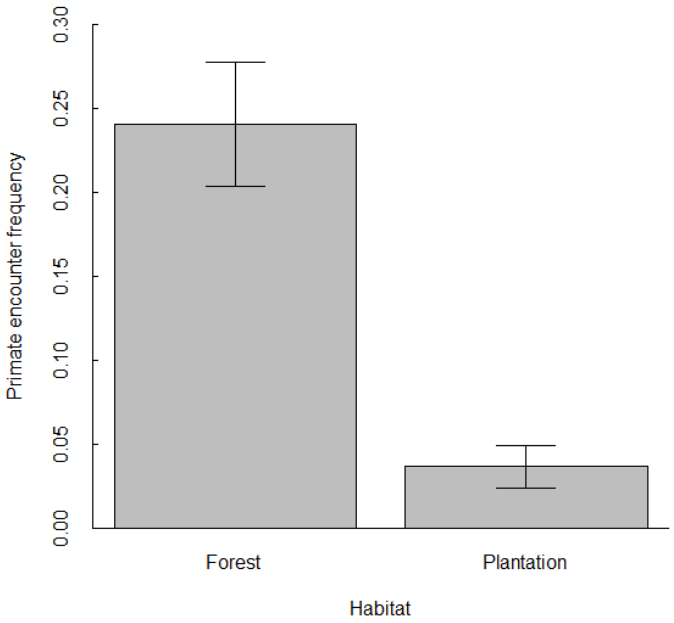

Fig. 10. Encounter frequency was significantly lower in plantation relative to secondary forest (negative binomial GLM; P<0.0001; coefficient = -1.91).

DISCUSSION

The five most prominent threats to the integrity of the world's biodiversity have been identified as either direct or indirect consequences of anthropogenic activity (COP 10 outcomes, 2010). Of these, four bear particular relevance to ecological and environmental issues facing the world's tropical rainforests: over-exploitation of wild flora and fauna, habitat loss and fragmentation, human population growth and pollution/climate change (Mepham, 2008; COP 10 outcomes, 2010). With 869 species forced into extinction in the last 500 years due to anthropogenic activities, and almost 17,000 plant and animal species currently threatened, uncertainty remains within the scientific community as to the optimum approach to mitigate current patterns of species extinctions and habitat loss (IUCN Red List Extinction List, 2007). This reiterates the importance of studies cataloguing species' responses to deforestation and fragmentation, since they can provide valuable information to facilitate the development of conservation and land management policies.

Although the present study highlighted some interesting drivers of primate distributions in human-modified landscapes, these unfortunately lack statistical integrity due to certain key limitations. I therefore feel it is necessary to address these first, before considering the broader context in which this study is placed.

LIMITATIONS TO THE INVESTIGATION

The most significant limitation to the investigation was a small sample size; this rendered statistical analyses ineffective in highlighting important drivers of primate distributions between plantation and secondary forest. Data deficiency arose primarily due to time constraints, and also to limitations associated with line transect surveys - particularly those which involve sampling social mammals. Although considered to be one of the most practical methods for sampling (Marshall *et al*., 2008), potential bias may be introduced if the same group is recorded more than once, either during one survey or between repeats. This is compounded further when sampling in disturbed, heterogeneous forest with low canopy density (where visibility and detectibility is limited and highly variable), and open, homogeneous plantation (Marshall *et al*., 2008). Visibility issues can be mitigated by estimating perpendicular distance to the group from the observer, however this is also difficult in secondary forest with dense understorey vegetation (Marshall *et al*., 2008).

The resulting dataset was subjected to thorough, although inconclusive, statistical testing. This included a zero-inflated negative binomial model using the pcsl package in R. This model is particularly suited to conducting regressions with zero-augmented count data - an occurrence which renders the classical poisson regression model of limited use (Zeileis *et al*., 2007). Zero-inflated regression was run using the function zeroinfl() in the pscl package, stipulating a negative binomial family, together with it's corresponding 'logit' link, using the following formula (Jackman, 2011):

```
model<-zeroinfl(yvar~xvar1+xvar2|xvar3+xvar4,data=mydata,dist="neg.bin",link="logit")
```

This reveals the parameters determining encounter frequency - which are conditional on (|) parameters which dictate whether an encounter event occurs. All parameters in the dataset

can be entered on both sides of the formula, which provides a more stringent assessment of the specific drivers of ecological processes (Zeileis *et al*., 2007; S Rushton, *pers. comm.*). However the zero-inflated model did not appear to be suitable for the present dataset, and would not run; again, a low sample size may have driven this outcome, meaning the ratio of encounters:zeros was too low.

A further GLM was attempted, for which an arc sin transformation was applied to the response. This model ran successfully and highlighted two particularly interesting variables as being (weakly) significant: proximity to the river (P=0.049) and lot (P=0.040). However, this model also presented problems: as with the negative binomial regression model, residuals could not be normalised; furthermore, interpreting why a power law would explain a particular response raises other issues in explaining the ecological process itself (S Rushton, *pers. comm.*), since the output no longer directly describes the actual events which occurred.

Further limitations encountered were primarily the effects of sampling in a highly fragmented landscape such as the Lower Kinabatangan floodplain. Although it should be noted that this type of environment is ideal for cataloguing responses of disturbance-sensitive taxa such as primates, heterogeneous land topography introduced several biases into the 'experimental design' and subsequent encounter frequencies. Since the plantations (many of which are above 20 years old) were developed much before the LKWS was gazetted in 2005, transects had to 'fit around' a pre-defined topographical layout. For example, it was initially intended that all transects would lie perpendicular to- and a minimum of 500m away from the Kinabatangan river; many primates, such as proboscis monkeys, long-tailed macaques and pig-tailed macaques, aggregate at riparian edges for roosting, and also as a predator-avoidance tactic (Sha *et al*., 2008; Matsuda *et al*., 2011). Ensuring all transects were equidistant from the river would have been one method of coping with this potential source of bias. However this was not always possible, due in part to the meandering of the river, but mainly because there was simply not always 500m of continuous habitat available. For example in lot 7, the plantation had been chopped down 471m from the river edge; this would accommodate neither the transect, nor the 150m gap from the river edge. Where the river meandered, such as near forest transects 3 and 4, one transect would have to be situated closer to the river edge; furthermore accessibility made it difficult here to situate forest transect 3 as far away as possible from the river edge, whilst still maintaining a minimum of 200m between itself and adjacent transect. In the case of transects alongside plantation edges, human-modification of the landscape made it difficult to position these where they would run in a straight line, and where the plantation, or part of it, had not been cut down. This was the case for edge transect 1, which was originally moved from lot 7 due to the plantation being cleared (see above); however one of the only other suitable areas it could be relocated to, also has experienced some (although less) cutting.

DRIVERS OF PRIMATE ENCOUNTER FREQUENCIES

The present study has highlighted some potentially interesting trends and significant predictors of primate distributions in fragmented and converted habitats. Although a larger data set is required to draw valid conclusions from these, several other studies have highlighted similar significant parameters which were alluded to in the present study - reiterating the need for longer-term research to see if these apply to the Kinabatangan situation.

It is becoming a universal truth that monoculture oil palm plantations support a considerably lower biodiversity compared to forest habitat (Marchal & Hill, 2009; Fitzherbert, 2008). Therefore results from the present study, of fewer encounters in plantation compared to secondary forest, and the suggestion that encounter frequencies increase with canopy density, alleviate some of the uncertainty surrounding issues with sample size. Canopy density has been positively correlated with group densities of the frugivorous, endangered Bare-face Tamarin (*Saguinus bicolor*) in Brazilian Amazonia, due to decreased conspicuousness to hawk and eagle predators (Vidal and Cintra, 2006). Decreased canopy density also reduces abundance of fruiting trees. Species such as leaf monkeys (including the proboscis monkey, silvered langur and maroon leaf monkey) have highly specialised diets, making them less-able to adapt in highly fragmented landscapes (Campbell-Smith *et al*., 2011); these species are therefore less likely to be encountered near plantations, as the present study highlighted - particularly when nutritious food resources are exchanged for tough, fibrous and unpalatable crops such as oil palm fruits (Campbell-Smith *et al*., 2011). Resource diversity is higher in forests by comparison, supporting a higher diversity of frugivores; the proboscis monkey, for example, feeds on fruits of the Lauraceae family - dominant on all forest transects; these quintessential tropical trees show predictable fruit production, and are second only to figs (*Ficus* sp.) in terms of their nutritional importance (LaFrankie, 2010).

Despite edge effects altering resource availability and canopy density, research has shown that primates are able to survive near plantation edges; for example one of the few remaining populations of bamboo lemur (*Latin name*) in Madagscar was found in forest at the periphery. The present study showed that, at habitat edges: higher primate densities were observed in forest- relative to plantation margins; this distribution pattern was not random, but determined by other ecological processes. Although habitat edges are associated with reduced resource availability and canopy density, this will still be higher in forest- relative to plantation margins. Furthermore, species demonstrating higher levels of dietary plasticity may be less prone to extinction in transformed habitats, and are thus more likely to be observed near plantations (Nahallage *et al*., 2008). This is reflected in my study, that all edge encounters except one (and all plantation encounters) were of the genus *Macaca*.

Furthermore, encounter frequencies were higher on the edge itself relative to plantation margin, and any observed on the plantation side were no more than 10 m away from the edge. This result suggests that primates don't venture too far into plantations, and once they leave, seek shelter further in the forest (Fig. 8). Consistent with this are observations from plantation transects, for which only one encounter was further than 250m into the habitat; this finding also suggests it is unlikely that primates use plantations as 'corridors' to travel between forest fragments, but simply to obtain food resources with are spatiotemporally predictable. Although this result must be treated conservatively, this may carry

implications with regards to working out exactly how we can reduce demographic and reproductive isolation in fragmented landscapes.

MITIGATING THE EFFECTS OF FRAGMENTATION

Managing the effects of oil palm agriculture is particularly interesting because of the wider socio-economic context in which the issue is placed. Palm oil provides a significant source of revenue for developing nations; as cultivation expands to match increasing demand (particularly in India, China and the West) (Wilcove and Koh, 2010), rates of species population declines and extinctions will only be exacerbated unless we find an effective compromise.

One current approach to facilitate human economic growth whilst preserving our fragile biodiversity, is establishing protected areas (PAs). There is debate within the literature as to the capacity for PAs to sufficiently reduce current rates of biodiversity loss. Some studies have cited PAs as one of the most important components of *in situ* conservation, since they can alleviate anthropogenic-induced threats to biodiversity by restricting human access (Chape *et al*., 2005; Gaveau *et al*., 2009). However, problems persist due to their limited coverage, vulnerability in areas of high deforestation rates and management issues (such as corruption of poorly-paid wardens) (Barlow *etal*., 2007b). Furthermore, many populations of threatened species currently exist outside of PAs; for example of the 11,000 orang-utans known to reside in Sabah, only 4,000 are within protected habitat (Ancrenaz *et al*., 2005).

Limitations surrounding PAs have facilitated growing interest in conserving human-modified landscapes such as plantations and secondary forest - a strategy that is listed in the Ecosystem Principles of the CBD (Barlow *etal*., 2007b). A new branch of conservation biology, coined 'reconciliation ecology' by Rosenzweig (2003), aims to encourage biodiversity in human-dominated landscapes. Secondary forest is of significant conservation value, due, for example, to high abundances of fruiting pioneer tree species, and have been shown to support a high diversity of primary forest species (Vidal and Cintra, 2006; Barlow *et al*., 2007b). Although exotic tree plantations can support some primary forest invertebrates where there is an understorey of native shrubs, they can only support to a few species of secondary forest primate (Barlow *et al*., 2007b; Fitzherbert *et al*., 2008). Primates are therefore less likely to benefit from reconciliation ecology, and is compounded by the clearing of plantations every 25-30 years.

These observations reiterate the need for effective conservation strategies to be taxon-specific. One approach to mitigate the effects of plantations on such disturbance-sensitive species that is currently gathering impetus in conservation planning, is to establish wildlife corridors to connect fragmented habitats (Newmark, 1996; Crooks and Sanjayan, 2006). Providing these zones remain protected from future expansions in oil palm agriculture, the potential exists to significantly reduce demographic and reproductive isolation, allowing dispersal between- and recolonization of fragmented sub-populations. For example, a VORTEX model designed by Bruford *et al*. (2010) showed that corridor establishment combined with translocation, could significantly reduce inbreeding and local extinction in isolated sub-populations of orang-utans in the Lower Kinabatangan floodplain.

Narrow riparian corridors are becoming increasingly common features in deforested landscapes of the humid tropics, and have been shown to be the most significant predictor of mammalian species richness (Lees and Peres, 2007). This is due in part to legislation that

stipulates a 20m buffer zone should exist between riverbanks and plantation edges, for rivers >30m wide (Environmental Conservation Department (2002). However narrow riparian corridors are ephemeral due to their vulnerability to natural river erosion, and may also exacerbate human-wildlife conflicts around plantations. The present study found higher encounter frequencies closer to river edges, and all plantation encounters occurred <300m from the riverbank. Therefore it could be argued that if the current 20m legislation were amended to increase riparian buffer widths, incidences of crop raiding may reduce since primate densities would be concentrated further away from the plantation edge.

Currently, research is lacking on optimum corridor width; existing small strips often do not contain enough forest habitat for many species, and are more vulnerable to edge effects (Lees and Peres, 2007). For rivers >10m, Lees and Peres (2007) recommend a critical-width threshold of 200m (either side) is necessary to maintain avian and mammalian species richness; this figure may need to be increased for large, arboreal primates, however, to maximise canopy cover and food availability.

RECOMMENDATIONS & FURTHER RESEARCH

Continued developments in global plantation agriculture means that deforestation and habitat fragmentation will continue to drive global patterns of species extinctions and population declines (Koh and Wilcove, 2010). As oil palm continues to expand, forests will become more and more fragmented unless previously-converted land is used instead (Fitzherbert *etal*., 2008). Habitat corridors are potentially a powerful tool in conservation planning, to increase connectivity and population viability in human-modified landscapes. However narrow riparian corridors may not provide a long-term solution to promoting connectivity in heterogeneous, human-modified landscapes; furthermore, more research is needed to determine optimum corridor width to maximise canopy cover and resource availability for arboreal primates.

The present study presented some interesting trends which should be investigated further, to generate statistically-valid conclusions about specific drivers of primate distributions in disturbed and fragmented habitats of the LKWS. In particular, more research is needed to investigate the affects of proximity to the river on primate abundances and crop raiding. Transects could be staggered away from the river, to analyse primate densities and interactions at riparian strips at the periphery of plantations. Each distance category would be fixed, and require more transects than were used in the present study. A second point of investigation would involve a direct comparison of primate density with primary forest (such as Danum Valley), would enable a more thorough and revealing analysis of the specific effects of plantation agriculture on primates in Sabah.

Combined, these studies could play an influential role in the development of detailed conservation programmes and land management strategies in Sabah. Many plantations in the Lower Kinabatangan floodplain are above 20 years of age, and approaching the time for clearing and replanting. This makes now an ideal time to push for legislation changes to riparian buffer widths and encourage the development of habitat corridors, to promote connectivity within the landscape; however to do this, we need to be able to present sound statistical analyses to prove that such proposals would benefit biodiversity of the LKWS, and effectively communicate the potential benefits to plantation companies.

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