

Assessing the effect of altitude on the medium and large mammal community in the protected rainforest of Sabah state, Malaysian Borneo

Heather Hemmingmoore
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Declaration

Between May 2015 and August 2015, I conducted a camera trapping study in Malaysian Borneo, based at the Stability for Altered Ecosystems (SAFE) Project and with the assistance of local field assistants. I was supervised by Dr. Robert Ewers and Dr. Oliver Wearn, neither of whom were present in the field at that time.

Dr. Ewers, Dr. Wearn and myself planned my sampling approach together, which was distinct from other camera trapping studies that they have conducted in the past; I was responsible for choosing and mapping out where sample points would be located, on which I received feedback from Dr. Ewers and Dr. Wearn.

Dr. Wearn provided templates that reflected his previous data collection methodology, and I collected the same covariate information for each trap point that he had collected for his own research in the past.

All data referred to in this document as “2015 data” or “my data” or “my transects” refers to the data collected by myself, accompanied by one to two of several field assistants.

Upon my return, Dr. Wearn offered to provide his data from his previous camera trapping studies in the same sampling blocks (but different locations, according to a different sampling design). We decided together that it would be best to combine the data, to increase the size of the data set.

All data referred to as “2011, 2012, or 2013 data”, or as “Dr. Wearn’s data” refers to the data he provided to me. I combined these data sets, cleansed them, and used the single resulting data set in my analysis.

I conducted three distinct analyses, which were developed as follows:

- To model abundance, I chose what type of models to use (zero inflated binomial generalised linear model) and how to display the outputs graphically. Dr. Wearn provided suggestions and guidance during this process, and Dr. David Orme also provided advice. I then developed the models, with assistance from Dr. Wearn when I encountered difficulty.
- To model species richness, I followed Dr. Wearn’s suggestion to use the iNext package in R (Hsieh, Ma & Chao 2014). Dr. Wearn provided code to generate values for estimating richness for each sampling point at a standard level of sample coverage, which I then used as inputs to model the change in species richness by altitude. I developed the code for this analysis.
- For community composition, I used code provided in the supplemental materials of Valle et. al. (2104) as a basis for my analysis. I carried out this analysis using the topicmodels package in R (Gruen and Hornik 2011), and Dr. Valle provided additional code to meet my graphing needs. Dr. Wearn debugged my code when I encountered difficulty, and Dr. Ewers originally suggested the method.

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Heather Hemmingmoore

Imperial College London

heather.hemmingmoore14@imperial.ac.uk

+44 (0) 7205613595

Abstract: Deforestation for oil palm plantation takes place more readily at low elevations and on gradual slopes. However, little is known about the effect of altitude and slope on medium and large mammals, and to what extent logging activities that are dependent on slope and altitude are likely to affect them. A camera trapping study was carried out in four primary and secondary forest locations in Sabah state, Malaysian Borneo to test the effect of altitude and related covariates on individual species abundance, species richness, and the composition of individual communities within the broader species assemblage. This study found that low elevation is only indicative of lower abundance for two species out of 15 assessed, while richness shows a slight increase at mid-elevations. Four distinct communities were identified, with one dominant at low altitudes, one at high altitudes, and the other two intermittently. These results indicate that medium and large mammals may be resilient to logging activities at low elevations, although the existing protected area network is likely inadequate to provide adequate refuge given future land use changes.

Key words: abundance, species richness, composition, sample coverage, latent dirichlet allocation, Heart of Borneo

1 Introduction

Borneo is one of the most biodiverse regions in the world, and also one of the most under threat (Myers et. al. 2000). Deforestation for the purpose of planting oil palm (*Elaeis guineensis*) has expanded rapidly in recent years; this expansion is unlikely to slow and the impact of this change has been called a “major concern” for tropical forests and biodiversity (Koh and Wilcove 2008a) and possibly “the single most immediate threat to the greatest number of species (Koh and Wilcove 2008b). Malaysia is the world’s second leading producer of palm oil, behind Indonesia. Together they account for more than 80% of global palm oil production (Koh and Wilcove 2008b), and deforestation occurred at a rate of 4.68% across the whole island of Borneo between 2007 and 2012, which is comprised of Malaysia, Indonesia, and Brunei (Wulffraat 2014). During the time period from 1990 and 2005, between 55% and 59% of new oil palm plantations in Malaysia displaced secondary forest (Koh and Wilcove 2008a), which provides important habitat for the region’s endemic species and supports at a similar level of biodiversity to old growth forest (Brodie et. al. 2015).

Borneo has been identified by the World Wildlife Fund for Nature (WWF) as a high-priority conservation area and in 2007 WWF facilitated the “Heart of Borneo” agreement, which defines a strategic action plan by Brunei, Indonesia, and Malaysia to protect an area within Borneo that covers nearly 30% of the island and contains one of Southeast Asia’s largest remaining continuous rainforests; this Heart of Borneo area includes all interior highlands, mountains, and major river head waters, as well as some in-tact lowlands and foothills (Wulffraat 2014).

The productivity, and therefore profitability, of oil palm decreases as elevation increases, with lower elevations yielding higher outputs (Edwards et. al. 2014). Of the 23,000 hectares of oil palm plantation assessed by Edwards and her team in Sabah state, it all occurs below 380 meters above sea level (m.a.s.l). Edwards et. al. (2014) also found that of the forest fragments retained within oil palm plantations, steepness is one of only two factors taken into consideration in deciding which areas to preserve (the other being unfavourable substrate). Other studies confirm these findings; Kinniard et. al. (2003) found deforestation for oil palm plantation to be more than six times higher below 500 m.a.s.l. than above, and to decrease as slope increases, with a factor of sixteen difference between flatlands (less than 10 degrees) and the steepest slopes of above 40 degrees. If deforestation for oil palm plantations continues following these trends, remaining forest fragments will potentially be disproportionately found at high elevations relative to the total high-altitude land area.

The implications of losing a disproportionate amount of lowland forest and biasing Borneo’s remaining habitat to higher elevations is unclear, and further information is needed regarding the

biodiversity value of high elevation and steep forest areas. This will be essential for assessing the biodiversity value of remnant forest within agricultural areas, as well as more broadly within the Heart of Borneo.

Few studies have focussed on the change in the mammalian community with elevation in Borneo. Brodie and Giordano (2011) conducted a camera trapping study in primary and logged forest at elevations between 230 and 1120 m.a.s.l., although assessing the effect of elevation was not their primary objective and therefore an altitudinal analysis of species abundances or richness were not conducted. Other medium and large mammal studies in the area, have focussed on mid elevation areas and have strived to control for altitude; as examples, Wearn et. al. (2013) controlled for a mean elevation of 432 m.a.s.l. and Bernard et. al. (2013) did not set any camera traps above 650 m.a.s.l. McCain (2005) found that in fifty-six elevational studies of small mammal communities, of which 32 were tropical, all but four showed a mid-elevation peak in richness, although the definition of “mid-elevation” changes with the absolute height of the mountain in question. However, all these studies focussed on small mammals only, with comparable studies lacking for the medium and large mammal community.

Given the rapid conversion of forest to oil palm, it is essential to develop an understanding of the change in the mammalian community with altitude in undisturbed forest, so as to assess which species will potentially be most affected by lowland deforestation. This will also provide a baseline from which to measure future changes in the composition of these communities by altitude.

A camera trapping study was conducted to assess the effect of altitude and slope on individual species abundance, species richness, and community composition for the large mammal community in Sabah state, Malaysian Borneo, with the following research questions:

- Does the relative abundance of remaining species decline as altitude and slope increase?
- Does species richness show a mid-elevation peak for medium and large mammals, as it appears to do for small mammals?
- Are mammalian communities at different altitudes distinctly different than one another, and how do these communities change along the gradient?

To test these question, a camera trapping study was conducted along four altitudinal transects in two protected areas in Sabah state, Malaysian Borneo between May and August 2015. All work was carried out in conjunction with the Stability for Altered Forest Ecosystems (SAFE) project, which monitors the long-term ecosystem changes occurring as forests are fragmented as a result of deforestation and palm oil plantation in Sabah state, Malaysian Borneo (Ewers et. al. 2011).

2 Methods

2.1 Study Area

Between May and August 2015, 61 trap camera stations were deployed along altitudinal transects in two protected areas in Sabah state, Malaysian Borneo. Thirteen to seventeen trap cameras were deployed per transect. The altitude range varied by transect, with the lowest camera deployed at 118 (m.a.s.l), and the highest camera deployed at 903 (m.a.s.l). Both protected areas where sampling took place fall within the WWF's Heart of Borneo special conservation area.

2.1.1 SAFE Virgin Jungle Reserve

Two transects were sampled in the Virgin Jungle Reserve (hereafter VJR), which is a reserve of 2200 hectares that has been logged around its edges in the past but not within its steep interior (Ewers et. al. 2011). The VJR was chosen for this study because it provides a protected area with relatively undisturbed forest and spans a sufficient elevational profile to assess the effect of altitude. Despite its previous logging activities, it is still considered appropriate for this study because forest sites in Malaysian Borneo that have been logged more than 10 years prior to assessment have been found to contain similar species richness to old growth forest (Brodie et. al. 2015). The VJR is used by the SAFE project as a control when testing the effects of forest fragmentation in the rest of the SAFE study site. Transect details are given in Table 1, with maps of the sampling area and design provided in Figure 1.

2.1.2 Maliau Basin

Maliau Basin is a crater-shaped bowl in central Sabah state encompassing 588 square kilometres and containing a single water catchment. It was designated as a conservation area in 1981, and in 1997 had its status changed to a Class 1 Protection Forest Reserve (MBMC 2015). It is one of the few remaining locations that still house low-altitude primary rainforest, and is one of the most intact sites in all of Southeast Asia (Brodie and Giordano 2011). Maliau was chosen for this study because it provides an appropriate elevational range in undisturbed forest. Two transects were conducted there in July and August 2015, each climbing a different ridge on the outside rim of the basin as shown in the topographical element in the upper panel of Figure 1. In addition to the data collected in 2015, sampling activities took place in three separate blocks at Maliau Basin and two blocks at the VJR in 2011 – 2013. Locations of earlier sampling blocks relative to 2015 transects are available in Figure 1.

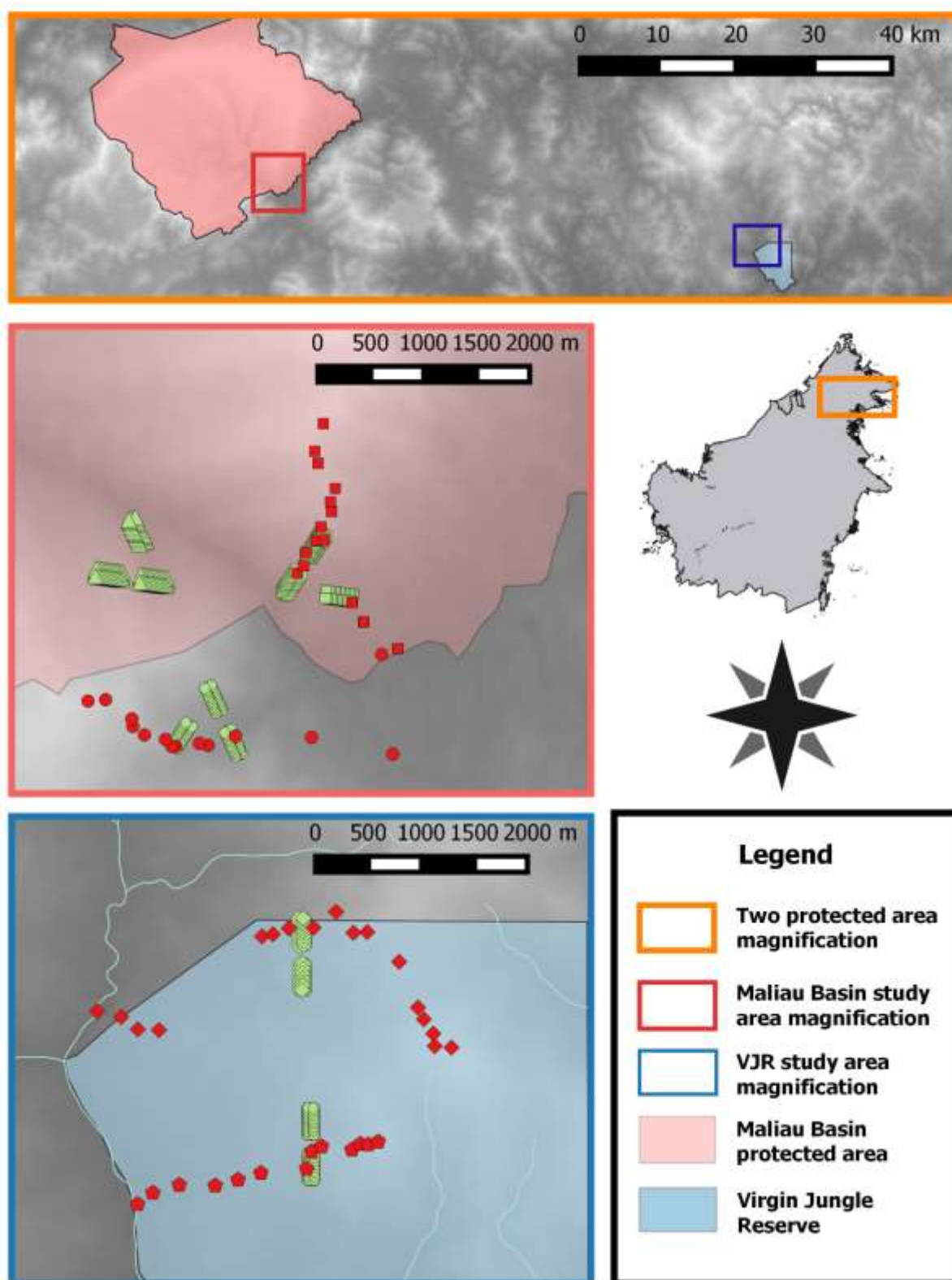


Fig 1 Map of study areas. Upper panel shows the location of each protected area, while panels (left) display sample point locations in Maliau Basin (above) and the Virgin Jungle Reserve (below). Red points indicate the 2015 study conducted solely for this analysis. Green points indicate 2011-2013 sampling points, for which further details are provided in Section 3.2. Sample points are shaped differently according to sampling block, as follows: Maliau North – triangle; Maliau East – square; Maliau west – circle; VJR North – diamond; VJR south – pentagon

2.2 Data collection

Thirty-one Reconyx HC500 Trail Cameras (Holmen, Wisconsin) were deployed successively in the two protected areas between May and August 2015, for a total of 61 sample points. They were deployed linearly and with one camera at each sample point to maximise altitudinal spread. The distance between cameras varied across the samples, as sampling points were spaced at 50 meters apart in altitude, with the linear distance between cameras varying according to slope. Cameras were deployed for 21-24 days at each location, for a total of 290 camera trap nights. All sampling was done in primary or mature secondary rainforest, as our hypotheses address the natural distribution of species, and not their response to habitat degradation or fragmentation. More traditional grid designs were dismissed because the objective of this study is not to estimate occupancy across a certain area, but to maximise altitudinal spread.

I supplemented these altitudinal transects with additional data collected by Oliver Wearn in 2011-2013. His sampling pattern did not focus on altitude and followed a grid design. Dr. Wearn's grids were aligned with the SAFE sampling blocks designated by Ewers et. al. (2011). Although my survey design did not stay within the SAFE blocks due to their altitudinal constraints, my transects did pass through four sampling blocks used by the SAFE project for control sites.

Although Dr. Wearn's sampling points did not have the same altitudinal spread as mine, the decision was made to combine them because his data were collected in the same sampling areas as my grids with the same covariate information collected. For more information on Dr. Wearn's survey design see Wearn et. al. 2013. All statements about methodology apply only to the 2015 sampling period unless otherwise noted, whereas all results are reported for the combined data set.

Sampling Block Name	SAFE Sampling Block*	Minimum Altitude	Maximum Altitude	Number of Sample Points	Dates deployed 2015	Dates deployed 2011-2013
SAFE VJR North	VJR	118	870	17 (2015) 30 (2012/13)	6-8 June – 29-30 June 2015	December 2012 – March 2013
SAFE VJR South	VJR	129	738	13 (2015) 27 (2012/13)	12-13 June 2015 – 3-4 July 2015	December 2012 – March 2013
Maliau East	OG2	215	930	15 (2015) 68 (2011/12)	8-10 July 2015 – 31 July-2 Aug 2015	Various April – July 2011 and 2012
Maliau West	OG3	216	877	14 (2015) 48 (2013)	11-13 July 2015 – 31 July – 2 Aug 2015	September – November 2013
Maliau North	OG1	285	610	61 (2012)	Not sampled	Various April – June 2012

Table 1 Altitude, number of sample points, and sampling dates for each block. * Information on SAFE sampling blocks is available in Ewers et. al. (2011).

Once the planned GPS point was reached, cameras were placed in the nearest area providing a clear detection zone, within five meters of the GPS location. GPS readings under the canopy were inexact and therefore sample points did not align exactly to planned points. The mean difference between intended altitude and actual altitude of sampling points was 11.72 meters.

The majority of area sampled did not follow a trail, and cameras were placed as randomly as possible subject to topographical constraints. Although it is common to try to increase detectability (O'Brien 2011), biased sampling designs have been shown to disproportionately affect the detectability of certain species (Wearn et. al. 2013, Sollmann et. al. 2013). No attempt was made to increase detectability beyond placing cameras in areas without interference from moving leaves. The number of cameras per transect was determined by the minimum and maximum altitude available (and the total number of functional cameras available for use), so not all transects had the same number of cameras. Habitat features were recorded for each sample point, as given in Table 2.

Measure	Variable Type	Units	Assessment method	Source
Elevation	Continuous	Meters above sea level	Plotted sample sites in QGIS version 2.8.1 and extracted elevation using the ASTER DEM data set	METI and NASA 2011
Slope – GIS	Continuous	Degrees	Generated in QGIS version 2.8	METI and NASA 2011; QGIS 2015
Slope where camera was placed – assessed in field	Ordinal	Scale, 1-4 as follows: 1 – Flat to slight slope 2 – Moderate slope 3 – Steep slope 4 – Extremely steep slope	Slope was assessed and recorded at each sampling point	Recommended by Dr. Wearn
SAFE Forest quality and Forest quality	Ordinal	Two separate 1-5 scales, ranging from extremely degraded to pristine.	Forest quality was assessed and recorded at each sampling point	Ewers et al. 2011, Wearn et. al. 2013
Canopy density	Continuous	Percentage of canopy openness	A densitometer was used to assess the percentage of leaf cover in each site and this total was subtracted from 100.	Densitometer
Basal area	Continuous	Square meters per hectare.	A two-factor relascope was constructed and readings taken at each sample point	Department of Environment, Climate Change and Water, NSW, Australia, 2010

Table 2 Covariate information collected while sampling and generated based on information collected while sampling

2.3 Data Analysis

Three metrics were used to assess the changes in the medium and large mammal community:

- Individual species abundance for those species with an adequate number of captures
- Species richness, or the number of species present at each sampling point, within the medium and large mammal community
- Community composition, or the number of individual communities within the larger species assembly, their species make-up, and the change in these communities with the elevation gradient.

Each of these metrics were calculated and modelled as described in their respective sections, below.

2.3.1 Abundance

Individual species abundance was assessed using the number of independent captures of each species, adjusted for effort by offsetting the capture count by the number of 24-hour periods for which the trap camera station was active (called camera trapping nights or CTNs) (O'Brien 2011). An independent capture was defined by any photograph identifiable to species level, separated from any previous detection of the same species for longer than one hour, or if the difference between individuals is visually identifiable. This metric, although arbitrary, is widely used to separate independent captures (Wearn et. al. 2013). Species were identified using (Payne, Francis and Phillips 1985).

Abundance was calculated for all medium and large mammal species that provided more than 20 independent captures, as this has been recognised as a sufficient number to calculate abundance information (Rowcliffe et. al. 2008). All species of squirrels, rats, and tree shrews were excluded. Greater and lesser mouse deer were grouped into a single category due to the difficulty to distinguish between species, which is commonly done (as examples, Bernard and Ahmad et. al. 2013, Brodie and Giordano 2011). A list of species is provided in Table 3.

For each species, a zero-inflated generalised linear model was fitted in R v3.1.1 with a negative binomial distribution and offset by the number of CTNs at that sample point using the “pscl” package (Zeileis, Kleiber & Jackman 2008). CTN number was log transformed, as offsets are input on the linear predictor scale. A zero-inflated model was chosen to compensate for the excessive number of zeros in the data, corresponding to the number of sampling points for which there were no captures of the species in question. The percentage of sampling points that yielded a zero are provided for each species in Table 3. A negative binomial distribution was used because the count data was over-dispersed, rendering a Poisson distribution inappropriate. The number of captures per species was offset by the number of CTNs to control for the difference in effort between stations due to camera failure, as per Table 4.

Common name	Latin name	Number of independent captures	Number of sample points with captures	% of sample points with 0 captures
Banded palm civet	<i>Hemigalus derbyanus</i>	285	117	55%
Bearded pig	<i>Sus barbatus</i>	715	130	51%
Leopard cat	<i>Prionailurus bengalensis</i>	24	18	93%
Long-tailed porcupine	<i>Trichys fasciculata</i>			
Malayan porcupine	<i>Hystrix brachyura</i>	230	68	74%
Malay civet	<i>Viverra zangalunga</i>	109	61	77%
Masked palm civet	<i>Paguma larvata</i>	43	27	90%
Mouse deer	<i>Tragulus spp.</i>	1130	151	43%
Orang-utan	<i>Pongo pygmaeus</i>	27	15	94%
Pig tailed macaque	<i>Macaca nemestrina</i>	979	160	39%
Red Muntjac	<i>Muntiacus muntjak</i>	1390	175	33%
Sambar deer	<i>Rusa unicolor</i>	123	58	78%
Short tailed mongoose	<i>Herpestes brachyurus</i>	64	31	88%
Thick spined porcupine	<i>Hystrix crassispinis</i>	83	23	91%
Yellow Muntjac	<i>Muntiacus atherodes</i>	597	116	56%
Yellow throated marten	<i>Martes flavigula</i>	21	15	94%

Table 3 Medium and large mammal species with more than 20 independent captures, each of which were analysed for abundance using a zero inflated negative binomial GLM

Explanatory variables used in the maximal models are a subset of those provided in Table 2 comprising sampling block, altitude, slope (GIS), and canopy openness. Covariates that were incomplete were excluded, and for those that were highly correlated according to a Person's product-moment correlation test, only one was chosen for this analysis. Percentage canopy cover was subtracted from 100 and log transformed to allow for a more even distribution of the data, effectively transforming canopy cover to "canopy openness" (i.e. the area not covered by leaves). All covariates had the scale() function applied, which centres them and divides them by the standard deviation, so they can be shown on the same scale. As the effect of altitude on the mammalian community is the primary research question, all two-way interactions between elevation and the other terms were included in the maximal model. Each model was reduced by removing non-significant interactions one at a time according to their p value, then single non-significant terms (with significance defined as $p < .05$). At each step of the process, the AIC of the simplified model and the lrttest() function within the lrttest package (Zeileis & Hothorn 2002) was used to compare the simplified model with the previous version. If the AIC of the new model was lower and the difference between the two models was not found to be significant at $p < .05$, the more simplified model was adopted.

A list of maximal and minimal models for all species that were assessed can be found in Appendix 1, with model outputs.

The practice of comparing abundances between species and sampling designs has been criticised based on the differences in detectability between species due to behaviour, body size, and survey design, and has led to the emergence of methodologies that seek to correct for imperfect detection (Tobler et. al. 2008, Rowcliffe & Carbone 2008, Sollmann et. al. 2013). No adjustment has been made to compensate for imperfect detection in this analysis. Banks- Leite et. al. (2013) found that the use of models adjusting for imperfect detection do not yield significantly more accurate results than traditional generalised linear models (GLMs) when studies aim to assess an ecological response to environmental factors or address rare or difficult-to-detect species. While using unadjusted estimates of occupancy, abundance, or richness can lead to underestimates of these values, the overall measure of strength and direction of the results are unaffected by imperfect detection (Banks-Leite et. al. 2013). Kelly 2008 also found that unadjusted capture frequencies were highly correlated with adjusted abundance using data from Tobler et. al. (2008). Additionally, Banks-Leite et. al. (2013) found that adjusted abundance estimates entail much higher data requirements including repeat analysis in each locations, which was not part of the sampling design for this study.

2.3.2 Species richness

Species richness, the number of species present at a given point, is difficult to estimate. Rarefaction methods are often used, which seek to standardise the number of samples between sites (Gotelli and Cowell 2001). For this analysis, standardising the coverage was chosen because rarefaction can lead to comparing samples with of different levels of completeness, as some samples are more diverse than others and therefore a standard size would not capture a standard level of coverage between communities (Chao and Jost 2012).

The iNEXT package (Hsieh, Ma & Chao 2014) in R was used to estimate the species richness at all sample points for a standard level of sample coverage, which was assessed at 80%. These species richness estimates were then assessed against the same covariates as the individual species abundance analysis above, with elevation modelled as a quadratic term (which can show curved lines) for the purpose of identifying any mid-elevation effects. Two-way interactions between elevation and covariates were also included in this model, as this analysis focusses on elevation. A quasi-Poisson generalised linear model was used, since species richness estimates were not integers and the data was found to be over-dispersed. The model was then manually simplified by dropping insignificant interaction terms then insignificant single terms one at a time. The minimal model was reached when either all terms showed as significant ($p < .05$), or when the simplified model was shown to be significantly different than the previous step using an ANOVA, test = 'F.'

Rats and squirrels were excluded with the exception of the tufted ground squirrel (*Rheithrosciurus macrotis*), the long-tailed giant rat (*Leopoldamys sabanus*), and the spiny rat (*Maxomys rajah*) because they were not identified to the species level during the 2015 sampling period.

2.3.3 Community composition

Community composition was assessed using the Latent Dirichlet Allocation (LDA) method, which is a probabilistic model that assesses the gradual change in component communities from larger species assemblages (Valle et. al. 2014). The LDA method was originally created for topic modelling within text (Blei et. al. 2003), and has subsequently been applied to species communities in an ecological context by Valle et. al. (2014) using species counts at each sampling points as inputs, rather than the count of terms within each document that would be used for text mining purposes. To my knowledge, this application of LDA to mammalian communities is novel. LDA was chosen over other methods for assessing community composition because it allows for each sampling point to contain more than one community, and it allows for the gradual change of communities along gradients, as opposed to the abrupt blocks of species that other methods rely upon (Valle et. al. 2104).

The same species assemblage was used as for the species richness analysis. Number of independent captures were amalgamated into bands spanning 100 vertical meters. The last sample point at 903 m.a.s.l. was combined with the 800-899 band due to its small sample size and proximity to this altitudinal band. Models were created using the “topicmodels” package (Gruen and Hornik 2011) in R v3.1.1 to assess the number of distinct mammalian communities present within each sampling block. The model that best represents the number of mammalian communities present was then chosen with the lowest AIC value was chosen from this group.

3 Results

3.1 Trapping effort

For the data collected in 2015 for the sole purpose of this analysis, trap cameras deployed were deployed for a mean of 17.5 days, as defined by the number of camera trap nights or CTNs. Of the 59 trap stations used in this study, 21 failed prior to the full 21-day term. For the data collected previously, trap cameras deployed were deployed for a mean of 31.5 days, as defined by the number of camera trap nights or CTNs.

Transect	No. of Points	Minimum CTNs	Maximum CTNs	Mean CTNs	No. of Failures	% Lasted Full Term
SAFE VJR North 2015	17	0	25	18.23	7	59%
SAFE VJR South 2105	13	1	23	16	6	54%
Maliau East 2015	15	0	23	18.33	5	86%
Maliau West 2015	14	1	21	18.36	2	64%
SAFE VJR North 2013	30	3	94	64.43	13	56%
SAFE VJR South 2012/13	27	0	94	61.35	14	86%
Maliau East 2011/12	68	0	65	21.88	16	67%
Maliau West 2013	48	0	63	52.00	13	73%
Maliau North 2012	61	0	64	36.18	14	77%

Table 4 Number of sample points and sampling success across all sampling blocks and periods

3.2 Abundance

Elevation was a significant factor in the abundance of seven of the 16 species assessed. Of these species, only the Bornean orang-utan and mouse deer displayed a negative coefficient, indicating that their abundance decreases with an increase in altitude. Slope showed significance for only two species, sambar deer and mouse deer, with sambar deer abundance responding positively to increasing slope and mouse deer responding negatively. Canopy openness was the most common indication of species abundance, as it was shown to be significant for nine species with a combination of positive and negative coefficients. The interaction between elevation and canopy openness showed significance for only the leopard cat, whereas interaction between elevation and slope showed significance for only the sambar deer. Both these effects are positive and are not strongly significant at $p < .05$. See Figure 2 for further detail. Minimal models and model outputs for all analysed species are available in Appendix I and have been excluded here due to their length.

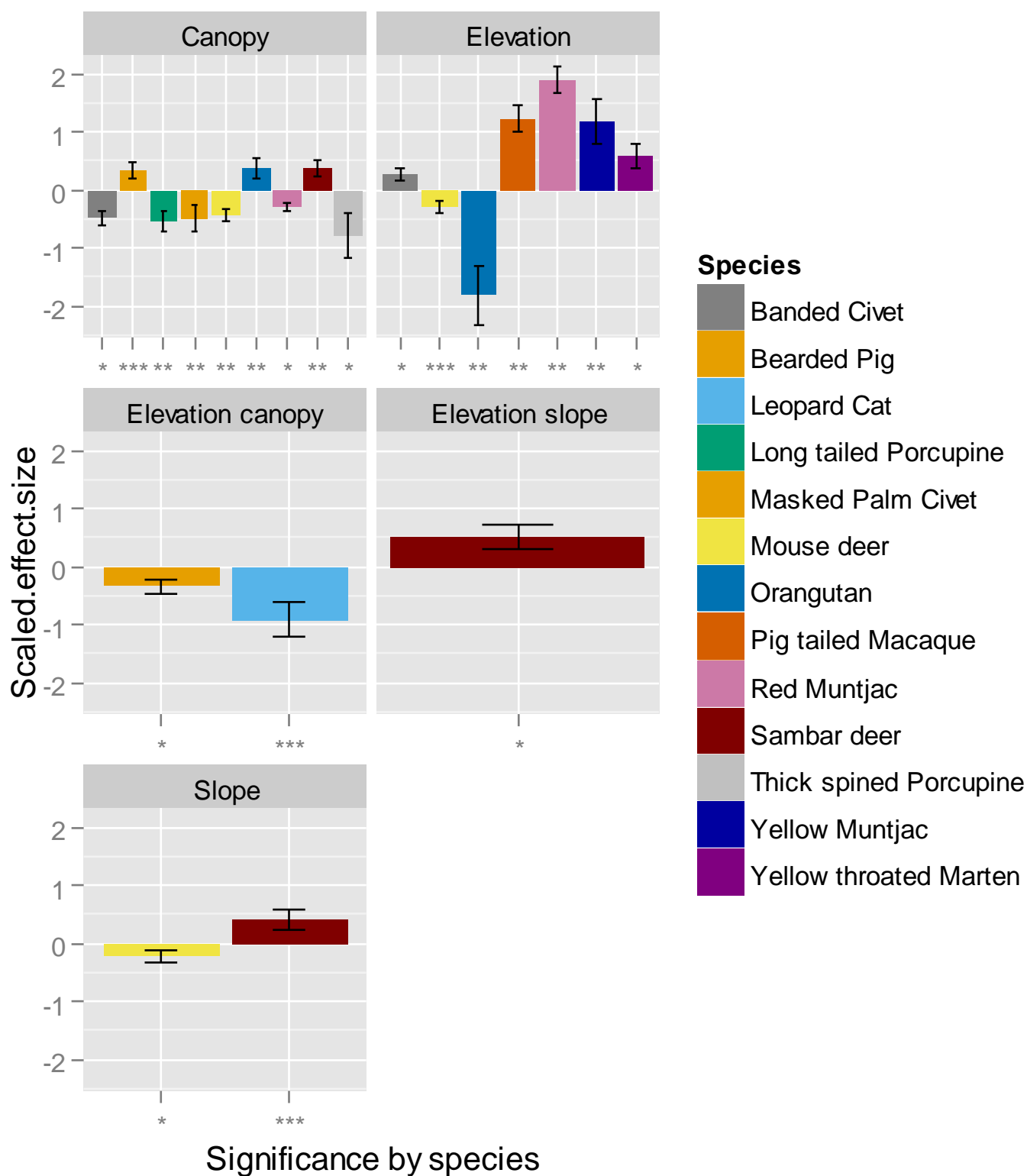


Fig 2 The scaled effect of single covariates elevation, canopy openness, and slope; and interaction terms elevation/canopy cover and elevation/slope on the mammal species for which it was found to be significant, using a zero inflated negative binomial GLM. Add new five and six and last. Remove 7 and last

Although elevation displayed a positive effect for five species on its own, the interaction between elevation and sampling block was negative and significant for three species across all four blocks, meaning that for these three species, higher altitudes are indicative of lower abundance within these specific blocks. The thick-spined porcupine was the only species that showed a positive effect for the interaction of elevation and sampling block, within Maliau East.

Sampling blocks were significant terms in 27 cases (the number of cases is higher than the number of assessed species because this interaction term can be significant for the same species with respect to different sampling blocks). When these interaction terms are significant, it indicates that the abundance of the species in question was significantly higher (if positive) or lower (if negative) in the given sampling block than in comparison to the intercept, which is set by the first covariate in alphabetical order, Maliau North in this case.

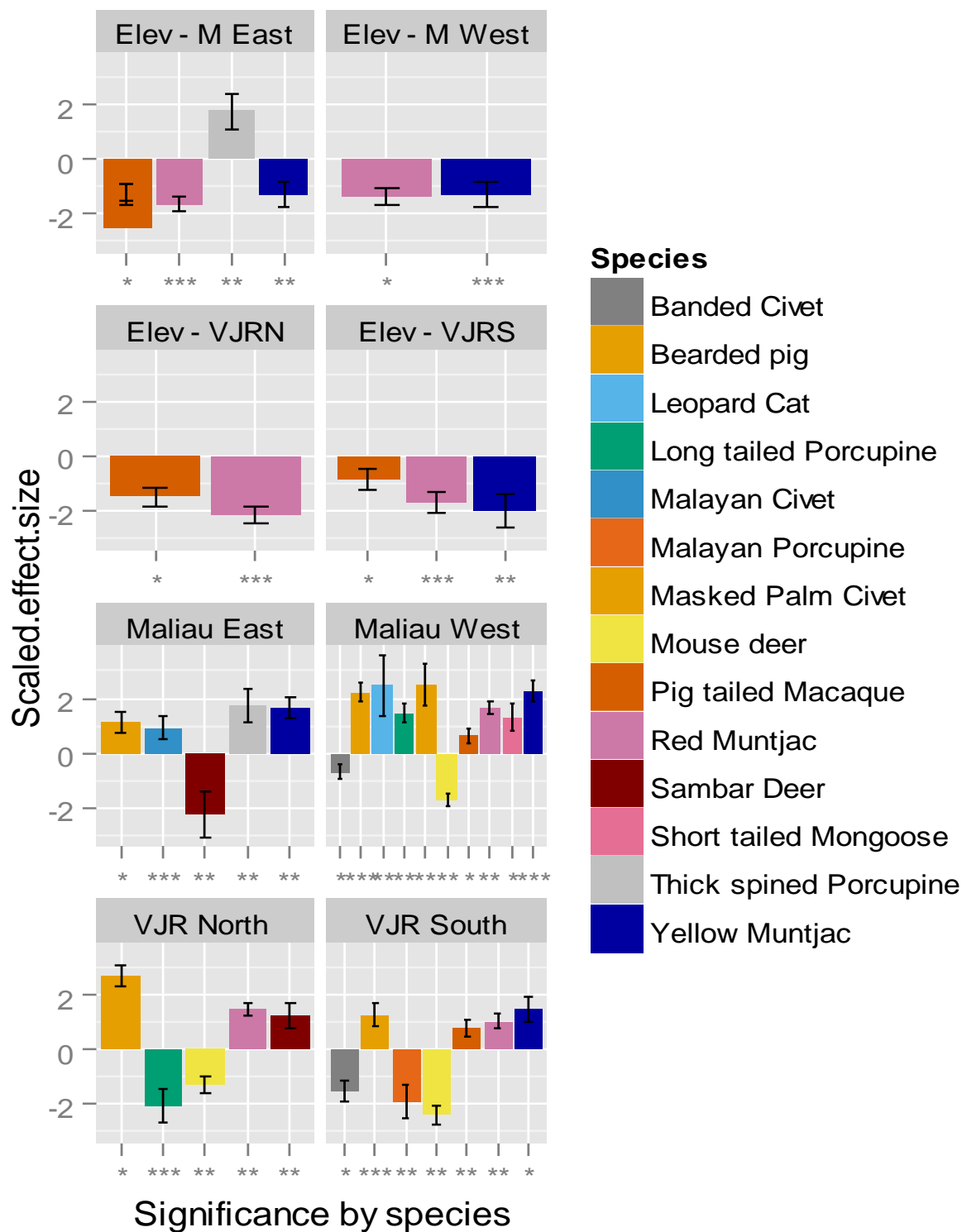


Fig 2 The scaled effect of single sampling blocks and the interaction between elevation and sampling blocks on all mammal species for which each respective term was found to be significant, using a zero inflated negative binomial GLM

3.3 Species richness

For estimated species richness at 80% sample coverage, only elevation, canopy openness, and sampling block were found to significantly affect richness estimates. Interactions between sampling block and elevation was insignificant, indicating that the five blocks do not show a significantly different degree of correlation between elevation and species richness. Only the Maliau West sampling block displayed a significantly different trend than the overall dataset, in that its species richness was significantly higher, as shown by its positive estimate given in Table 5 below. The minimal model is as follows, and results are provided in Table 5:

Min.mod = glm(Richness ~ Elevation + I(Elevation^2) + Canopy Cover, data=fullnew, family=quasipoisson).

	Estimate	Std.Error	t value	p value
(Intercept)	6.44E-01	4.34E-01	1.484	p > .05
BlockOG2	1.38E-01	9.98E-02	1.379	p > .05
BlockOG3	3.63E-01	9.58E-02	3.793	p < .0001
BlockVJRN	-1.68E-01	1.23E-01	-1.362	p > .05
BlockVJRS	2.11E-01	1.20E-01	1.764	p > .05
Elevation	3.76E-03	1.71E-03	2.197	p < .05
Elevation as squared term	-3.71E-06	1.69E-06	-2.191	p < .05
Canopy openness	-1.28E-01	4.23E-02	-3.014	p < .01

Table 5 Minimal model coefficients, standard errors, significance tests and resulting p values for a generalised linear model with quasi Poisson errors on species richness as a function of sampling block, elevation, slope, and canopy cover. Significant terms are in bold.

The modelled predictions for estimated species richness at 80% sample coverage were graphed for each numeric variable, holding other variables at their mean. Richness predictions display a gradually increasing trend with elevation until the mid-elevations of 400-600 meters above sea level, at which time it gradually declines. Estimated richness declines as canopy cover gets increasingly less dense.

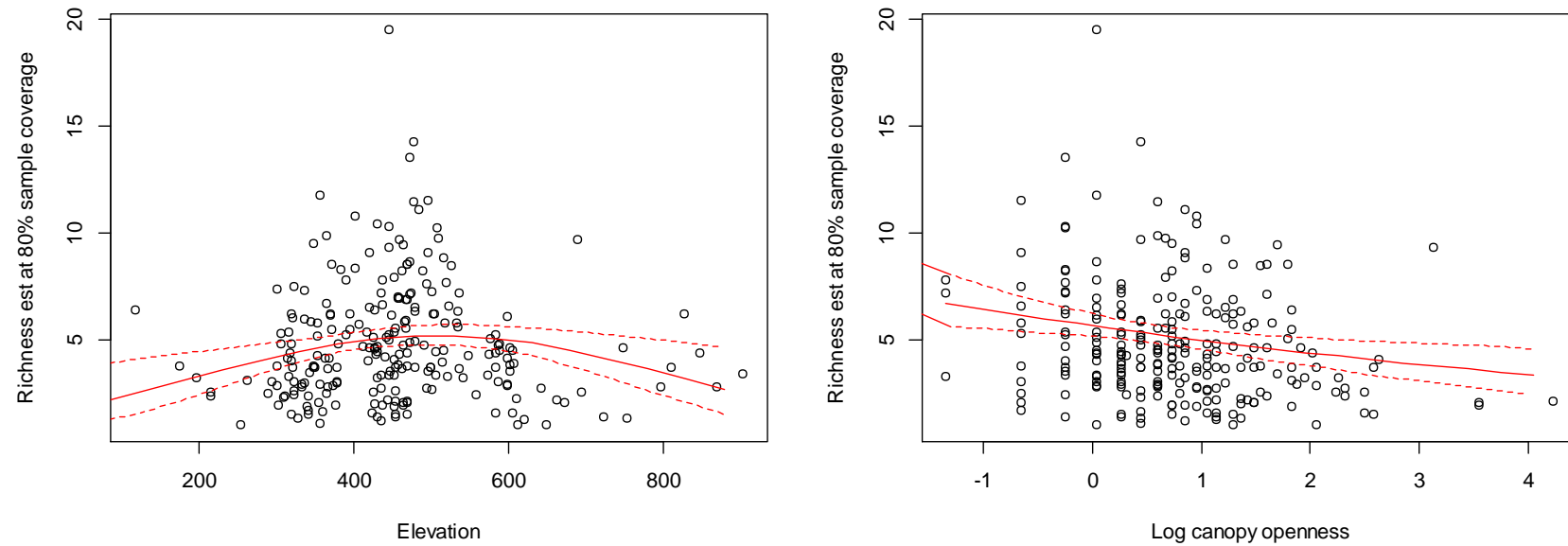


Fig 6 Estimated species richness for the mammalian community as a function of elevation (left) and canopy openness as defined by canopy cover percentage subtracted from 100% and log transformed (right). Dots show data while predictions of a quasipoisson generalised linear model are shown as the solid red line, with a 95% confidence interval shown as dashed lines. Terms related to sampling block were removed from the model used to generate the graph as they are non-numeric.

3.4 Community composition

Our LDA analysis shows one dominant community at low altitudes, a different dominant community at high altitudes, and two more emerging then declining at mid-altitudes, one of which makes a small resurgence in the highest altitudinal band. The top six species comprising each of these distinct communities are provided in Table 6, and their relative abundance in relation to each other is provided in Figure 8.

Community 1	Community 2	Community 3	Community 4
Bearded.Pig	Red.Muntjac	Mouse.deer	Bearded.Pig
Pig.tailed.Macaque	Pig.tailed.Macaque	Yellow.Muntjac	Red.Muntjac
Mouse.deer	Mouse.deer	Pig.tailed.Macaque	Pig.tailed.Macaque
Sambar.Deer	Spiny.Rat	Banded.Civet	Yellow.Muntjac
Red.Muntjac	Yellow.Muntjac	Bearded.Pig	Sun.Bear
Yellow.Muntjac	Bearded.Pig	Thick.spined.Porcupine	Banded.Civet

Table 6 Species comprising each individual mammalian community in our study area as assessed using the LDA method

Although the rank of each species in terms of how prominently it features in each community varies, some species are prominent in more than one community with bearded pigs and pig-tailed macaques featuring in all four communities.

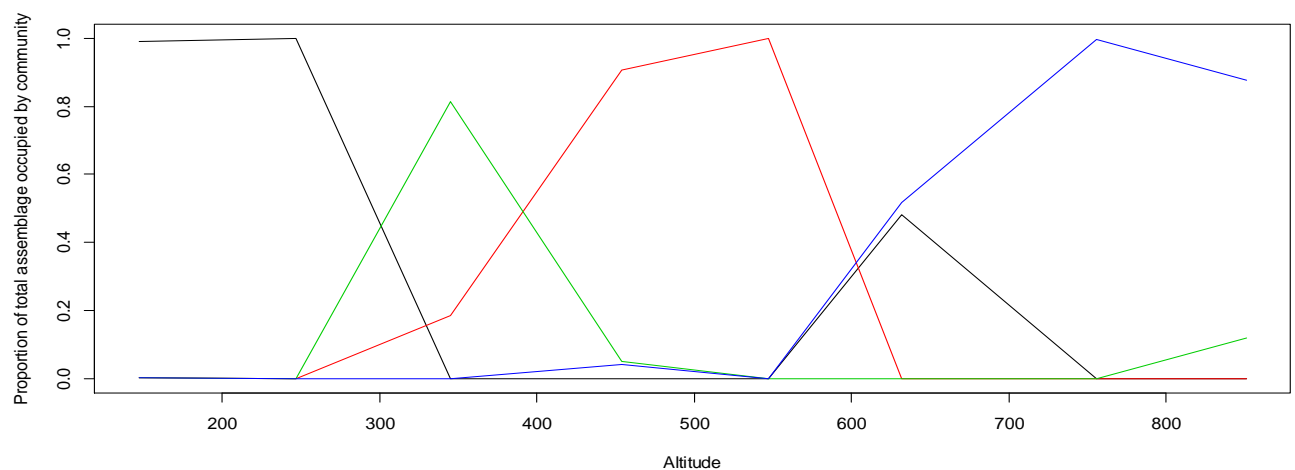


Fig 8 Change in the relative abundance of each of five mammalian communities along the altitudinal gradient for all five sampling blocks in Malaysian Borneo. Line colours are as follows: Community 1 (black), Community 2 (green), Community 3 (red), Community 4 (blue).

4 Discussion

4.1 Abundance

Our findings suggest that altitude and slope are not indicative of individual species abundance in primary and previously logged forest on their own with a few exceptions, although abundance does decline for three species with altitude within individual sampling blocks. These findings may indicate that many medium and large mammal species could persist well in higher altitude and steeper forested areas, which could provide much-needed habitat and therefore facilitate the continued persistence of the species as this topographical environment will increasingly become mammals' only option as land is cleared more readily for oil palm at lower altitudes and more gradual slopes.

These results are surprising and bode positively for many species. However, they also highlight an important exception; orang-utans stand out from the rest of the mammalian community in that their abundance declines strongly and significantly as elevation increases (see Figure 2 above), and therefore they may not be able to persist in higher elevations like other mammals. The vulnerability of this endangered and charismatic species is further supported by their recent and projected decline; WWF found that their population declined by 14% in only five years between 2007 and 2012 (Wullfraat 2014). Struebig et. al. (2015a) have projected that they could face up to a 74% loss of habitat by 2080 when the effects of climate change are combined with the continuation of the current deforestation trend. However, it is worth noting that orang-utans are largely arboreal and therefore our detection of them on the ground may not be representative of their presence.

4.2 Richness and community composition

The results show a mid-elevation peak in species richness between 400 and 600 m.a.s.l., which we would have expected based on common richness patterns in small mammals across elevational gradients (McCain 2005). However, the definition of "mid-elevation" changes relative to the elevational spread of the study in question, mammalian communities appear to peak at mid-elevations, regardless of the absolute elevation of the study area. Our findings align with this trend, although our peak is very slight when the 95% confidence interval is taken into account. For example, Nor et. al. (2001) found that small mammal communities peak at 1400-1500 m.a.s.l. on Mt. Kinabalu, the tallest mountain in Sabah state; these altitudes are considered mid-elevation for the area but is actually higher in absolute terms than the maximum elevation of our study areas. It is interesting that our results mirror this trend, especially considering that the low altitude sampling points from all transects assessed in this study occur near large rivers (see Figure 1). If these mid-altitude peaks occur more broadly, this indicates that areas of higher species richness will potentially face less pressure than their low-altitude counterparts.

Regarding community composition, single communities dominate the species assemblage at low and high elevations, with different communities popping up in emerging then declining in the middle. . High and low altitude communities display overlap between the prominent species, therefore suggesting that the differences lie in some of the less common members of the community. This trend indicates that not only is there higher richness at mid-elevations, but the way in which communities are composed changes with altitude, even when common species feature in all of them.

4.3 Implications for protected area design

Our results together indicate that most mammal species are relatively resilient to changes in altitude. Given these results, Borneo's medium and large mammals could likely persist in a protected area network that provides refuge above the altitudes most at risk for deforestation.

In absolute terms, the highest amount of protected land area in Malaysian Borneo occurs in lower elevational bands but the percentage of total land in each altitudinal band that is part of a protected area actually rises with altitude (see Figure 9). This means that although less land is available at higher altitudes, the chance of that land being protected rises with altitude. Seventeen percent of the forest inside the Heart of Borneo is protected (Wulffraat 2014) although their connectivity disappearing (Ewers et. al. 2011).

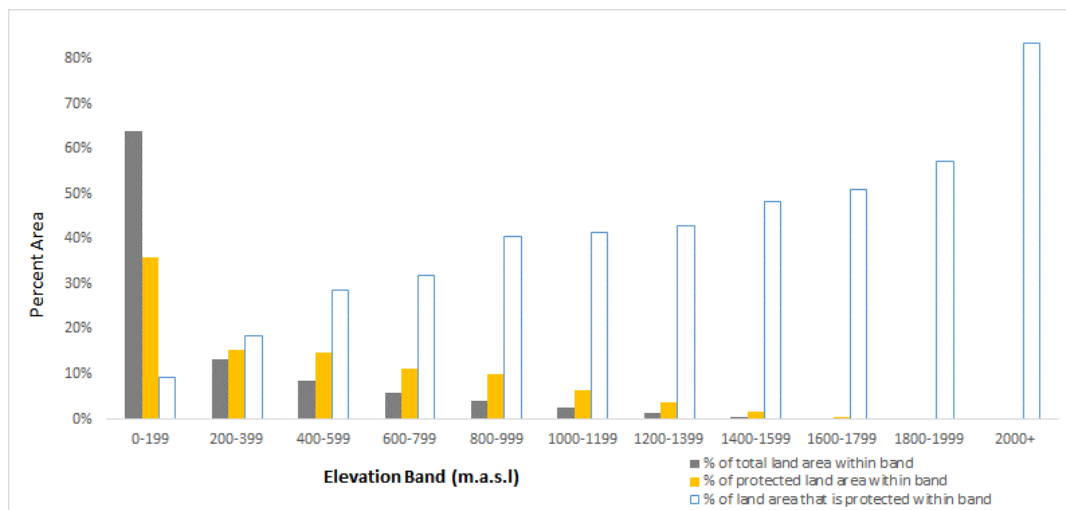


Fig 9 Protected area as a percentage of total land area in Malaysian Borneo. Protected area information was taken from the World Protected Area Network (protectedplanet.net); land area was taken from ASTER DEM (asterweb.jpl.nasa.gov/gdem.asp). Graph format was based on a similar analysis in Scriven et. al. 2015.

Although Borneo's existing protected areas appears to meet the needs of mammals, there is not adequate connectivity to facilitate the movement to higher elevations, which will worsen in the future (Scriven et. al. 2015). Struebig et. al. (2015b) demonstrate that this shift up slope will become

increasingly necessary as the climate warms, and have called for increased protected area at high altitudes to facilitate it.

As over 30% of land area in each band over 400 m.a.s.l. is already protected and many mammals' abundances would likely not be affected by an upward shift, I suggest that future protected area development should focus on providing corridors that will facilitate this shift. Conservation corridors were found to be most effective for Bornean mammals when built with ecological considerations for similar multi-species groups (Brodie et. al. 2015), but connectivity is not built into the current protected area system (Struebig et. al. 2015b). Therefore, although our analysis appears to support the existing altitudinal distribution of the protected area network, connectivity issues at low altitudes need to be addressed.

4.4 Limitations and suggested further study

Although our findings suggest that most mammal populations could persist at higher elevations and on steeper slopes, this finding comes with caveats due to the limitations of the study. This study did not consider the effects of the habitat fragmentation that is occurring due to the continuing deforestation for oil palm. Covariates related to this process have been found to be important in influencing the persistence of mammals along the altitudinal gradient, especially as forest fragments shrink (Kinniard et. al. 2003). The effect of fragmentation was not addressed in this study because our purpose was to establish a baseline in undisturbed forest. However, it represents the reality of the environment that Borneo's mammals will increasingly face, and any conservation implications must consider it. A long-term study of the effects of fragmentation is being carried out at the SAFE Project which will provide some of this much-needed information (Ewers et. al. 2011), although the altitudinal gradient available at their fragmented sampling sites is narrower than the one used in this study.

Other covariates that were not measured in this study could be exerting an effect on mammal abundance, richness, and community compositions, such as those related to climate, weather, and food sources. As examples, proximity to water is a primary factor driving the species distribution of the flat headed cat (*Prionailurus planiceps*) due to its dietary reliance on fish and amphibians (Wilting et. al. 2010), and orang-utans are known to be limited by fruit availability, which is connected to temperature and rainfall (Struebig et. al. 2015). Other species could have similarly specific habitat requirements which are as yet unknown.

Our findings potentially provide hope for the future survival of mammals in Malaysian Borneo and potentially in other tropical areas that face similar land-use pressures. Aside from the mid-altitude species richness peak, it is unknown whether our findings are more broadly applicable across orders,

or whether they are specific to medium and large mammals, potentially due to their relatively high mobility and tolerance of microclimatic conditions. It would be interesting to conduct similar studies of birds, reptiles, and even invertebrates across the same gradients, to assess whether higher altitude and steeper habitat represents a viable refuge for all of Borneo's animals as deforestation continues to affect their habitat.

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7 Appendices

7.1 Minimal models and outputs for species abundance

The following code provides the minimal models and model outputs for the zero inflated negative binomial generalised linear models used to assess the relationship between individual species abundance and altitude and other covariates.

7.1.1 Maximal model

The maximal model that served as a starting point for all species models is as follows:

```
Maximal.model = zeroinfl(Species.name ~ Block + scale(Elevation) + scale(SlopeGIS) +
scale(Canopy.Cover)) + scale(Elevation)*Block + scale(Elevation)*scale(SlopeGIS) +
scale(Elevation)*scale (Canopy.Cover)) + offset(log(CTNs)) | 1, data = full, dist = "negbin")
```

7.1.2 Banded palm civet

```
(bpcivmodzf3)
```

Call:

```
zeroinfl(formula = Banded.Civet ~ Block + scale(Elevation..DEM.) + scale(log(100 - Densimeter.Average)) +
offset(log(CTNs)) | 1, data = full, dist = "negbin")
```

Pearson residuals:

```
Min 1Q Median 3Q Max
-0.8495 -0.6458 -0.3814 0.2156 5.3804
```

Count model coefficients (negbin with log link):

# Banded Palm Civet	Estimate	Standard Error	z value	p value	Significance
#(Intercept)	-3.2805	0.1835	-17.88	<2.00E-16	***
#BlockOG2	-0.2701	0.265	-1.019	3.08E-01	
#BlockOG3	-0.6938	0.2732	-2.54	1.11E-02	*
#BlockVJRN	-0.4243	0.3074	-1.38	1.67E-01	
#BlockVJRS	-1.5251	0.396	-3.851	1.18E-04	***
#scale(Elevation..DEM.)	0.2782	0.1111	2.504	1.23E-02	*
#scale(log(100- Densimeter.Average))	-0.4735	0.1246	-3.8	0.000145	***
#Log(theta)	-0.1311	0.2008	-0.653	0.513928	

Zero-inflation model coefficients (binomial with logit link):

```
Estimate Std. Error z value Pr(>|z|)
(Intercept) -11.82 134.03 -0.088 0.93
---
Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
```

Theta = 0.8771

Number of iterations in BFGS optimization: 39

Log-likelihood: -342.4 on 9 Df

7.1.3 Bearded pig

```
> summary(pigmodzf3)
```

Call:

```
zeroinfl(formula = Bearded.Pig ~ Block + scale(Elevation..DEM.) + scale(log(100 - Densimeter.Average)) +
scale(Elevation..DEM.) * scale(log(100 - Densimeter.Average)) + offset(log(CTNs)) | 1, data = full,
dist = "negbin")
```

Pearson residuals:

Min 1Q Median 3Q Max
-0.64712 -0.55014 -0.42546 0.01319 10.02694

# Bearded Pig	Estimate	Standard Error	z value	p value	Significance
#(Intercept)	-4.3042	0.2865	-15.026	<2.00E-16	***
#BlockOG2	1.0864	0.3775	2.878	4.00E-03	**
#BlockOG3	2.2093	0.3565	6.197	5.74E-10	***
#BlockVJRN	2.7228	0.3968	6.861	6.83E-12	***
#BlockVJRS	1.2625	0.4153	3.04	2.37E-03	**
#scale(Elevation..DEM.)	0.2403	0.1377	1.745	8.10E-02	.
#scale(log(100-Densimeter.Average))	0.3396	1.30E-01	2.613	0.00898	**
#scale(Elevation..DEM.):scale(log(100-Densimeter.Average))	-0.3345	0.1213	-2.758	0.00582	**
#Log(theta)	-0.8475	0.1306	-6.491	8.53E-11	***

Zero-inflation model coefficients (binomial with logit link):

Estimate Std. Error z value Pr(>|z|)
(Intercept) -15.28 575.82 -0.027 0.979

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Theta = 0.4285

Number of iterations in BFGS optimization: 43

Log-likelihood: -474.1 on 10 Df

7.1.4 Leopard cat

> summary(catmodzf3)

Call:

```
zeroinfl(formula = Leopard.Cat ~ Block + scale(Elevation..DEM.) + scale(log(100 - Densimeter.Average)) +  
  scale(Elevation..DEM.) * scale(log(100 - Densimeter.Average)) + offset(log(CTNs)) | 1, data = full,  
  dist = "negbin")
```

Pearson residuals:

Min 1Q Median 3Q Max
-0.6825 -0.2781 -0.1252 -0.0851 7.3966

Count model coefficients (negbin with log link):

#Leopard Cat	Estimate	Standard Error	z value	p value	Significance
#(Intercept)	-7.0444	1.1187	-6.297	3.03E-10	***
#BlockOG2	0.2886	1.4734	0.196	8.45E-01	
#BlockOG3	2.4827	1.1017	2.254	2.42E-02	*
#BlockVJRN	1.4961	1.2125	1.234	2.17E-01	
#BlockVJRS	1.4913	1.1957	1.247	2.12E-01	
#scale(Elevation..DEM.)	0.3287	0.4012	0.819	4.13E-01	
#scale(log(100-Densimeter.Average))	-0.4051	0.2884	-1.405	0.16013	
#scale(Elevation..DEM.):scale(log(100-Densimeter.Average))	-0.9168	0.2964	-3.094	0.00198	**
#Log(theta)	12.2634	463.8972	0.026	9.79E-01	

Zero-inflation model coefficients (binomial with logit link):

Estimate Std. Error z value Pr(>|z|)

```
(Intercept) 0.3842 0.5426 0.708 0.479
---
Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
```

```
Theta = 211796.8887
Number of iterations in BFGS optimization: 53
Log-likelihood: -62.9 on 10 Df
```

7.1.5 Long-tailed porcupine

```
> summary(ltpmodzf5)
```

Call:

```
zeroinfl(formula = Long.tailed.Porcupine ~ Block + scale(log(100 - Densimeter.Average)) + offset(log(CTNs)) | 1, data = full, dist = "negbin")
```

Pearson residuals:

```
Min 1Q Median 3Q Max
-0.6229 -0.4786 -0.3541 -0.1396 11.2217
```

Count model coefficients (negbin with log link):

	Estimate	Std. Error	z value	Pr(> z)
(Intercept)	-4.1024	0.2753	-14.901	< 2e-16 ***
BlockOG2	-0.7864	0.4290	-1.833	0.06678 .
BlockOG3	1.4340	0.3513	4.082	4.46e-05 ***
BlockVJRN	-2.0408	0.6221	-3.280	0.00104 **
BlockVJRS	-0.8694	0.5005	-1.737	0.08236 .
scale(log(100 - Densimeter.Average))	-0.5315	0.1728	-3.075	0.00210 **
Log(theta)	-0.8881	0.2110	-4.210	2.56e-05 ***

Zero-inflation model coefficients (binomial with logit link):

	Estimate	Std. Error	z value	Pr(> z)
(Intercept)	-11.15	109.48	-0.102	0.919

```
---
Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
```

```
Theta = 0.4115
Number of iterations in BFGS optimization: 35
Log-likelihood: -270.4 on 8 Df
```

7.1.6 Malayan civet

```
> summary(mcivmodzf2)
```

Call:

```
zeroinfl(formula = Malayan.Civet ~ Block + scale(Elevation..DEM.) + scale(SlopeGIS) + scale(log(100 - Densimeter.Average)) + scale(Elevation..DEM.) * scale(SlopeGIS) + offset(log(CTNs)) | 1, data = full, dist = "negbin")
```

Pearson residuals:

```
Min 1Q Median 3Q Max
-0.6868 -0.5123 -0.3860 -0.1589 5.6602
```

Count model coefficients (negbin with log link):

	Estimate	Std. Error	z value	Pr(> z)
(Intercept)	-4.67935	0.53000	-8.829	<2e-16 ***
BlockOG2	0.91342	0.39939	2.287	0.0222 *
BlockOG3	0.56928	0.41023	1.388	0.1652
BlockVJRN	-0.12258	0.50683	-0.242	0.8089
BlockVJRS	-0.02679	0.47975	-0.056	0.9555
scale(Elevation..DEM.)	-0.18133	0.17143	-1.058	0.2902
scale(SlopeGIS)	-0.02576	0.13960	-0.185	0.8536
scale(log(100 - Densimeter.Average))	0.07012	0.14618	0.480	0.6314

```
scale(Elevation...DEM.):scale(SlopeGIS) -0.33426 0.17103 -1.954 0.0507 .
Log(theta) 0.24467 1.23379 0.198 0.8428
```

Zero-inflation model coefficients (binomial with logit link):

```
Estimate Std. Error z value Pr(>|z|)
(Intercept) -1.010 1.767 -0.572 0.568
```

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Theta = 1.2772

Number of iterations in BFGS optimization: 24

Log-likelihood: -195.1 on 11 Df

7.1.7 Malayan (common) porcupine

```
> summary(mpmozdf6)
```

Call:

```
zeroinfl(formula = Malayan.Porcupine ~ Block + offset(log(CTNs)) | 1, data = full, dist = "negbin")
```

Pearson residuals:

```
Min 1Q Median 3Q Max
-0.4902 -0.4461 -0.3742 -0.1626 11.4463
```

Count model coefficients (negbin with log link):

```
Estimate Std. Error z value Pr(>|z|)
(Intercept) -3.6785 0.2999 -12.268 < 2e-16 ***
BlockOG2 -0.7094 0.4440 -1.598 0.11009
BlockOG3 0.5181 0.4003 1.294 0.19558
BlockVJRN -0.8273 0.5247 -1.577 0.11484
BlockVJRS -1.8734 0.6084 -3.079 0.00208 **
Log(theta) -1.3310 0.2135 -6.234 4.54e-10 ***
```

Zero-inflation model coefficients (binomial with logit link):

```
Estimate Std. Error z value Pr(>|z|)
(Intercept) -7.441 87.361 -0.085 0.932
```

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Theta = 0.2642

Number of iterations in BFGS optimization: 69

Log-likelihood: -268 on 7 Df

7.1.8 Masked palm civet

```
> summary(mpcivmodzf4)
```

Call:

```
zeroinfl(formula = Masked.Palm.Civet ~ Block + scale(SlopeGIS) + scale(log(100 - Densimeter.Average)) +
offset(log(CTNs)) | 1, data = full, dist = "negbin")
```

Pearson residuals:

```
Min 1Q Median 3Q Max
-0.87127 -0.23404 -0.16068 -0.09532 7.14453
```

Count model coefficients (negbin with log link):

```
Estimate Std. Error z value Pr(>|z|)
(Intercept) -7.2860 0.7349 -9.914 < 2e-16 ***
BlockOG2 0.1826 1.0303 0.177 0.85934
BlockOG3 2.5129 0.7562 3.323 0.00089 ***
BlockVJRN -0.2054 1.2818 -0.160 0.87271
```

```
BlockVJRS          0.2699  1.0433  0.259 0.79589
scale(SlopeGIS)     0.4072  0.2128  1.913 0.05569 .
scale(log(100 - Densimeter.Average)) -0.5010  0.2274 -2.203 0.02762 *
Log(theta)         0.1658  0.5866  0.283 0.77739
```

Zero-inflation model coefficients (binomial with logit link):

```
Estimate Std. Error z value Pr(>|z|)
(Intercept) -11.74  252.54 -0.046  0.963
```

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Theta = 1.1804

Number of iterations in BFGS optimization: 45

Log-likelihood: -81.92 on 9 Df

7.1.9 Mouse deer

```
> summary(mdmodzf3)
```

Call:

```
zeroinfl(formula = Mouse.deer ~ Block + scale(Elevation..DEM.) + scale(SlopeGIS) + scale(log(100 - Densimeter.Average))
+
offset(log(CTNs)) | 1, data = full, dist = "negbin")
```

Pearson residuals:

```
Min 1Q Median 3Q Max
-0.8178 -0.6436 -0.4129 0.2621 6.9034
```

Count model coefficients (negbin with log link):

```
Estimate Std. Error z value Pr(>|z|)
(Intercept) -1.6456  0.1700 -9.682 < 2e-16 ***
BlockOG2     -0.3265  0.2352 -1.388 0.16514
BlockOG3     -1.7335  0.2549 -6.802 1.03e-11 ***
BlockVJRN    -1.2794  0.3143 -4.070 4.69e-05 ***
BlockVJRS    -2.3934  0.3377 -7.086 1.38e-12 ***
scale(Elevation..DEM.) -0.2840  0.1097 -2.590 0.00961 **
scale(SlopeGIS) -0.2256  0.1007 -2.241 0.02504 *
scale(log(100 - Densimeter.Average)) -0.4321  0.1094 -3.950 7.81e-05 ***
Log(theta)    -0.2979  0.1340 -2.223 0.02623 *
```

Zero-inflation model coefficients (binomial with logit link):

```
Estimate Std. Error z value Pr(>|z|)
(Intercept) -14.37  349.57 -0.041  0.967
```

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Theta = 0.7424

Number of iterations in BFGS optimization: 43

Log-likelihood: -561.9 on 10 Df

7.1.10 Orangutan

```
> summary(ormodzf2)
```

Call:

```
zeroinfl(formula = Orangutan ~ Block + scale(Elevation..DEM.) + scale(SlopeGIS) + scale(log(100 - Densimeter.Average)) +
scale(Elevation..DEM.) * scale(SlopeGIS) + offset(log(CTNs)) | 1, data = full, dist = "negbin")
```

Pearson residuals:

```
Min 1Q Median 3Q Max
-1.251e+00 -9.512e-05 -2.416e-05 -1.207e-05 4.046e+00
```

Count model coefficients (negbin with log link):

Orangutan	Estimate	Standard Error	z value	p value	Significance
#(Intercept)	-24.9199	3391.6054	-0.007	0.994138	
#BlockOG2	0.6186	4611.4841	0	1.00E+00	
#BlockOG3	0.1183	6327.8515	0	1.00E+00	
#BlockVJRN	19.7742	3391.6053	0.006	9.95E-01	
#BlockVJRS	20.1837	3391.6054	0.006	9.95E-01	
#scale(Elevation..DEM.)	-1.813	0.5084	-3.566	3.62E-04	***
#scale(SlopeGIS)	0.3547	2.16E-01	1.641	1.01E-01	
#scale(log(100-Densimeter.Average))	0.3767	1.84E-01	2.047	0.040677	*
#scale(Elevation..DEM.):scale(SlopeGIS)	-1.0559	0.5741	-1.839	6.59E-02	.
#Log(theta)	15.1501	197.3797	0.077	9.39E-01	

Zero-inflation model coefficients (binomial with logit link):

Estimate Std. Error z value Pr(>|z|)
 (Intercept) -0.5133 0.6290 -0.816 0.415

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Theta = 3798592.4793

Number of iterations in BFGS optimization: 49

Log-likelihood: -43.42 on 11 Df

7.1.11 Pig tailed macaque

summary(ptmmodzf4)

Call:

```
zeroinfl(formula = Pig.tailed.Macaque ~ Block + scale(Elevation..DEM.) + scale(Elevation..DEM.) *  
Block + offset(log(CTNs)) | 1, data = full, dist = "negbin")
```

Pearson residuals:

Min 1Q Median 3Q Max
 -0.7546 -0.6439 -0.4154 0.1408 9.8411

Count model coefficients (negbin with log link):

Pig tailed macaque	Estimate	Standard Error	z value	p value	Significance
#(Intercept)	-2.77991	0.20285	-13.704	<2.00E-16	***
#BlockOG2	-0.02939	0.2771	-0.106	9.16E-01	
#BlockOG3	0.62298	0.27831	2.238	2.52E-02	*
#BlockVJRN	-0.39457	0.31691	-1.245	2.13E-01	
#BlockVJRS	0.79626	0.31265	2.547	1.09E-02	*
#scale(Elevation..DEM.)	1.2234	0.22609	5.411	6.26E-08	***
#BlockOG2:scale(Elevation..DEM.)	-1.21639	3.19E-01	-3.808	1.40E-04	***
#BlockOG3:scale(Elevation..DEM.)	-1.26374	0.36404	-3.471	5.18E-04	***
#BlockVJRN:scale(Elevation..DEM.)	-1.46764	0.34254	-4.285	1.83E-05	***
#BlockVJRS:scale(Elevation..DEM.)	-0.83053	0.37701	-2.203	2.76E-02	*
#Log(theta)	-0.48182	0.12573	-3.832	1.27E-04	***

Zero-inflation model coefficients (binomial with logit link):

Estimate Std. Error z value Pr(>|z|)
 (Intercept) -10.04 30.51 -0.329 0.742

 Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Theta = 0.6177
 Number of iterations in BFGS optimization: 29
 Log-likelihood: -549.1 on 12 Df

7.1.12 Red muntjac

summary(redmodzf3)

Call:

zeroinfl(formula = Red.Muntjac ~ Block + scale(Elevation..DEM.) + scale(log(100 - Densimeter.Average)) +
 scale(Elevation..DEM.) * Block + offset(log(CTNs)) | 1, data = full, dist = "negbin")

Pearson residuals:

Min 1Q Median 3Q Max
 -1.1846 -0.7196 -0.3900 0.5368 3.5153

Count model coefficients (negbin with log link):

Red muntjac	Estimate	Standard Error	z value	p value	Significance
#(Intercept)	-3.43836	0.20595	-16.695	<2.00E-16	***
#BlockOG2	0.15611	0.25798	0.605	5.45E-01	
#BlockOG3	1.63002	0.23983	6.797	1.07E-11	***
#BlockVJRN	1.47506	0.25178	5.858	4.67E-09	***
#BlockVJRS	1.04467	0.26721	3.91	9.25E-05	***
#scale(Elevation..DEM.)	1.88873	0.22909	8.245	<2.00E-16	***
#scale(log(100- Densimeter.Average))	-0.28305	6.99E-02	-4.049	5.15E-05	***
#BlockOG2:scale(Elevation..DEM.)	-1.63229	0.27022	-6.041	1.53E-09	***
#BlockOG3:scale(Elevation..DEM.)	-1.35808	0.30184	-4.499	6.82E-06	***
#BlockVJRN:scale(Elevation..DEM.)	-2.15951	0.30503	-7.08	1.45E-12	***
#BlockVJRS:scale(Elevation..DEM.)	-1.67792	0.36657	-4.577	4.71E-06	***
#Log(theta)	0.52474	0.1543	3.401	6.72E-04	***

Zero-inflation model coefficients (binomial with logit link):

Estimate Std. Error z value Pr(>|z|)
 (Intercept) -14.84 640.48 -0.023 0.982

 Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Theta = 1.69
 Number of iterations in BFGS optimization: 55
 Log-likelihood: -555.5 on 13 Df

7.1.13 Sambar Deer

> summary(sammodzf2)

Call:

zeroinfl(formula = Sambar.Deer ~ Block + scale(Elevation..DEM.) + scale(SlopeGIS) + scale(log(100 -
 Densimeter.Average)) + scale(Elevation..DEM.) * scale(SlopeGIS) + offset(log(CTNs)) | 1,
 data = full, dist = "negbin")

Pearson residuals:

Min 1Q Median 3Q Max

-0.6170 -0.4508 -0.2938 -0.1069 5.9664

Count model coefficients (negbin with log link):

Sambar.Deer	Estimate	Standard Error	z value	p value	Significance
#(Intercept)	-4.93953	0.33222	-14.868	<2.00E-16	***
#BlockOG2	-2.26127	0.83248	-2.716	6.60E-03	**
#BlockOG3	0.07733	0.42694	0.181	8.56E-01	
#BlockVJRN	1.23917	0.48713	2.544	0.01096	*
#BlockVJRS	0.64931	0.45213	1.436	0.15097	
#scale(Elevation..DEM.)	0.04525	0.18179	0.249	0.80341	
#scale(SlopeGIS)	0.40718	0.18282	2.227	2.59E-02	*
#scale(log(100-Densimeter.Average))	0.36939	0.12802	2.885	0.00391	**
#scale(Elevation..DEM.):scale(SlopeGIS)	0.52274	0.20782	2.515	0.01189	*
#Log(theta)	-0.78094	0.25362	-3.079	0.00208	**

Zero-inflation model coefficients (binomial with logit link):

Estimate Std. Error z value Pr(>|z|)
 (Intercept) -14.71 663.90 -0.022 0.982

 Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Theta = 0.458

Number of iterations in BFGS optimization: 47

Log-likelihood: -191.7 on 11 Df

7.1.14 Short tailed mongoose

> summary(stmmmodzf6)

Call:

zeroinfl(formula = Short.tailed.Mongoose ~ Block + offset(log(CTNs)) | 1, data = full, dist = "negbin")

Pearson residuals:

Min 1Q Median 3Q Max
 -0.484848 -0.330660 -0.232161 -0.000114 9.715822

Count model coefficients (negbin with log link):

Short tailed mongoose	Estimate	Standard Error	z value	p value	Significance
#(Intercept)	-5.474	0.464	-11.798	<2e-16	***
#BlockOG2	-0.5131	0.6313	-0.813	4.16E-01	
#BlockOG3	1.2842	0.5038	2.549	1.08E-02	*
#BlockVJRN	-17.2262	2003.3463	-0.009	0.9931	
#BlockVJRS	-0.4491	0.7067	-0.635	0.5251	
#Log(theta)	-1.1616	0.4746	-2.447	0.0144	*

Zero-inflation model coefficients (binomial with logit link):

Estimate Std. Error z value Pr(>|z|)
 (Intercept) -6.153 100.439 -0.061 0.951

 Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Theta = 0.313

Number of iterations in BFGS optimization: 52

Log-likelihood: -117.4 on 7 Df

7.1.15 Thick-spined porcupine summary(tspmodzf5)

Call:

```
zeroinfl(formula = Thick.spined.Porcupine ~ Block + scale(log(100 - Densimeter.Average)) + offset(log(CTNs)) | 1, data = full, dist = "negbin")
```

Pearson residuals:

```
Min      1Q  Median      3Q      Max
-3.552e-01 -2.810e-01 -1.980e-01 -8.211e-05  8.133e+00
```

Count model coefficients (negbin with log link):

Thick-spined porcupine	Estimate	Standard Error	z value	p value	Significance
#(Intercept)	-5.5731	0.5161	-10.798	<2.00E-16	***
#BlockOG2	1.7683	0.6306	2.804	5.04E-03	**
#BlockOG3	-1.3344	0.8471	-1.575	1.15E-01	
#BlockVJRN	-17.3764	1688.8118	-0.01	0.99179	
#BlockVJRS	-17.2891	2022.5879	-0.009	0.99318	
#scale(log(100-Densimeter.Average))	-0.7832	0.3953	-1.982	0.04753	*
#Log(theta)	-2.0466	0.3177	-6.441	1.18E-10	***

Zero-inflation model coefficients (binomial with logit link):

```
Estimate Std. Error z value Pr(>|z|)
(Intercept) -9.049 138.288 -0.065 0.948
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
```

Theta = 0.1292

Number of iterations in BFGS optimization: 40

Log-likelihood: -106.4 on 8 Df

7.1.16 Yellow muntjac > summary(yelmodzf3)

Call:

```
zeroinfl(formula = Yellow.Muntjac ~ Block + scale(Elevation..DEM.) + scale(log(100 - Densimeter.Average)) + scale(Elevation..DEM.) * Block + offset(log(CTNs)) | 1, data = full, dist = "negbin")
```

Pearson residuals:

```
Min      1Q  Median      3Q      Max
-0.6876504 -0.5823315 -0.3486070  0.0007762  4.9997690
```

Count model coefficients (negbin with log link):

	Estimate	Standard Error	z value	p value	Significance
Yellow muntjac					
#(Intercept)	-4.5563	0.3174	-14.354	<2.00E-16	***
#BlockOG2	1.6437	0.3772	4.357	1.32E-05	***
#BlockOG3	2.298	0.3764	6.104	1.03E-09	***
#BlockVJRN	0.1356	0.4779	0.284	0.776579	
#BlockVJRS	1.4735	0.437	3.372	0.000747	***
#scale(Elevation..DEM.)	1.1705	0.3913	2.991	0.002779	**
#scale(log(100-Densimeter.Average))	-0.2268	0.1319	-1.72	0.085375	.
#BlockOG2:scale(Elevation..DEM.)	-1.2884	0.4414	-2.919	0.003511	**

#BlockOG3:scale(Elevation..DEM.)	-1.2773	0.4859	-2.629	0.008568	**
#BlockVJRN:scale(Elevation..DEM.)	-0.7291	0.5144	-1.417	0.156374	
#BlockVJRS:scale(Elevation..DEM.)	-1.9736	0.6205	-3.181	0.001468	**
#Log(theta)	-0.6975	0.1517	-4.599	4.25E-06	***

Zero-inflation model coefficients (binomial with logit link):

Estimate Std. Error z value Pr(>|z|)
(Intercept) -15.18 1440.24 -0.011 0.992

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Theta = 0.4978

Number of iterations in BFGS optimization: 55

Log-likelihood: -419.9 on 13 Df

7.1.17 Yellow throated marten

> summary(ytmmodzf6)

Call:

zeroinfl(formula = Yellow.throated.Marten ~ scale(Elevation..DEM.) + offset(log(CTNs)) | 1, data = full, dist = "negbin")

Pearson residuals:

Min 1Q Median 3Q Max
-0.3505 -0.2679 -0.2106 -0.1541 7.9916

Yellow throated marten	Estimate	Standard Error	z value	p value	Significance
#(Intercept)	-4.7638	0.4253	-11.201	<2E-16	***
#scale(Elevation..DEM.)	0.5771	0.2159	2.673	0.00752	**
#Log(theta)	8.6207	148.7985	0.058	0.9538	

Zero-inflation model coefficients (binomial with logit link):

Estimate Std. Error z value Pr(>|z|)
(Intercept) 1.3935 0.4949 2.816 0.00487 **

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Theta = 5545.0187

Number of iterations in BFGS optimization: 77

Log-likelihood: -64.93 on 4 Df