Impact of logging on Paleotropical bat assemblages: What value do secondary forests hold for biodiversity conservation?

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ABSTRACT

Tropical forests around the world are being dramatically altered by human activities. Secondary forests are an increasingly common occurrence throughout the tropics. In Malaysia, unsustainable logging practices are resulting in the conversion of vast expanses of secondary forest to more profitable land-use such as oil palm agriculture. With more than half of Borneo's remaining forest cover in active timber concessions it is important to quantify what value these forests have with regard to biodiversity conservation before they are lost. To inform this goal this study sampled insectivorous bats, which forage in the forest understory, at ten forest sites across a disturbance gradient in Sabah, Borneo. Bat abundance was significantly lower in the most-disturbed sites than in the least-disturbed sites. Species richness did not change in association with the level of disturbance. Changes in the composition of the bat community were driven by three, tree-cavity and foliage-roosting, species: *Kerivoula papillosa; K. hardwickii* and; *Murina suilla*. *K. papillosa* is shown to be particularly vulnerable to logging-disturbance, whereas *K. hardwickii* and *M. suilla* benefit from it. This study found compelling evidence for retaining secondary forests as important tools in biodiversity conservation. It requests that the IUCN Red List status of *K. papillosa* be re-assessed. Finally it offers some broad recommendations with regards to future conservation of tropical rainforests and improving reduced-impact logging practices.

INTRODUCTION

Tropical forests around the world are being dramatically altered by human activities through industrial logging, fragmentation and clearance for agriculture (Achard et al. 2002). This has led to renewed debate regarding the value of disturbed forests for wildlife: a debate that has important implications for conservation management. Dirzo and Raven (2003), for example, predicted that 50-75% of tropical species could face extinction this century if high deforestation rates persist. On the other hand, Wright and Muller-Landau (2006) claim that extinction and deforestation estimates are too high and that the outlook for tropical biodiversity is not quite as catastrophic as projected. Such predictions usually rely on Species Area Relationship (SAR) models and the former viewpoint assumes that secondary forests have near-zero value for biodiversity conservation (Laurance and Wright 2009). The opposing view held by Wright and Muller-Landau (2006) assumes that old growth and secondary forests hold the same value for biodiversity. It is widely accepted that we are facing an extinction crisis of some sort so if we are to influence management that will dampen the effects on tropical wildlife, it is important to quantify the value of secondary forests for biodiversity conservation and determine the species that are most at risk (Dent and Wright 2009).

The extent of disturbed and fragmented forests is rapidly increasing in Southeast Asia (Koh 2007; Koh and Sodhi 2010), where rates of deforestation are proportionally higher than elsewhere in the tropics (Bradshaw et al. 2009). Secondary forests account for the majority (67.5% , 129 million ha) of native forest cover in Southeast Asia (Koh 2007). Critically, unsustainable logging practises are reducing the economical productivity of poorly managed concessions (Dennis et al. 2008) which increases the pressure for conversion of these forests to more profitable land-use, such as oil palm (Fitzherbert et al. 2008; Koh and Wilcove 2009; McMorrow and Talip 2001). Half of the forests in Borneo are in active timber concessions, so there is a need to develop more sustainable management and better include these disturbed forests in conservation strategies (Meijaard and Sheil 2007). Unfortunately, substantial information on the biodiversity value of these forests relative

to old growth forests is still lacking despite many years of tropical biodiversity research (Chazdon et al. 2009).

Disturbance events are expected to result in a reduction of species diversity (Berry et al. 2010; Edwards et al. 2010; Magurran 2004; Peh et al. 2005; Wells et al. 2007). Berry et al (2010) showed that disturbed forest on Borneo typically contained >90% of species found in old growth forest, but notably this study did not include bats in the analyses. Despite a multitude of logging-impact studies in Southeast Asia (Sodhi et al. 2009), very few have focussed on bats. Bats are considered to have great potential as bioindicators (Jones et al. 2009). They perform important ecosystem services such as seed dispersal (Fujita and Tuttle 1991), pollination (Fleming et al. 2009; Hodgkison et al. 2003), and help to control invertebrate populations (Cleveland et al. 2006; Williams-Guillen and Perfecto 2008). Bat communities form predictable assemblages that can give insights into the structure of their surrounding habitat (Hodgkison et al. 2004; Kingston et al. 2003). Wing morphology (Norberg and Rayner 1987), roosting ecology (Struebig et al. 2008) and echolocation characteristics (for microchiropterans) (Kingston et al. 1999; Schnitzler and Kalko 2001) are all considered to be important in predicting the sensitivity of bat species to disturbance events. For example, bat species that roost in tree cavities or foliage, have rounded wing tips with low-wing loading and low aspect ratio, and highly specialised echolocation calls for finding prey in cluttered environments, may be particularly vulnerable to forest degradation (Kingston et al. 2003; Struebig et al. 2008).

Most studies investigating the effects of habitat disturbance on bats have been done in the neotropics, where a) some bat assemblages can show predictable declines in species richness and abundance (Fenton et al. 1992; Medellín et al. 2000; Peters et al. 2006), b) some species may actually benefit from disturbed successional forest (Willig et al. 2007) or c) bats may remain largely unaffected within sustainable, well-managed logging concessions (Clarke et al. 2005). However, these findings are not necessarily indicative of how paleotropical bat communities may respond to forest

disturbance, since bat communities in the old world tropics are structured differently to those in the neotropics (Kingston et al. 2003). To date only four studies have assessed the impacts of logging on bats in Southeast Asia. Danielson and Heegaard (1995) and Zubaid (1993) limited their sampling effort to using mist nets, and in a recent study by Fukuda et al (2009), harp traps were not systematically used and as a result, many Kerivoulinids and Murinids that are otherwise common in Southeast Asian forests were notably absent from all habitat types in their studies. The use of harp traps in Southeast Asian forests is essential in order to successfully sample insectivorous bats of the forest interior (Kingston et al. 2003). A recent study into the effects of forest disturbance on bats in Vietnamese limestone karst areas accounted for this bias by including a high proportion of harp trapping in their sampling (Furey et al. 2010), but low capture rates limited the power of their analyses to detect statistically significant responses to logging. Together, these studies have provided the foundations to develop a more detailed and informative study of the effects of forest disturbance on Southeast Asian bat communities.

This study focussed on one group of insectivorous bats that forage in the forest understory known collectively as the narrow-space bats. In Southeast Asia, insectivorous bats belonging to the families Nycteridae; Megadermatidae; Rhinolophidae; Hipposideridae; and the Vespertilionidae sub-families Murininae and Kerivoulinae contribute the majority of species that make up the narrow-space bats. These bats are predicted to be particularly sensitive to the effects of habitat disturbance (Furey et al. 2010; Kingston et al. 2003). They can be divided into two subgroups: cave-roosting species and; species that roost in tree cavities and foliage (referred to as foliage-roosting bats in this paper) (Struebig et al. 2008). It is important to clarify these predictions and to quantify what constitutes an irreversible level of disturbance in terms of a loss of narrow-space bat diversity. The prediction of a 40% decline in Southeast Asian bat diversity by 2100 with current habitat destruction rates (Lane et al. 2006) reinforces the importance of that need (Kingston 2010).

The specific aims of this study were to:-

1. Sample insectivorous bats of the forest understory in ten rainforest sites in Sabah, Borneo. Effort was directed at one guild of bats to maximise the explanatory power of any findings.

2. Determine a gradient of disturbance across these rainforest sites using environmental variables. Forest sites were classified as old growth or secondary forest in the analyses.

3. Relate the level of disturbance to changes in abundance, species-richness and species composition of narrow-space bat communities, with particular reference to the foliage-roosting bats. The foliage-roosting bats are dependent on the forest as both a foraging and roosting environment. Therefore it is likely that they are particularly sensitive to changes in forest structure.

4. Collect important baseline data for a future fragmentation study as part of the Stability of Forest Ecosystems (SAFE) project. Six of the sites sampled in this study will become fragments within an oil palm development, commencing November 2011 (SAFE 2011).

METHODS

STUDY SITE:

The study took place in Sabah, Borneo, between 28th March and 31st July 2011, as part of the SAFE project. The SAFE project is a multi-disciplinary study investigating a whole suite of ecological patterns and processes across a forest disturbance gradient (old growth, secondary, forest fragments, riparian strips and oil palm plantations). This study sampled insectivorous bat communities at 10 SAFE project sites which represent a disturbance gradient from old growth forest, through once-logged forest into heavily disturbed, 2-3 times logged forest (figure 1). All 10 sites are located within a one million hectare expanse of contiguous rainforest, the majority of which is within timber concessions belonging to the Yayasan Sabah Group.

Two of the 10 study sites were located in the old growth forest of the Maliau Basin Conservation Area (MBCA), which lies in the southern central region of Sabah. MBCA was designated as a

conservation area in 1981 and was upgraded to a Protection Forest Reserve (*Class I*) in 1997. MBCA comprises 58 800 hectares of old growth rainforest that has, in the most part, never been logged – largely because the site is inaccessible to logging due to the difficult terrain. However, one of the study sites within MBCA was lightly logged in the mid-1990s (figure 1c) to provide timber for the construction of a research centre. This site is still representative of old-growth forest in both vertical structure and species composition of the canopy and understory (SAFEproject unpublished data). The other eight sites located in the Kalabakan Forest Reserve were selected and matched for topography and elevation (200-500m) and represent a gradient of disturbance, from undisturbed through to heavily disturbed rainforest.

Sampling Design

Four-bank harp traps were used to target insectivorous bats that forage in the forest understory.

Three transects contributing 14 trap positions each were sampled at every site. There were 42 trap positions per site, giving a total effort of 420 harp trap nights. Traps were set for a single night and were typically ca. 50m apart along trails, streams and other flyways, which bats use for travelling and foraging (Francis 1989). Transects ran through and between SAFE sampling points, where detailed environmental data was collected by other researchers on the SAFE project. Supplementary environmental data was collected at each trap location. Transects were arranged in the same spatial pattern (figure 2) with the exception of two sites (C & D). Crucially, the length of each transect was comparable; each being approximately 600m in length.
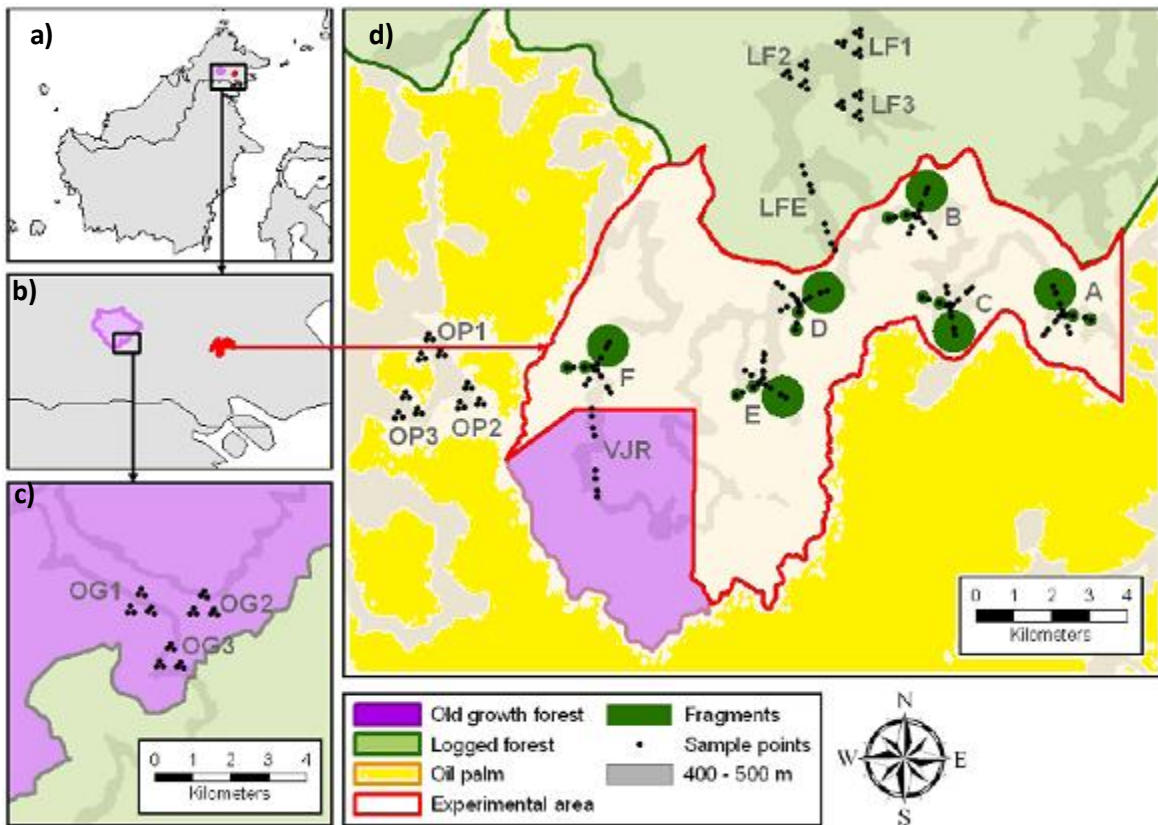
Figure 1. SAFE project overview. a) Borneo. b) Maliau Basin Conservation Area (MBCA) in purple, SAFE experimental area in red. The two sites are connected within a 1million ha tract of forest, the majority of which is in active logging concessions. c) Old Growth forest sites of the SAFE project. This study sampled at OG2 and OG3. OG3 was lightly logged in the 1990s but remains representative of primary old-growth forest. d) The SAFE project experimental area located 60km to the East of MBCA, in a 1million ha block of forest. The area outlined in red represents a 7,900ha tract of twice-logged forest, which will be cleared and converted to oil palm in late 2011. Sites A-F will remain as fragments within the oil palm estate after the clearance event. These sites represent twice-logged forest that is largely heavily disturbed but sites were quite variable in forest condition. Two sites to the North of this area were also sampled (LFE and LF2). These two sites were less-disturbed than sites A-F. Figure reproduced by permission from the SAFE project, Imperial College London.

Bat Sampling

Insectivorous bats that forage in the forest understory (the narrow-space bat guild) are most commonly caught in harp traps (Francis 1989; Kingston 2009). In order to adequately sample other guilds of bats, different methods are required. Therefore any captures of bats that belong to a different guild were removed from subsequent analyses as the sampling methods used in this study are only appropriate for effectively sampling insectivorous narrow-space bats.

Harp traps were set 0.5-1.5m off the ground along access trails, streams and flyways. Where needed, vegetation was cut, off-trail, and used to close any gaps around the trap in order to funnel bats into it (Struebig and Sujarno 2006). Seven traps were set each night before sunset and checked at 20:00 and then again at 07:30 the following morning. Insectivorous bats exhibit two peaks of foraging activity, which follow peaks of insect activity, for 1-2 hours after sunset and 1-2 hours before sunrise (Kingston 2010). Bats were identified by external features and measurements following an identification key based on Payne & Francis (1985) and updated by M. Struebig (Struebig and Sujarno 2006). Age, sex and reproduction status was determined. To reliably identify recaptured individuals, wing biopsies were taken using a 3mm biopsy punch, on the right wing between the 2nd and 3rd digit.

Weather conditions were unpredictable throughout the survey period and there was an unusually high occurrence of rain for the 'dry' season in Borneo (April-October). However, rain was only considered to have had an effect on two survey nights. On both occasions the capture rate dropped significantly below the expected minimum encounter rate of 2 bats per trap (i.e. 14 bats per 7 traps). On both occasions, traps were re-set the following evening 5-10 m from their original position. When it rains, water droplets collect on the strings of the harp traps potentially making it more visible to bats due to the thickness of the strings being increased. Therefore moving the trap removes any possible trap-avoidance behaviour from bats that have potentially learnt where the trap/obstacle is.

Environmental Data

Four environmental variables were collected to serve as proxies for forest disturbance. Preliminary analysis indicated that two of these were not suitable for determining a gradient of disturbance (see Appendix A). The two variables used in analyses were canopy height and canopy openness. At each trap position, canopy height was estimated and given a score of 0-4 (where; 0=<5m; 1= 5-10m; 2= 10-20m; 3= 20-30m and; 4= >30m). Canopy openness was measured using a spherical canopy densiometer. Measurements were taken at 18 points within a ca. 56mx734m area in which each harp trap transect was located. The spatial arrangement of sampling points is based on fractal geometry and was the same for each transect (see Appendix B for further information). Four readings were taken (N, E, S, W) in each location and the mean value used to give a canopy-openness score (where; low scores = closed canopy and; high scores = open canopy).

Two further environmental variables were recorded to explore species-environment relationships but were not used to classify disturbance. Understory (0-3m) clutter was scored 1-5 (where 1 = open, little or no understory vegetation and 5= dense, impenetrable understory vegetation) within a 5m radius surrounding each trap. Number of streams within a 15m radius of each trap was recorded.

Data Analysis

Disturbance Gradient

Canopy openness and canopy height were strongly negatively correlated with each other (r = -0.871, n=30, p<0.001). For this reason, they were used separately to give two possible disturbance gradients. The disturbance gradient for canopy height was obtained using the mean value per transect. Although it is not common practice to use the mean of categorical data, the categories were continuous and fairly evenly-spaced. Using the median was considered but based on observations in the field, the mean values seemed more representative of the disturbance gradient as they also illustrate the variability of forest structure at sites. Furthermore the mean values were

highly correlated with the SAFE forest-quality score (appendix A). Mean canopy openness score per transect was used as the second disturbance gradient. Both sets of data were used independently to illustrate the relative accuracy of the canopy height method.

Abundance of bats

To assess whether the abundance of foraging bats was affected by disturbance levels, linear regression was performed in PASW Statistics18 (SPSS) using the Log10 transformed data on the abundance of narrow-space bats per transect and two different predictors of disturbance (canopy height and canopy openness).

Species Richness

Differences in observed species richness between sites were investigated by constructing individual-based rarefaction curves using EstimateS vers 8.2 (Colwell 2006). Inputted data were computed analytically using the formulae of Colwell et al (2004). Species richness was plotted as a function of the accumulated number of individuals. To compare richness between sites, curves were reduced to a common sample size and 95% confidence intervals for the most disturbed and least disturbed sites were plotted separately to assess whether any sites lay outside of these limits. To further assess potential site-level differences in species diversity, Simpson's reciprocal diversity index (1/D) was calculated. Assemblage evenness ($E_{1/D}$) was determined by dividing index values by S (number of species) (Krebs 1999).

Community analyses

Ordination techniques were employed to relate species abundance data to the environmental variables using the software programme CANOCO. The gradient length in the species composition data, which was determined using de-trended correspondence analysis (DCA), was short (<2) so a linear ordination method was required. Redundancy Analysis (RDA), constrained by environmental

variables, was used (Leps and Smilauer 2003). Assemblage data are often largely composed of rare species. Removing some of these species can improve our ability to detect important species-species and species-environment relationships (McCune and Grace 2002). For this reason, several ordinations were performed, initially including all bat species before separating the assemblage data into guilds and relatively common individuals. A species was considered rare if it was represented by fewer than five individuals because it could not be present at more than half of the sites in the study. Species were also considered rare if they were only recorded in one site as their abundance could not be related to the disturbance gradient being used. Species-species associations were explored further using Spearman's correlation in PASW Statistics18 (SPSS). Environmental variables (canopy height, canopy openness, number of streams per transect, and understory clutter) were added to the ordination and their relative importance was investigated by assessing their correlation coefficients. Streams were not included in the final ordination because they were not found to be having any influence on the bat observation data and CANOCO identified streams as being slightly correlated with understory clutter, which had no biological explanation.

Habitat Associations

Generalised Linear Models, for Poisson distributions, were built using CANOCO to investigate species-axis associations (constrained by environmental variables). Habitat associations of species exhibiting strong axis-associations, and species for which there were >30 records, were explored using General Linear Models with the environmental variables, in PASW Statistics18 (SPSS). Species abundance data was log10 transformed to achieve normal distribution.
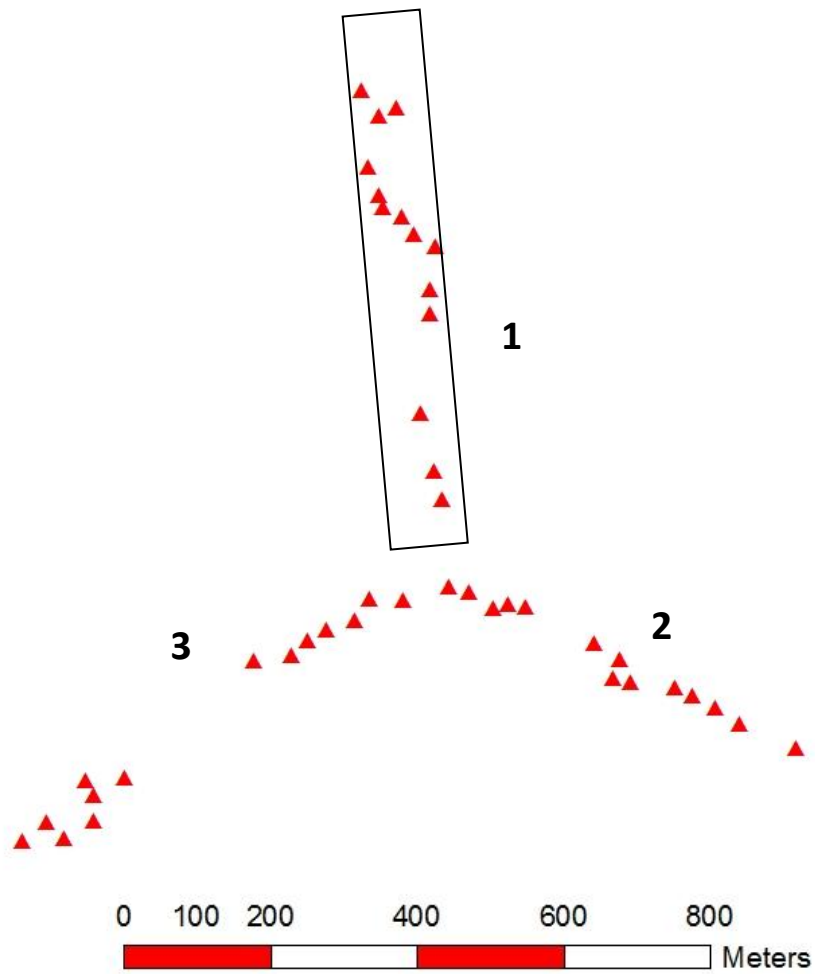
Figure 2. Layout of harp trap transects at a disturbed forest site in Sabah, Borneo (site B is displayed). Triangles indicate harp traps. The rectangle represents the ca.56m x 734m area in which canopy densiometer readings were taken. This layout was typical across most of the sites.

RESULTS

Disturbance gradient

Two disturbance gradients were determined: one using canopy height and; one using canopy openness (Table1). The least disturbed site was OG2 which is the only site that has never experienced any logging. The most heavily disturbed site was site C. This site had the second lowest and most open canopy. Sites A, C, E and F were also more variable than the other sites despite all being referred to as 'twice-logged' forest (Table1 – SE), which indicates the patchy nature of logging activities. All regression analyses were performed using transect-level data, so this patchiness was reduced when considering the effects of disturbance on bat communities.

Bat Abundance

A total of 1390 insectivorous bats, representing 32 species were captured over the course of 420 harp trap nights at the 10 sampling sites. Of these bats, 28 species, comprising 1349 individuals were classified as narrow-space bats; 8 of these species, comprising 551 individuals were cave-roosting bats and; 17 species comprising 798 individuals were foliage-roosting bats (table 2). The remainder were edge and open-space species (4species; 41 individuals) and were excluded from analyses due to the sampling methods being unsuitable for adequately sampling these bats.

At the transect level (n=30), total abundance of narrow-space bats was influenced by both canopy height and canopy openness. Narrow-space bat abundance was typically lower at sites with a lower, more open and fragmented canopy (figure 3a). At sites with a high canopy, narrow-space bat abundance increased (figure 3b). This relationship disappeared when cave-roosting bats were removed from the analyses suggesting that they were having a disproportionate effect on the assemblage signal detected. Old growth forest sites (n=2) contributed 42% of cave-roosting bat observations in the whole study (n=10). Foliage-roosting bat abundance was similar across all sites,

except for block F and LF2, however total abundance of narrow-space bats was still comparable to other sites.

Species Richness

For all narrow-space bat species, the sample based rarefaction curves for most sites fell within the 95% confidence intervals for block C, which was one of the most heavily disturbed sites (figure 4a). Only the curve for block F lay outside the lower 95%confidence interval. This was not considered to be significant, in terms of disturbance, because Block F was characterised as being moderately disturbed. The foliage-roosting bat species rarefaction curves for all sites fell within the 95% confidence intervals of OG2, which was the least disturbed of all the sites (figure 4b). Furthermore, there was no clear pattern between the level of forest disturbance and foliage-roosting bat species richness (figure 5). Cave-roosting bats were not considered separately as there was no data available on the presence/absence or abundance of caves for any of the sites, which is likely to be a major contributor to cave-roosting bat species richness.

The lack of a predictable trend in foliage-roosting bat species richness along the disturbance gradient was mirrored in indices of species diversity. Block E (heavily disturbed) and LFE (moderately disturbed) had the highest reciprocal Simpson's diversity index ($1/D$ = 5.8 each) and OG2 (not-disturbed) had the lowest ($1/D$ = 3.8). These differences are not explained by level of disturbance. Estimates of assemblage evenness ($E_{1/D}$) were similar across all sites (table2).

Table1. Forest disturbance gradient as defined by two different environmental variables: Estimated canopy height and; spherical densiometer, canopy openness readings. The disturbance level increases from left to right. Canopy height values are given as the mean estimated height score (n=42 per site). Canopy openness are given as the mean spherical densiometer reading per site (n=54 per site). Standard errors (SE) are presented below the mean.

| Variable	Site ID									
	OG2	OG3	LF2	LFE	F	D	B	A	C	E
Canopy Height	2.58	2.49	2.1	1.43	1.38	1.12	1.02	0.95	0.95	0.71
CH Standard Error	0.01	0.20	0.05	0.04	0.23	0.086	0.06	0.13	0.26	0.24
	OG2	OG3	F	LF2	LFE	B	A	E	D	C
Canopy Openness	4.55	6.0	11.23	12.43	13.96	19.76	20.42	22.54	22.77	23.51
CO Standard Error	0.86	0.93	2.64	0.98	1.03	0.96	2.16	5.4	1.10	3.35

Table 2. Narrow-space bat species composition, abundance and diversity for 10 sites sampled in Sabah, Borneo. OG2 and OG3 were located within Maliau Basin Conservation Area. The other 8 sites were located in the Kalabakan Forest Reserve, all within a Yayasan Sabah logging concession ca. 60km east of MBCA. Sites are ordered from left to right with decreasing canopy height (increasing levels of disturbance).

Taxon (family; species)	Species abb.	OG2	OG3	LF2	LFE	F	D	B	A	C	E
Hipposideridae											
Hipposideros ater [c]	Hiat	10	5								
Hipposideros cervinus [c]	Hice	56	56	36	19	36	8	31	2	37	8
Hipposideros diadema [c]	Hidi	2	2		1						
Hipposideros doriae [f]	Hido				3						
Hipposideros dyacorum [c]	Hidy	22	14	2	1	32	1		12	1	6
Hipposideros galeritus [c]	Higa	2	1		1			2	1		
Hipposideros ridleyi [f]	Hiri		3	1	11		1	2	8	2	3
Nycteridae											
Nycteris tragata [f]	Nytr	1	2		1				2	1	2
Rhinolophidae											
Rhinolophus acuminatus [c]	Rhac	10	2								
Rhinolophus borneensis [c]	Rhbo	14	34	7	4	7	1	5	5	10	7
Rhinolophus creaghi [c]	Rhcr			22							
Rhinolophus sedulus [f]	Rhse	8	4	3	12	2	8	14	8	7	12
Rhinolophus sp. * [f]	Rhsp	1	1								
Rhinolophus trifoliatus [f]	Rhtr	9	15	3	6	14	1	12	6	18	8
Vespertilionidae											
Kerivoula hardwickii [f]	Keha	4	4	3	13	11	1	17	10	19	22
Kerivoula intermedia [f]	Kein	41	31	17	26	11	3	30	34	12	21
Kerivoula minuta [f]	Kemi									1	
Kerivoula papillosa [f]	Kepa	24	21	10	3	5	4	7	3		
Kerivoula pellucida [f]	Kepe	4	7	14	2		3	1		2	4
Harpiocephalus harpia [f]	Haha										1
Murina aenea [f]	Muae	1	2		1						
Murina cyclotis [f]	Mucy		4		1	1	1		4	3	3
Murina rozendaali [f]	Muro			1					2	1	
Murina suilla [f]	Musu	2		1	3	9	5	2	10	4	9
Phoniscus atrox [f]	Phat	2							1	1	
Total Abundance		214	211	120	110	145	1	125	112	127	107

Table 2 continued

Taxon	Species	OG2	OG3	LF2	LFE	F	D	B	A	C	E
No. of species [f]		13	8	12	9	10	7	9	13	11	11
Simpson's diversity index (1/D) [f]		3.8	5.1	4.6	5.8	5.1	4	4.6	5.2	5.5	5.8
Evenness ($E_{1/D}$) [f]		0.4	0.6	0.5	0.5	0.6	0	0.5	0.4	0.3	0.5

Cave-roosting bats [c], foliage-roosting bats [f] and un-described species *(closely related to Rhtr and Rhse in morphological features so same ecological niche assumed).
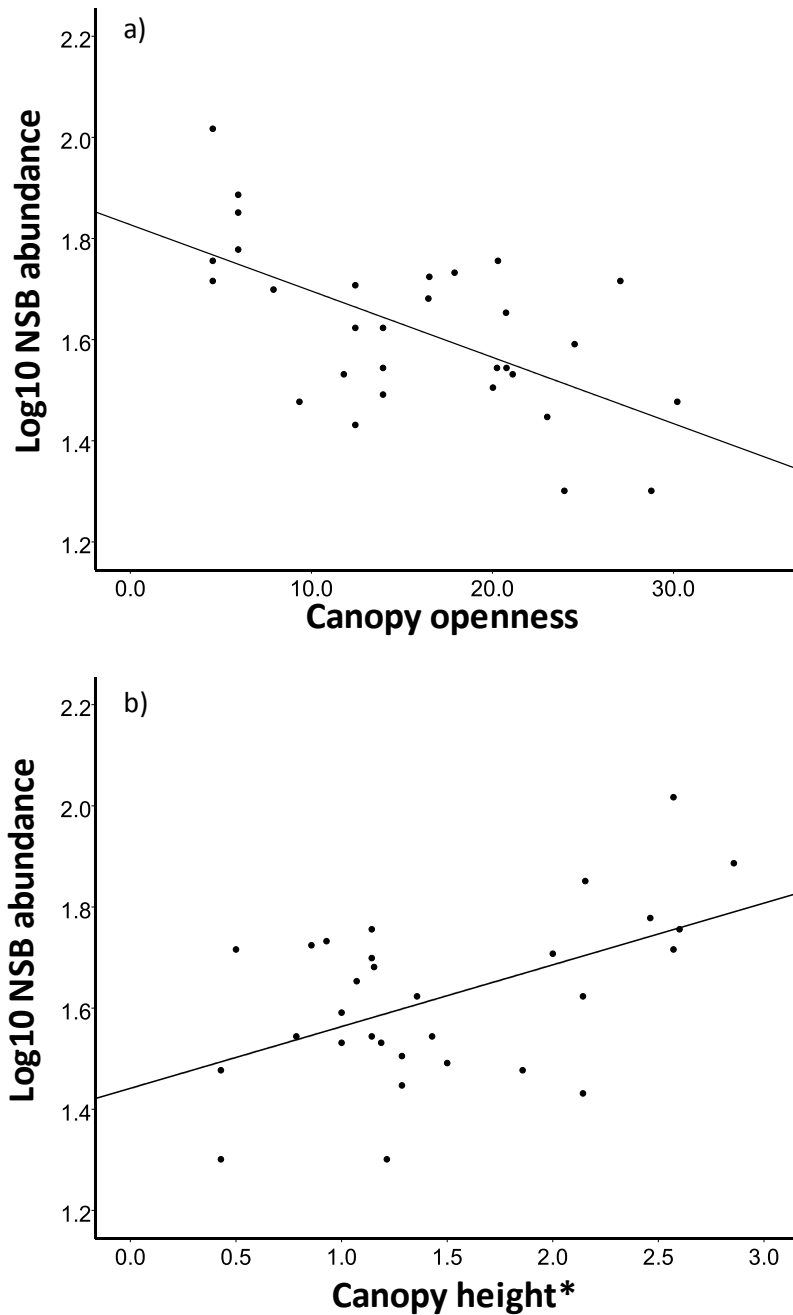
Figure 3. a) Narrow-space bat (NSB) abundance decreases with increasing canopy openness (y= -0.013x + 1.827, r^2 = 0.370, p<0.001). b) NSB abundance increases with increasing canopy height (y= 0.122x + 1.441, r^2 = 0.266, p<0.01). * Estimated canopy height - refer to methods for scoring protocol.
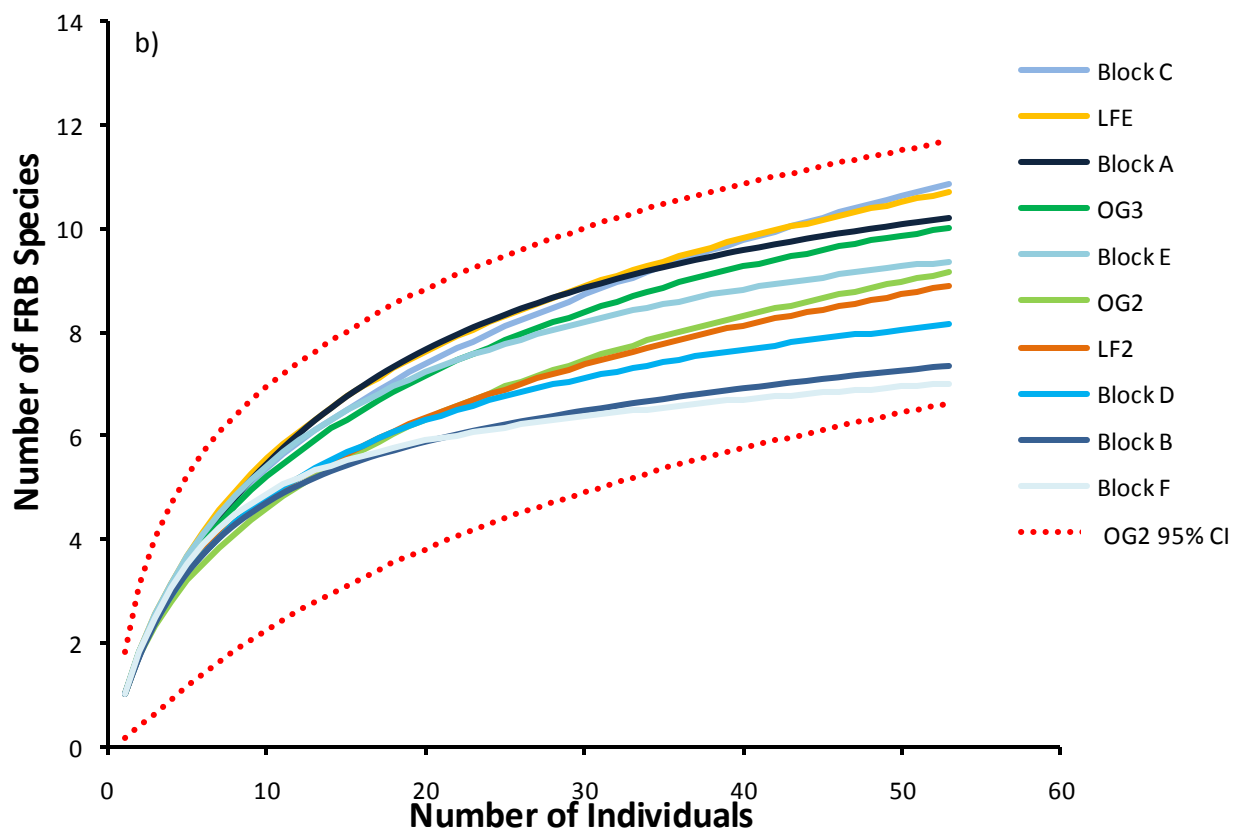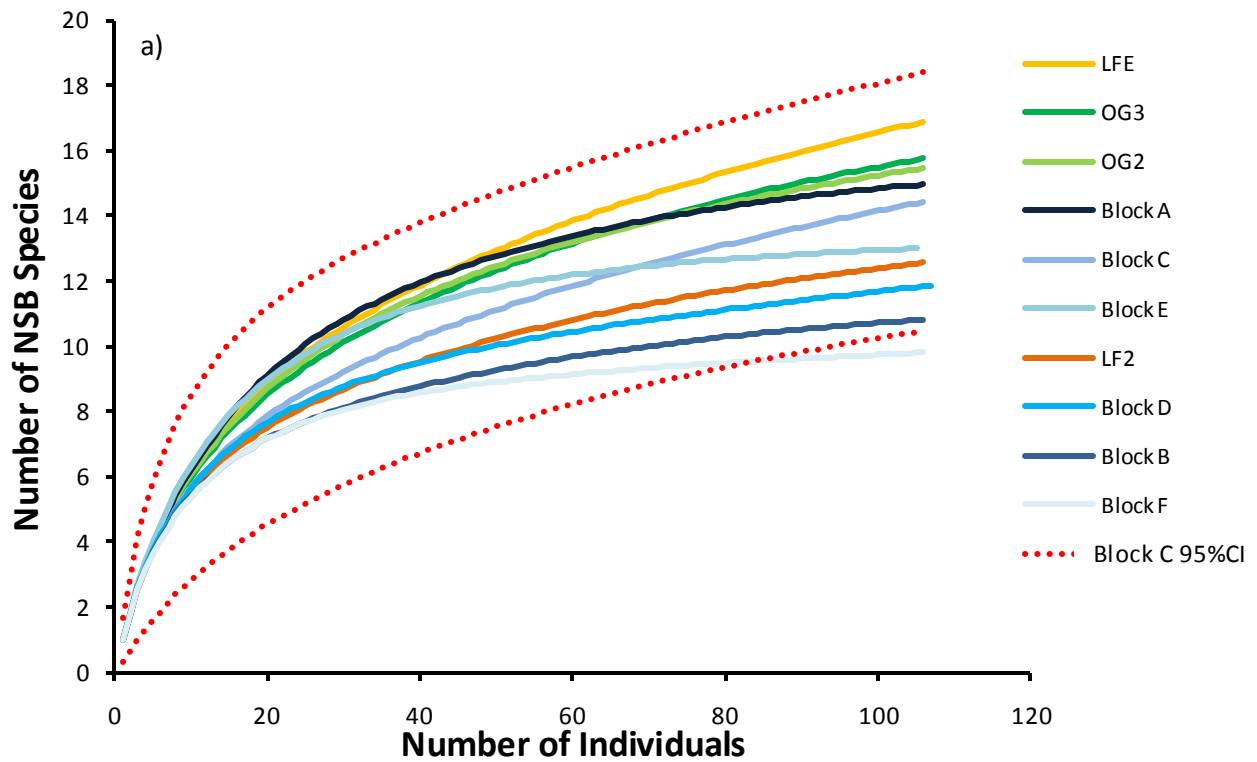
Figure 4. Individual-based rarefaction curves of 10 rainforests sites with varying levels of disturbance in Sabah, Borneo. a) Accumulation of narrow-space bat (NSB) species per randomised sample of the observed population. The 95% confidence intervals are those for the most heavily disturbed site, Block C b) Accumulation of narrow-space foliage-roosting bat species (FRB) per randomised sample of the observed population. The 95% confidence intervals represent the least disturbed site, OG2.

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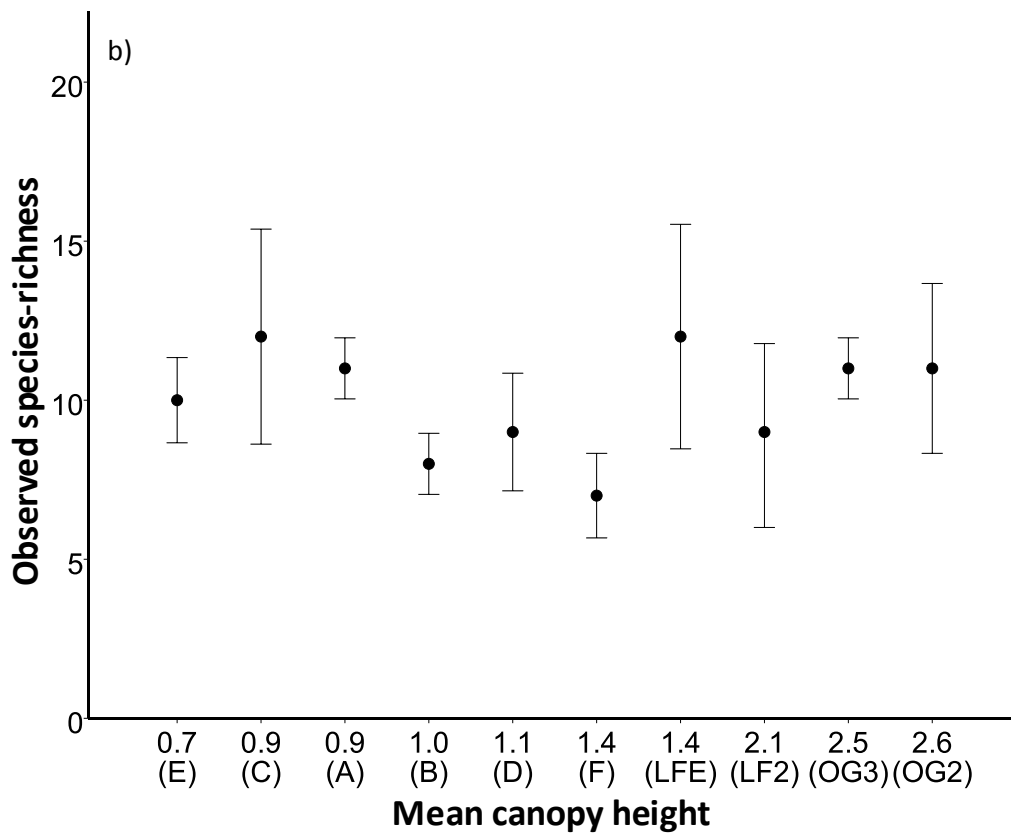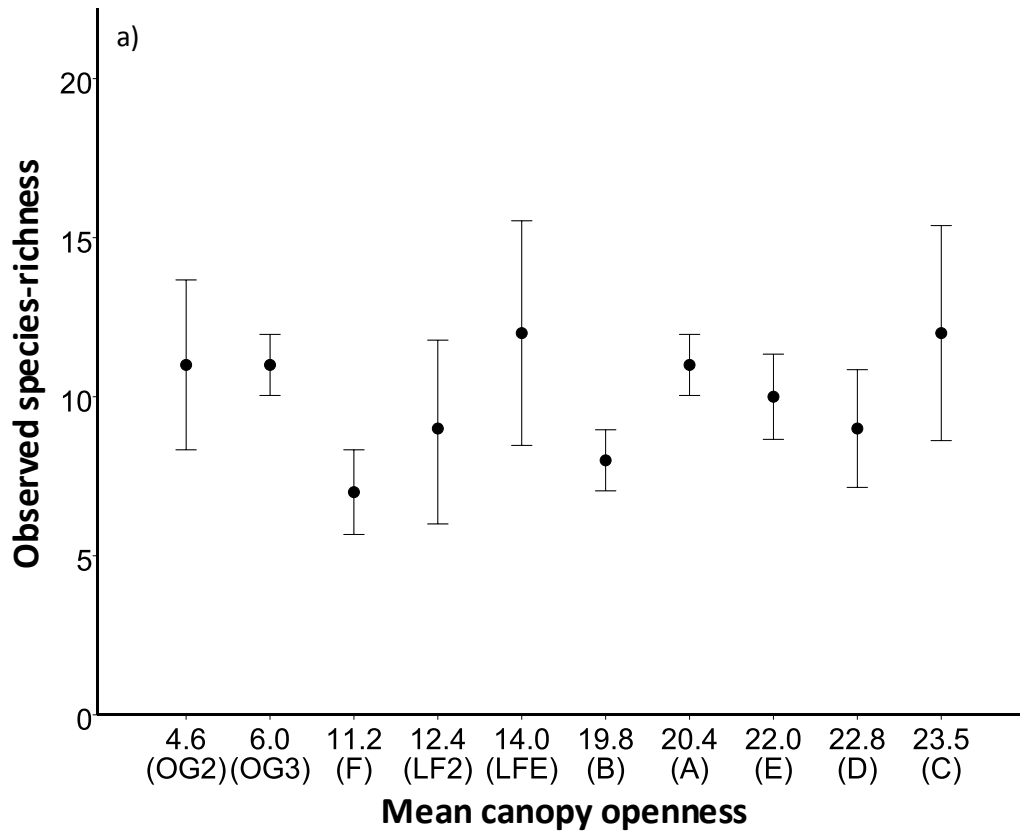
Figure 5. Foliage-roosting bat species richness and the level of disturbance at 10 rainforest sites in Sabah, Borneo. a) No clear trend between canopy openness and species richness (± rarefied 95% confidence intervals). Smaller values, on the x axis, indicate a denser, closed canopy. Larger values indicate a more open canopy (site ID in brackets). b) No clear trend between canopy height and FRB species richness (site ID in brackets).

*Community composition and habitat preference analysis*

Narrow-space foliage-roosting bats were considered to be the only community that could be fully explored using ordination due to a lack of data on distance to caves, which is likely to be an important causal factor in determining relationships involving cave-roosting species. Ten foliage-roosting species were considered common enough to be used in RDA (lowest n = 9 individuals). The final unconstrained ordination explained 24% of the variance in species composition data. Three Vespertilionid species (*Kerivoula hardwickii*, *K. papillosa* and *Murina suilla*) were associated with (unconstrained) axis 1 (Table 3) which accounted for most of the variance in the species data (20.2%). *K. hardwickii* abundance was found to be high at sites with low *K. papillosa* abundance (r_s= -0.5, p <0.01, n = 30). Likewise, *M. suilla* abundance was found to be high at sites with low *K. papillosa* abundance (r_s= -0.65, p <0.001, n = 30) (see Appendix C). Axis 2 (unconstrained) was significantly associated with *Hipposideros ridleyi*, *K. intermedia* and *Rhinolophus trifoliatus*. There was a significant, but weak, positive relationship between *K. intermedia* and *H. ridleyi* (r_s= 0.367, p<0.05) which could not be explained using the environmental variables.

The constrained ordination included three environmental variables: understory clutter; canopy height and; canopy openness. Axis 1 explained the majority of the variance in species composition and characterised a gradient of disturbance (Figure 6). *K. hardwickii* and *Murina suilla* abundances were higher as the forest became more disturbed, whilst *K. papillosa* abundance was lower (figure 7). These trends largely remained after removing old growth forest to assess whether the 60km distance between sites was having a disproportionate effect on the data (Appendix D). *K. papillosa* is the largest of these three species (Forearm (FA) = 40-49mm; Weight (WT) = 6.0 − 12g) and; *K. hardwickii* and *M. suilla* are a similar size to each other (FA=31-34mm; WT=3.5-4g and; FA=28-31mm; WT=3.0-4.7g respectively). *Kerivoula pellucida* was more prominent in sites with a taller canopy, though there were no significant predictors to explain this. There were no significant relationships between any cave-roosting bat species and an environmental predictor.

Table 3. Generalised linear model (GLM) species responses to unconstrained RDA ordination axes, according to Poisson distributions. Unconstrained analysis focuses solely on species data.

Species	Axes	$F_{1,28}$	T
Kerivoula hardwickii	Axis1	35.36[***]	-5.0
K. papillosa		76.30[***]	7.8
Murina suilla		6.06[*]	-3.1
Hipposideros ridleyi	Axis2	6.12[*]	-3.3
K. intermedia		5.57[*]	-3.8
Rhinolophus trifoliatus		13.75[*]	3.5

*P<0.05; ***P<0.001
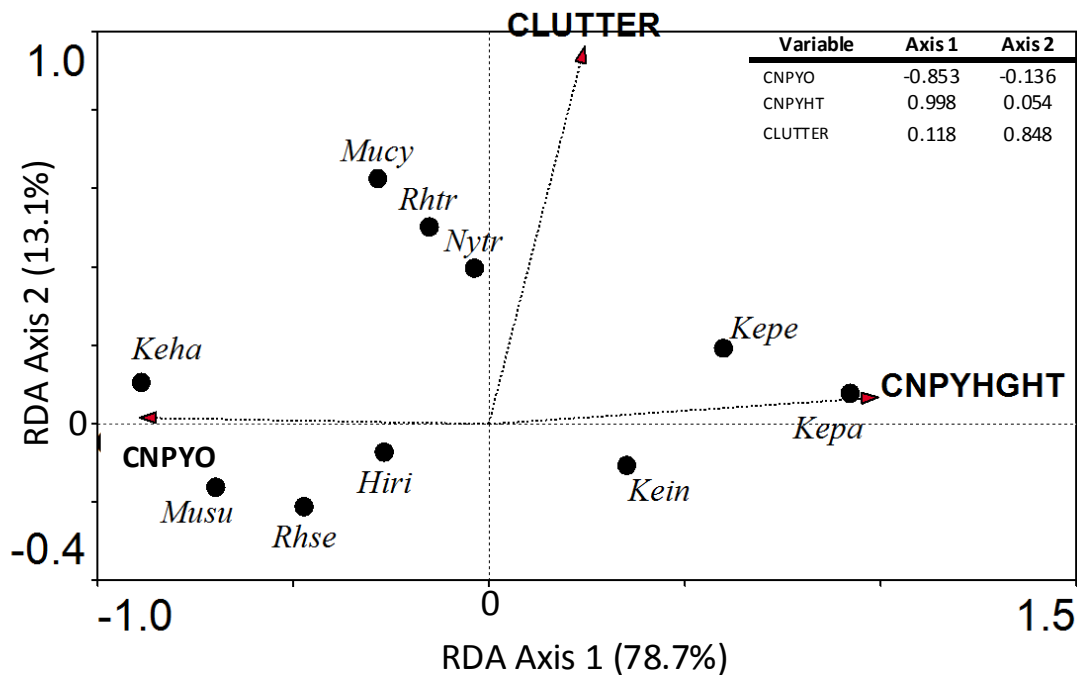
Figure 6. Biplot based on redundancy analysis (RDA) of 10 insectivorous, narrow-space, foliage-roosting bat species constrained by 4 environmental variables (correlation coefficients presented in top right). Axis 1 represented the majority of the variance in assemblage differences (77.4%) and the overall model produced 4 axes which cumulatively accounted for accounted for all of the variance (100%). The orientation of environmental variables in relation to each axis is represented by an arrow, the length of which indicates the degree of correlation with those axes. Axis 1 is characterised by a taller closed canopy. Axis 2 is characterised as having slightly more understory clutter. CNPYO-Canopy openness; CNPYHGHT – Canopy height and; Clutter – Understory clutter.
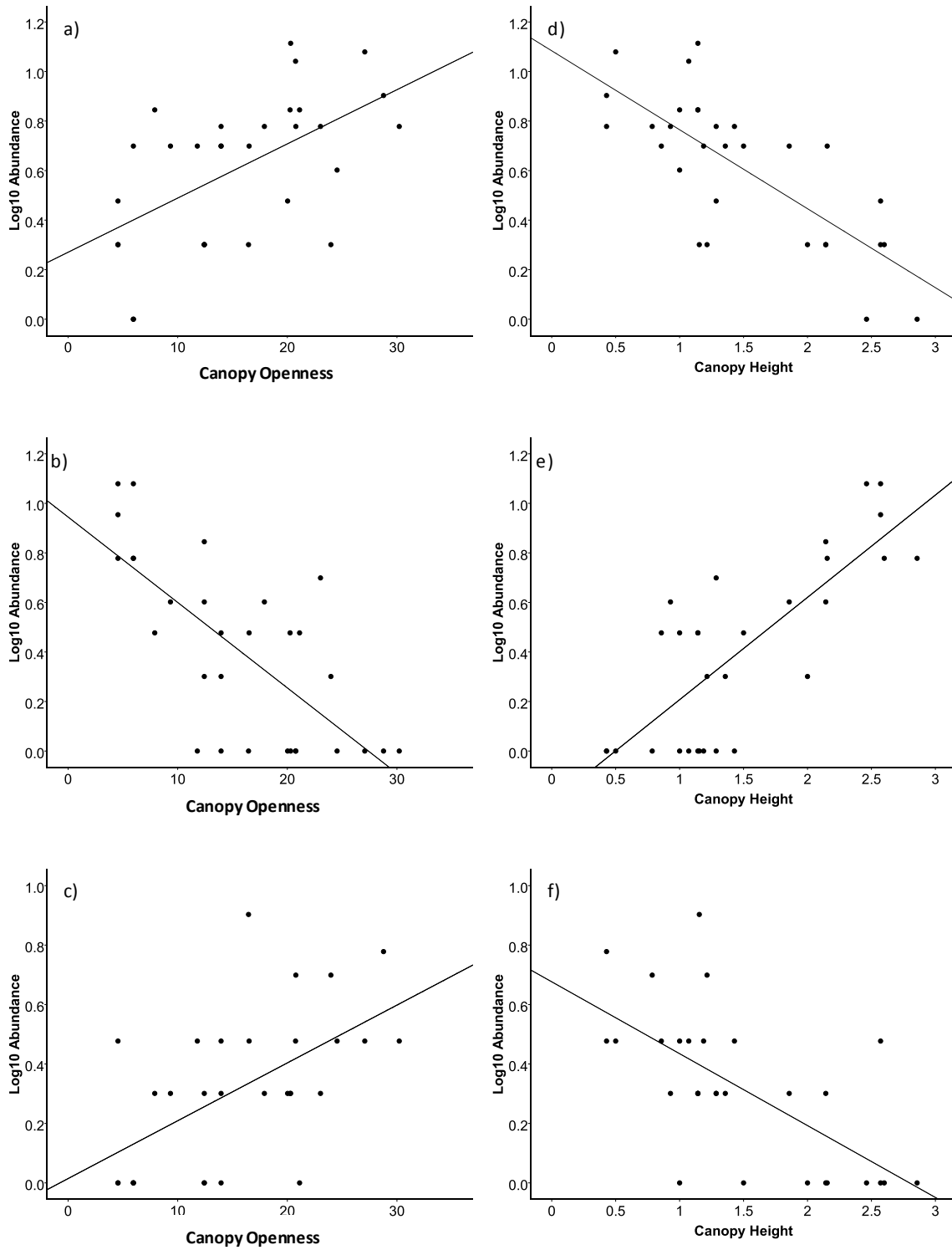
Figure 7. Scatterplots of three foliage-roosting bat species responses to two different habitat disturbance predictors, canopy openness and canopy height. a) *Kerivoula hardwickii* abundance was greater at sites with a more open canopy (y=0.022x + 0.27; r^2=0.314; p<0.01); b) *K. papillosa* abundance was lower at sites with a more open canopy (y= -0.034x + 0.945; r^2=0.512; p<0.001); c) Abundance of *Murina suilla* was greater at sites with a more open canopy (y=0.019x + 0.014; r^2=0.323; p<0.01); d) *K. hardwickii* abundance was greater at sites with a shorter canopy (y= -0.32x + 1.08; r^2=0.56; p<0.001); e) *Kerivoula papillosa* abundance increases was greater at sites with a taller canopy (y=0.413x + -0.21; r^2=0.611; p<0.001); f) *M. suilla* abundance was greater at sites with a shorter canopy (y= -0.24x + 0.68; r^2=0.415; p<0.001).

Discussion

The narrow-space bats of South East Asia are predicted to be particularly vulnerable to the effects of habitat disturbance (Kingston 2010). This study provides insights into these predictions and identifies three species that display marked responses to logging activities. *Kerivoula papillosa* declines in logged forests whereas *K.hardwickii* and *Murina suilla* seem to benefit. Overall abundance of narrow-space bats declined along a disturbance gradient but species-richness did not. This study also identified the potential for using rapid estimates of canopy height in determining a disturbance gradient. This method was comparable to the more expensive and time-consuming method of using a spherical canopy densitometer. This may be a particularly useful method in studies, where the time and effort required to adequately sample a faunal community, leaves little time for collecting detailed habitat data.

Many logging-impact studies that sample across disturbance gradients arbitrarily classify forest as old growth forest and secondary forest (or unlogged and logged forest). Secondary forest can be classified in a number of ways and the definitions used are crucial for assessing land-use change and relating that to conservation strategies (Chazdon et al. 2009). Determining a disturbance-gradient may help to overcome generalisations made when referring to the 'number of logging-events' and/or 'time since logging'. Providing basic information about the current state of a forest stand may be more meaningful when interpreting the current state of its faunal community. However, it is widely accepted that faunal species-richness typically declines in response to logging. In Borneo these declines are often not more than 25% in heavily disturbed forest (Edwards et al. 2010) and are often less than 10% (Berry et al. 2010; Willott 1999). Abundance usually declines after logging across a range of taxa (Basset et al. 2008; Cleary et al. 2005; Furey et al. 2010; Ghazoul 2002; Poulsen et al. 2011), but this is not always the case (Slade et al. 2011). Logging disturbance almost always results in a shift in species-composition across taxa (Castro-Arellano et al. 2007; Cleary et al. 2009; Ghazoul

2002; Sodhi et al. 2005; Wells et al. 2007). Changes in plant communities result in changes in herbivore communities, which can have knock-on effects at higher trophic levels (Callaham et al. 2000). The consequences of this may be far reaching and only noticeable in the long-term. For example a decline in the relative abundance of large-bodied seed-dispersers is likely to have noticeable impacts on future forest structure and tree-species composition (Corlett 2009; Kirika et al. 2008).

There is a demonstrable negative effect of logging in tropical forests on insectivores; notably in birds (Cleary et al. 2007; Felton et al. 2008; Sodhi et al. 2005) and bats (Fenton et al. 1992; Peters et al. 2006). Abundance of insect-prey is not considered a driver of decline for insectivorous bats (Peters et al. 2006) because arthropod abundance and species richness can remain un-changed after logging (Basset et al. 2008; Law and Chidel 2002; Slade et al. 2011). However, shifts in arthropod community composition may contribute to shifts in bat abundance. Relatively little is known about the diets of the bat species in this study, though inferences can be made from the structure of their echolocation calls (Bogdanowicz et al. 1999; Schnitzler and Kalko 2001). Broadly speaking Rhinolophidae and Hipposideridae bats are aerial-insectivores, which catch their, nocturnal-flying, prey in-flight (Schnitzler and Kalko 2001). Kerivoulinae and Murininae bats are primarily gleaners, taking their, diurnal-resting/nocturnal-walking, prey from foliage, bark and other surfaces (Kingston et al. 1999).

Slade et al (2011) recently noted significant declines in large-bodied nocturnal dung beetle species, in logged forests in Borneo, though total community abundance did not change. Cicadas in Mexico are particularly sensitive to disturbance events, especially those that depend on particular tree-species in the nymph-stage of their life-cycle (Smith et al. 2006). This may have consequences for bats that are aerial-insectivores, since scarab-beetles, cicadas and moths are major components of their diets (Bogdanowicz et al. 1999; Hutson et al. 2001). Furthermore, changes in insect-community composition can determine bat-species and bat-activity within a habitat (Wickramasinghe et al. 2004). In this study, aerial-insectivores (Rhinolophidae and Hipposideridae) were less abundant in

more disturbed forest sites. The majority of these bats are cave-roosting species, so interpreting the results is hindered by a lack of data on caves in the study sites. However, Furey et al (2010) noted that, in Vietnam, bats from these two families declined in disturbed forest where caves were likely to be present, so shifts in prey-species composition may be important in determining their relative abundance. Body-size also determines the diet of insectivorous bats (Bogdanowicz et al. 1999). The relatively large body-size of *K. papillosa* indicates that its diet may be quite different to that of *K. hardwickii* and *M. suilla*, who are a similar size to each other.

Structural changes to the forest are likely to affect bats (Kingston 2010; Meyer et al. 2010). As the rainforest canopy becomes fragmented and opens up, light penetrates through to the understory, which becomes overgrown and cluttered with vines and other vegetation (Brown et al. 2000; Whitmore 1990). This can increase the energetic demands of foraging bats due to difficulties associated with manoeuvring through a cluttered environment (Peters et al. 2006). More importantly, insect prey becomes difficult to detect in highly cluttered environments due to an increase in background interference with echolocation calls (Arlettaz et al. 2001). Roosting ecology is also important with regard to the foliage-roosting (and tree-cavity roosting) bats. *K. papillosa* roosts in small tree-cavities (Kingston et al. 2006). Interestingly, density of tree-cavities is typically lower in logged forests, which results in declines of tree-cavity nesting birds (Cockle et al. 2010; Politi et al. 2010). Little is known about the roosting-ecology of the smallest bats (such as *K. hardwickii* and *M. suilla*). However, recent improvements in radio-telemetry technology have enabled research, in the peat swamp forests of Brunei, that found a population of *K. hardwickii,* which roosts almost exclusively in the pitcher plant species *Nepenthes rafflesiana* (Grafe et al. 2011). A study into the roosting-ecology of a *Kerivoulinae* species in Australian rainforests found that 77% of roost-sites were in the nests of two bird species (Law and Chidel 2004). Such highly specific roosting behaviours will make some bats vulnerable to environmental change, whilst others may stand to benefit.

This study is the most comprehensive to-date, outlining the impacts of logging on narrow-space bats in South East Asia. However, the conclusions that can be drawn from it remain limited at this stage. The old growth sites were located 60km from the disturbed forest sites and they yielded the majority of cave-roosting bat observations. Although sites were matched for topography, elevation and soil-type (as part of the SAFE project), the lack of data on caves limits the power of the disturbance gradient to explain the differences in abundance of cave-roosting bats. The conclusion that narrow-space bat abundance has declined along the disturbance-gradient assumes that old growth forest has a carrying-capacity, which is filled by foliage-roosting bats or cave-roosting bats or a combination of both, dependent on distance from caves. In Peninsular Malaysia, cave-roosting bat abundance declines in forest fragments with increasing distance from caves, whilst foliage-roosting bat abundance increases (Struebig et al. 2009). A similar pattern is likely in continuous forest though there are no studies to clarify this point. Although species-richness did not decline with disturbance there may be a more subtle response that sees a gradual extinctions in the coming years (Krauss et al. 2010). This 'extinction debt' has been observed in fragmentation studies in Brazil (Ferraz et al. 2003; Stouffer et al. 2009) and on Barro Colorado Island in Panama, since its isolation in 1913 (Robinson 1999). However, Clarke et al (2005) showed that bat communities recover with time since logging and a similar trend has been observed in birds (Kavanagh and Stanton 2003) so an extinction debt may not necessarily be cause for concern in continuous forest.

The relationship between declines in abundance and level of disturbance are a little crude as there were relatively few old growth forest sites and moderately disturbed forest sites sampled in this study. Removal of the old growth sites from analyses results in some relationships becoming weaker though the general trend of abundance decline was observed in most cases. Sampling more relatively undisturbed sites would clarify this issue. The disturbance gradient used in this study was rather basic and only gave a rough idea of simple structural differences of forest between sites. Understory clutter should have exhibited some association with canopy openness (Brown et al. 2000; Whitmore 1990) and the lack of any relationship between these two variables indicated that

the scoring system for understory clutter was not adequate to detect differences along the disturbance gradient. The main purpose for using these variables was to move away from broad land-use classifications to a potentially more meaningful forest-quality gradient, and to highlight the relative ease with which it can be done.

Conservation Implications/Recommendations

Kerivoula papillosa is potentially extremely vulnerable to rainforest disturbance. This species is currently listed as 'least concern' on the IUCN Red List of Threatened Species. The findings from this study suggest that this species should be reconsidered and moved to a higher-level threat category. *K. papillosa* also declines in abundance and genetic diversity in forest fragments (Struebig et al. 2011) and because it roosts in tree-cavities, its recovery in logged forest is likely to take a long time (Kavanagh and Stanton 2003). Further research into the roosting and feeding behaviours of *K. papillosa, K. hardwickii* and *M. suilla* may help to identify specific drivers of change in their populations, and subsequently improve habitat in disturbed areas for *K. papillosa*.

In the current literature, there is a plethora of data on a suite of taxonomic groups in both disturbed and undisturbed forests (Berry et al. 2010; Chazdon et al. 2009; Gray et al. 2007). However, there is a paucity of studies that provide data on the disturbance-response of different taxonomic groups, at the same sites, sampling points and time-period. This is a barrier to our attempts at understanding, and ultimately conserving, tropical rainforests. As part of the SAFE project, this study will contribute a vital component to the understanding of biodiversity response in a human-disturbed rainforest. At the time of writing, there were no data available to enhance the explanatory power of this study. However, SAFE scientists are processing invertebrate samples collected from combined pit-fall and flight-interception traps from over 720 sampling points along the same transects used in this study. The data presented here will undergo further analysis once those samples have been processed. On-going research into plant, arthropod, avian, mammal and amphibian communities based on the

same sampling points will allow for greater insights into the effects of tropical forest disturbance on biodiversity.

It is clear from this study and others like it, that logged forests have the potential to be havens for wildlife and they are extremely important for the conservation of tropical biodiversity (Chazdon et al. 2009). Secondary forests should be considered research priorities not only for biodiversity assessments, but for all aspects of ecological research. Aside from improving our understanding of human caused disturbance on rainforest ecosystems, it may also contribute to the regeneration of already-disturbed forests directly; through increased funding from research projects and potentially eco-tourism. Furthermore, conservation scientists need to work with the logging industry to develop reduced-impact logging techniques, for the benefit of both wildlife and the logging industry (Sist et al. 2003).This need is immediate and imperative because unsustainable logging practices facilitate the expansion of the oil palm industry (Dennis et al. 2008; Fitzherbert et al. 2008).

Unfortunately 7,900 hectares of logged forest in which sites A to F are situated (Figure 1) will be converted to oil palm plantation in November 2011. From a biodiversity conservation perspective, this development is unfounded and will result in the loss of an unimaginable number of individuals. In Malaysia, more than 1.1million hectares of secondary forests were clear-felled for agriculture between 1990 and 2005 - 94% of which was for oil palm (Wilcove and Koh 2010). Conversion of logged forests to oil palm results in major declines of vertebrate species-richness and is perhaps, the most destructive and absolute threat to tropical rainforest species in South East Asia and globally (Danielsen et al. 2009; Wilcove and Koh 2010).

Effective conservation of tropical rainforests requires a much improved and better-managed logging industry, which should be directly informed through research developments. Legislation reform is required to ensure the proper labelling of food products containing palm oil sold in the UK and globally. Better education in the developed world to inform people what impacts the contents of their cupboards are having on the planet is needed to allow consumers to make more informed

decisions. The aim of this study was to assess the value of secondary forests for bat communities in

Borneo. It provides further evidence to support the increasingly popular view; that secondary forests

are extremely important for the conservation of tropical biodiversity.

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Appendix A

Canopy cover was measured using a canopy viewing tube (a piece of drainpipe), with a plastic-mounted 4x4cm, 25 point grid built into it. The forest canopy was viewed through the tube, which was held vertically, aided by a built-in level, and the number of dots that were 'touching' vegetation was counted. Each dot represents 4%; therefore percentage canopy cover was determined by multiplying the number of dots touching vegetation by four. This design is based on the moosehorn technique for estimating canopy cover, developed for forestry surveys. Canopy cover readings were taken from 5 locations at each trap – one from the centre of the trap and one each from, 2-3metres, North, East, South and West of the central position, depending on accessibility. This data was not used in analysis as the variation between sites did not describe a disturbance gradient. Although the 4x4cm grid translated into a larger area at canopy level, the grid was, perhaps, too small to signal any major changes in canopy cover. Further modifications to this (relatively cheap) method may result in improved data accuracy.

The SAFE forest-quality score was not used in the final analyses as it was highly correlated with both canopy height (+ive) and canopy openness (-ive). The scoring system is outlined in Table 4 below.

Table 4. Forest quality scores as outlined by SAFE protocol.

Forest type	Quality	Description - vegetation in the area immediately around sample point
1	Very poor	No trees - open canopy with ginger/vines or low scrub
2	Poor	Open with occasional small trees over ginger/vine layer
3	Ok	Small trees fairly abundant/canopy at least partially closed
4	Good	Lots of trees, some large, canopy closed
5	very good	No evidence of logging at all, closed canopy with large trees

Appendix B
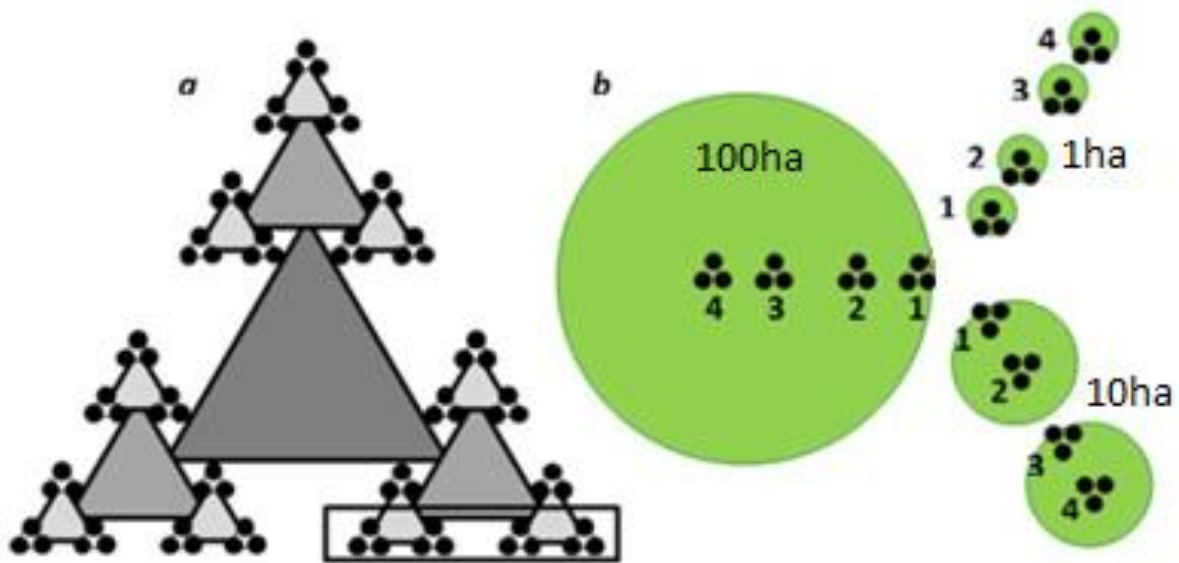
Figure8 . Fractal arrangement of sampling points being used at the SAFE project. (a) Old Growth sample points. The rectangle represents one sampling transect. Black dots form the smallest sampling point triangles and are 56m apart. Within the centre of these triangles will be the 25mx25m plots for collection of detailed environmental data – the distance between the centre of two plots is 178m. (b) Secondary forest sites. The green circles represent the proposed forest fragments at each site. Bat sampling took place on the 3 transects that run through the green circles. (see www.SAFEproject.net for further information).
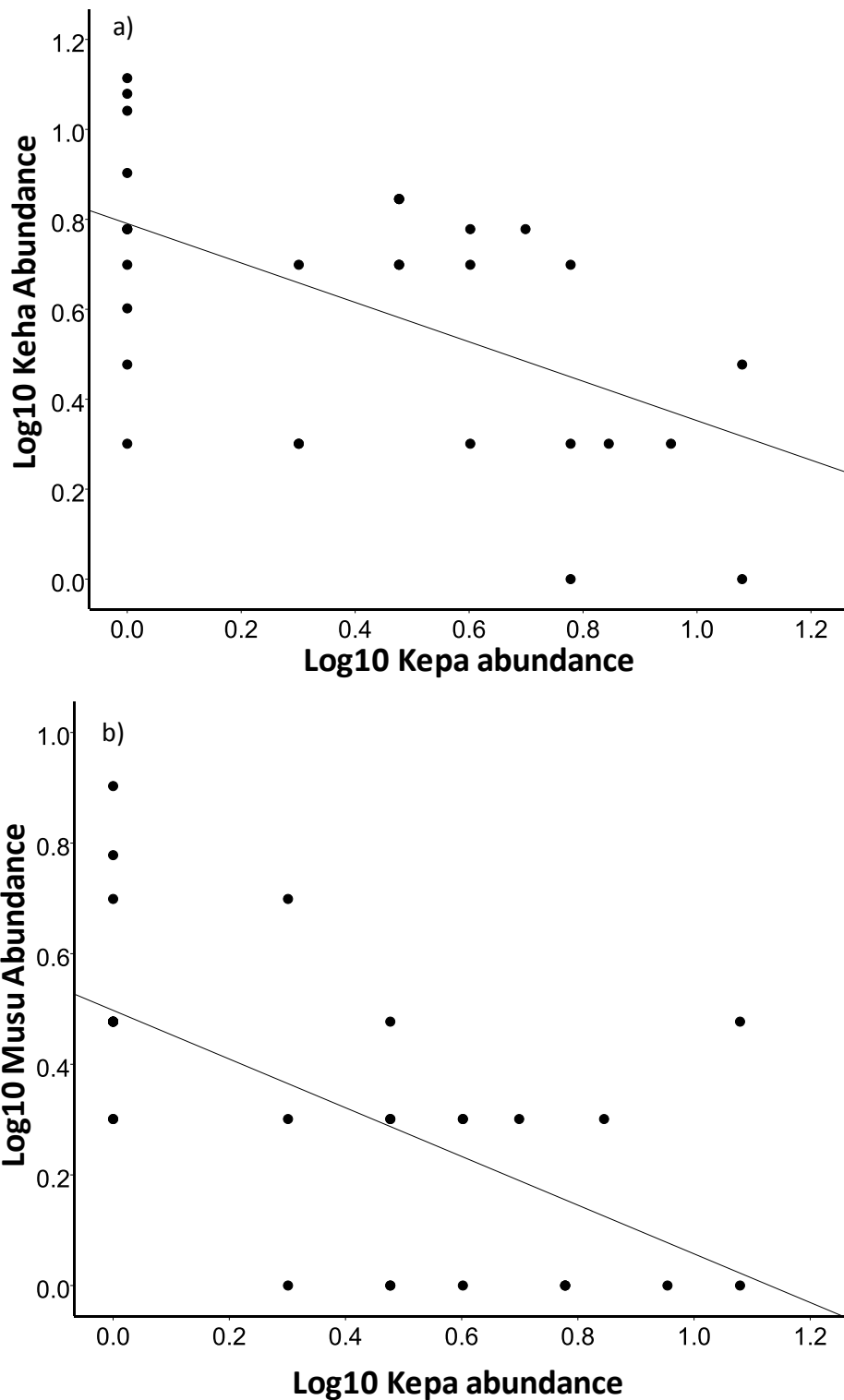
Appendix C

Figure 9. Specie-specie relationships a) *Kerivoula hardwickii* abundance increases as *Kerivoula papillosa* abundance decreases (r_s = -0.5, p <0.01, n = 30). b) *Murina suilla* abundance increases as *Kerivoula papillosa* abundance decreases (r_s = -0.65, p <0.001, n = 30) (Appendix B).

Appendix D

Table 5. R^2 values from linear regressions of three species versus two separate disturbance predictors excluding old growth forest (n=24).

Species	Canopy Openness (R^2)	Canopy height (R^2)
Kerivoula hardwickii	0.118^{ns}	0.384***
K. papillosa	0.204*	0.309**
Murina suilla	0.173*	0.310**

ns not significant; *p<0.05; **P<0.01; ***p<0.001