Imperial College London

Quantifying Predation Pressure Along a Gradient of
Land-Use Intensity in Sabah, Borneo

Michael Boyle

2012

Abstract

Tropical forests around the world are being altered and modified by human activities. Secondary forests are becoming an increasingly common feature of the tropical landscape, and it is important that we assess their potential for biodiversity conservation before they are lost. Many studies focus on abundance and diversity of certain species groups to ascertain the worth of secondary forests, but studies into the functional processes that regulate biotic systems are lacking. This study used a new experimental technique to quantify predation pressure at four forest sites along a gradient of disturbance in Sabah, Borneo. Predation pressure was significantly higher in old growth forest and declined with increasing levels of disturbance. Evidence of a taxa shift in the drivers of predation in disturbed forest was also uncovered. The study suggests that more research should focus on functional diversity and ecosystem processes to truly assess the potential of secondary forests for long-term conservation.

Introduction

Tropical forests around the world are being dramatically modified by human activities through logging, agriculture and associated fragmentation (Achard et al. 2002). South East Asia possesses a particularly high level of biodiversity and endemism associated with its tropical forests, but also experiences some of the highest levels of deforestation worldwide (Koh et al. 2008; Myers et al. 2000). Some predictions suggest that South East Asia will have lost 75% of its forest and 42% of its biodiversity by 2100 (Sodhi et al. 2004). Deforestation rates in Malaysia are proportionally higher than in other Asian countries, with around 250,000 hectares logged annually (McMorrow & Tallip 2001). Much of this deforestation is driven by the global demand for palm oil (Fitzherbert et al. 2008). Between 1990-2005 around 59% of the oil palm industry's expansion throughout Malaysia was via the conversion of forest to agricultural land (Koh & Wilcove 2009). Global production of palm oil is expanding by 9% per annum (Fitzherbert et al. 2008) and Malaysia's economy is heavily dependent

on the industry. It is likely therefore that secondary forests and plantations will become an increasing feature of the Malaysian landscape. There is now an urgent need to study the effects of fragmentation and degradation of natural systems in order to identify appropriate management solutions (Didham et al. 1996).

Habitat conversion causes an overall loss of habitat area and also the degradation and fragmentation of remaining patches (Tscharntke et al. 2002). The effects of disturbance, structural modification, and changing microclimate on species assemblages and systematic processes often lead to loss of biodiversity (Barlow et al. 2006; Bihn et al 2010; Ding et al. 2012; Krauss et al. 2010). The effects of disturbance may vary greatly between and even within taxa however, and their detection obscured by the spatial scale of study (Hill & Hamer 2004). It is likely that fragmentation induced changes may effect the biological processes that maintain ecosystem function and biodiversity, such as nutrient cycling, seed dispersal, herbivory and pollination (Didham et al. 1996). These processes are often mediated by insects, yet the effects of fragmentation on insect populations and their higher order interactions remains poorly understood (Gardner et al. 2008).

Habitat disturbance may impact invertebrate species by decreasing reproductive success, reducing survivorship, or causing direct mortality (Schlaepfer et al. 2002; Sih et al. 2000; Sodhi et al. 2004; Stork et al. 2009). All three ecological processes are potentially strongly affected by predation (Posa et al. 2008). In Lepidopteran larvae predation is the main cause of mortality (Feeny et al. 1985), and therefore has a strong influence on habitat selection, community structure and species distribution (Morris 2003, Shiojiri & Takabayashi 2003). Pressure from natural enemies can depend on forest type and also level of disturbance, both of which can impact on predator abundance and diversity (Edwards 2011) and also on their ability to locate prey items (Kareiva 1987; Kruess & Tscanrtke 1994).

Some insect groups have the ability to act as 'ecosystem engineers', in that they can cause physical changes to their environment or regulate the

availability of resources to other species (Jones et al. 1994). Herbivory for example is a major factor controlling plant communities (Crawley 1983), and altered patterns could have important consequences for forest dynamics (Faveri et al, 2008). Populations of insects are often controlled by a tritrophic interaction involving food resources (bottom-up control) and natural enemies (top-down control) (Hairston et al 1960). Many studies have attempted to highlight the relative importance of these forces in the regulation of invertebrate populations (Lewinsohn et al. 2005; Richards & Coley 2007; Walker & Jones 2001)

Top-down control may vary both spatially and temporally between and within habitats due to differences in structural complexity, microclimate, predator assemblages and human interference (Posa et al. 2008). Some studies have suggested that fragmentation can negatively affect the abundance and diversity of insect predators and parasitoids (Kruess and Tshcanrtke, 1994). Yet literature and data on the direct effects of disturbance on predation are often conflicting. Faveri et al. (2008) showed that levels of predation on phytophagous invertebrate larvae were significantly higher in continuous forest than in fragments. Tvardikova & Novotny (2012) recorded increased rates of predation in disturbed patches compared to undisturbed forest, and Posa et al. (2008) measured higher rates of predation in habitat islands, potentially owing to edge effects. Information on how disturbance affects these ecological processes in the Paleotropics is lacking (Sodhi & Brook 2006). Within Malaysia, altered predation patterns resulting from habitat conversion could negatively impact native fauna, and could be one of the processes affecting species declines and extinctions in fragmented systems.

Because actual predation events are rarely observed, previous studies have used artificial models of insect larvae to evaluate predation pressure (Faveri et al. 2008; Koh & Menge 2006; Loiselle & Farji-Brener 2002; Posa et al. 2008). While this method allows for a rapid assessment of relative predation pressures (Howe et al 2009), it is subject to many biases, and could be one reason why the results of some previous studies fail to reach consensus. Many predators rely on a complex array of visual and chemical cues to locate prey (Brodie

1993; Kielty et al. 1996). Models do not provide these cues, potentially biasing results towards disturbed sites where higher proportions of generalists occur.

This study implemented a new experimental technique wherein live mealworms where used as proxy for local invertebrate larvae to examine levels of predation across four habitat types. Sites varied in their land use and level of human disturbance from old growth rainforest, through once and twice logged forest to oil palm plantation. Predation was also compared across two microhabitats of litter layer and vegetation layer, and two temporal periods of nocturnal and diurnal activity. Exclusion treatments were employed in an attempt to identify the proportion of predation pressure attributable to different predator types. Questions posed by the study were:

1. Does predation pressure change along a gradient of land use intensity?
2. If so, what habitat features might be driving these changes?
3. Does predation pressure vary between diurnal and nocturnal activity periods?
4. Does predation pressure vary between vegetation layer and litter layer microhabitats?

The study aims to provide empirical information on predation pressure in a human modified landscape, which is a factor potentially affecting declines and extinctions of certain species groups. The study also aims to critically examine a new technique for quantifying predation pressure using exclusion treatments and live prey.

Methods

All fieldwork was carried out in Sabah, Malaysia as part of the Stability of Altered Forest Ecosystems (SAFE) project. Data were collected from old growth forest sites in Maliau Basin Conservation Area, logged forest and secondary forest sites in the Kalabakan Forest Reserve and oil palm plantation sites at Benta Wawasan.

Mailau Basin is a 58,800ha expanse of mostly undisturbed forest in Southern Central Sabah that was afforded protected area status by Yayasan Sabah in 1981, and promoted to a Class 1 Protection Forest Reserve by the Sabah State Assembly in 1997. Old growth sites sampled within Maliau have therefore never been commercially logged and forest quality is exceptionally high, however other sites in the locality were lightly logged during the 1990s to provide timber for the construction of the Maliau Basin field center. Logged forest sites lay inside a semi protected area of 2200ha within the Kalabakan Forest Reserve. The forest was selectively logged around 20 years ago, removing many of the largest canopy leaders, but has been undisturbed since and retains between 35–60% tree cover with some regenerating patches of dense understory. Secondary forest sites have been repeatedly selectively logged and between 8-15 trees of >60cm DBH removed per hectare. Within these sites remains a mosaic of heavily disturbed regenerating patches with tree cover varying from 18–54%. Oil palm sites constituted of intensive *Elaeis guineensis* monoculture. The area sampled includes a single age class that was planted in 2000 and lies 1km away from the forest edge. The canopy is generally low and open with little to no understory in most areas. Oil palm sites are also subject to high levels of human disturbance (Fitzherbert et al. 2008).

All forest sample sites were located within a 1,000,000ha expanse of continuous forest and were selected to represent a gradient of land use intensity from undisturbed virgin forest through logged forest to highly disturbed secondary forest. Oil palm was sampled to represent the ultimate stage of land use intensity in the area.

All study sites used in the collection of data form part of the SAFE project's long-term research into the effects of habitat fragmentation and disturbance on species assemblages and ecosystem processes. The multi-discipline project aims to take advantage of planned logging and conversion of a large swathe of secondary forest into oil palm plantation to create forest fragments of varying sizes. Changes in the dynamics of species assemblages

and systematic processes will be monitored during and after conversion, with the ambition of aiding the understanding of the impacts of land use change on the structure and function of tropical systems.

Within the framework of the project a network of survey points has been established across old growth, logged forest and oil palm control sites, as well as secondary forest fragment arrays that will be allowed to remain after logging. The locations of survey points are derived from a hierarchical fractal based design system using nested triangles of increasing spatial scale.

First order points occur at the vertices of equilateral triangles with sides of 56m. These 1st order fractals are arranged so that their centers form the vertices of 2nd order fractals with sides of 178m. 2nd order fractals are then in turn nested within 3rd and 4th order fractals with sides of 564m and 1780m respectively (Ewers et al. 2011). All survey points occur at similar altitude, on similar slope and suitably far away from converted habitats to avoid edge effects (Ewers et al. 2011).
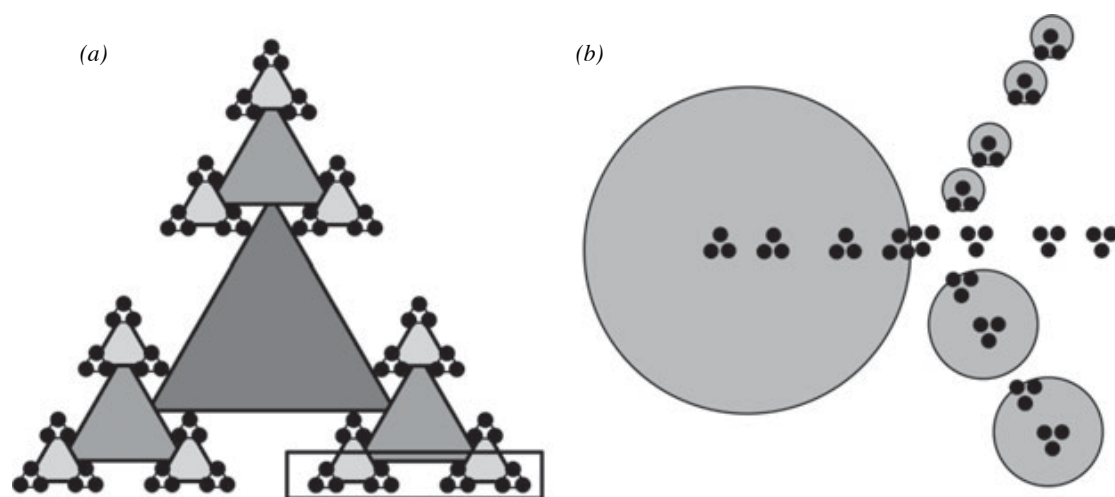

Fig.1 – (a) Fractal geometry of the sampling network in a continuous habitat. Points on the light grey triangles represent sampling locations, and triangles of progressively darker shades represent the progression from first to fourth order of the fractal pattern. *(b)* Spatial layout of a fragment array, showing how the fractal sampling scheme is embedded within each fragment. (Ewers et al. 2011).

102 1st order points were sampled within this study across 4 habitat types. 21 old growth, 24 logged forest, 30 secondary forest and 27 oil palm. Secondary

forest sites were situated within continuous forest, and will become fragment arrays when logging commences in the area in 2012. Data were collected between May 20th and July 24th 2012 and all specific times and dates of work were recorded.

The design of the experiment took inspiration from the nested fractal framework of the SAFE project. Smaller triangles with 4m sides were established with SAFE project 1st order points at their centres. The vertices of these triangles constituted sampling points where a single live prey item would be placed at vegetation layer (1.5m) and litter layer (0m) and randomly assigned one of three exclusion treatments. In this way each individual treated with the same exclusion were a minimum of 56m apart, but each exclusion was represented at every 1st order point at vegetation and litter layer. Exclusions were designed to differentiate between aerial and terrestrial predators:

Exclusion A – No exclusion: all groups can predate

Exclusion B – Terrestrial predator exclusion: leaves were attached to a pole and insect-trapping glue applied liberally 20cm above and 20cm below where the leaf joined the stem. This exclusion was only initiated at vegetation layer as falling debris compromised the effectiveness of the exclusion at litter layer.

Exclusion C – Aerial predator exclusion: 30cm x 30cm x 30cm metal cages were constructed using wire with a mesh size of 1cm x 1cm. These were placed around leaves attached to vegetation or pinned into the ground around leaves at the litter layer.

Mealworms were attached to the center of standardised acrylic 'leaves' (green at vegetation layer, brown at litter layer) of dimension 80mm x 120mm x 5mm using fine cotton thread and a small strip of clear tape. Acrylic leaves were fabricated in an attempt to control for plant species, leaf size, shape and chemistry. For vegetation layer measurements leaves were attached to
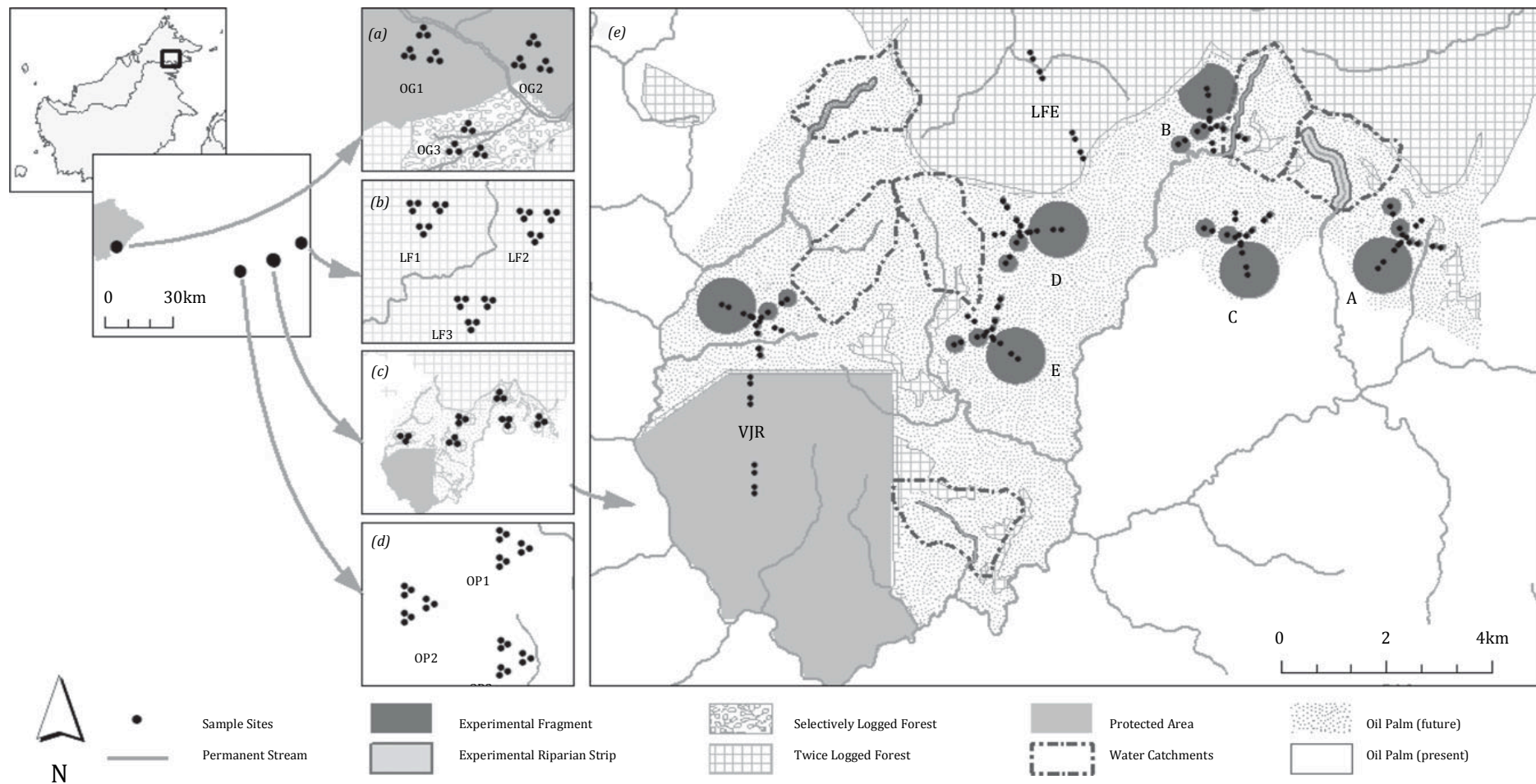
Fig. 2 – Map of the SAFE Project site in Sabah, Malaysia. *(a)* Old growth sites *(b)* Continuous twice logged forest *(c)* Twice logged and fragmented forest in an oil palm matrix *(d)* Oil palm sites *(e)* Blocks A-F, logged forest edge (LFE) and virgin jungle reserve (VJR). Fragments are currently embedded in a twice logged forest landscape that is due to be cleared and converted to oil palm commencing late 2012. Sites sampled in the collection of data for study were OG2, VJR, E and OP3 (Ewers et al. 2011).

stems at 1.5m using green rubberized fencing wire, litter layer leaves were simply placed on the ground. All leaves were positioned to face outwards from the triangle. Where no suitable substrate was present to attach leaves at the vegetation layer a 2m pole was cut and driven into the ground at the correct point. Enough cotton thread was attached to enable the mealworm to crawl around on the leaf as it was assumed that movement would be an important cue for potential predators. Very fine thread was used so that it would not be confused for an urticating defense, and clear tape chosen over coloured tape so that it would not affect other visual signals given off by the mealworm. Size of prey items has been shown to affect predation rates (Remmel et al. 2011) and so mealworms of similar size were used throughout the experiment.

The method of attaching the mealworm using thread was preferred after extensive trials comparing superglue, trapping glue, putty and combinations thereof. It was deemed the most suitable as it allowed for the removal of the prey item by a predator but did not allow the mealworm to break free if not predated. In trials where no predators were present, no mealworms (n=15) became unattached to the leaf after 48 hours. Similarly the method was deemed least likely to kill the mealworm; in all trials mealworms that had not been predated were still alive after 24 hours, except after periods of extended heavy rain. Latex gloves were worn when handling mealworms and no insect guard or other potentially repellent chemicals were worn at any time during the entire data collection period to ensure that no equipment would in any way deter potential predators.

Triangles were set up around six 1st order points every morning at dawn between 6-7am. They were then visited 12 hours later at dusk between 6-7pm where the numbers of mealworms predated during the diurnal activity period were recorded. New mealworms were then attached to the leaves, which were revisited at dawn the following morning when the numbers of mealworms predated during the nocturnal activity period were recorded. Equipment would then be moved to six new points in readiness for the next sampling period. Mealworms were considered predated if they had been

removed with no evidence of them having become detached by other means, if they were seen being eaten, or if there was clear evidence of them having been partially eaten. In this way, data on the proportions of diurnal and nocturnal predation pressure from different taxa could be recorded at vegetation level and ground level across four classes of habitat degradation.

Environmental variables recorded included aspect, percentage vegetation cover at 0m, percentage vegetation cover at 1.5m, percentage vegetation cover at 2m, canopy height, canopy density, litter depth, and forest quality. These were selected as they were considered to be the simplest factors explaining the basic structure of the forest in each area. Rainfall was measured as a temporal confounding effect.

Aspect was recorded using a compass facing downhill from the 1st order point at the centre of each 4m triangle. Percentage vegetation cover at each level was estimated using a 1.2m x 1.2m quadrat. Estimates were recorded at each vertex of the triangle and the mean values taken as a representation of the cover characteristics surrounding each 1st order point. Canopy height was estimated by eye or by using a clinometer where possible. Canopy density was measured using a spherical densiometer. The number of open quarter-squares were counted to the north, south, east and west of each vertex of the triangle and used to calculate canopy openness. The mean values were then taken and converted to give a measurement of canopy density. Litter depth was measured using a ruler. Forest quality was taken from second order points at the centre of each 1st order triangle according to the SAFE project forest quality scale from 0 (very poor) to 5 (very good) based on visible vegetation around each survey point. Rainfall intensity was given a score of 0-5, 0 being no rain and 5 being torrential rain. Scores were given based on rainfall events lasting more than 30 minutes in the locality of the study sites. Latitude and longitude data for every point were also obtained from the SAFE project.

Analyses

All statistical analyses were carried out in the R 2.13.2 statistical package for Mac OSX.

Initially the question of potential spatial autocorrelation between survey points had to be addressed in order to choose the correct models for the core analysis. To test for this, the longitude and latitude data for every point was converted from spherical coordinates to Cartesian coordinates using the GeoXY function in the SoDA package for R. Distance matrices were then constructed using these coordinates and the status (predated or not predated) of each individual mealworm for every exclusion at each point within each disturbance class. Mantel tests were run using the package Ade4 to test for spatial autocorrelation between points within each disturbance class. No significant spatial correlation was detected meaning that the use of a generalised linear model rather than a linear mixed effects model was justified for the core analysis.

Habitat variables were then examined in a correlation matrix (test = Spearman). Variables were considered correlated if $P > 0.5$ (test = Spearman). If correlation occurred then the most explanatory variable was kept in as a proxy for it's correlates. This led to % cover at 0m and % cover at 2m being removed from the analysis as % cover at 1m was significantly correlated with both. No other variables were significantly correlated.

Data on the proportions of predated mealworms in each exclusion were tested against disturbance class, level and time using a generalised linear model with binomial errors. Having run these models to examine the basic relationships between disturbance and predation, more complex models were initiated. These tested levels of predation from each exclusion against habitat variable interactions using a generalised linear model with binomial errors to try to explain any observed effects on predation rates. Full interactions were entered into each model and then simplified until the minimal adequate models were obtained.

Results

In total the predation status of 1020 individual mealworms was recorded across all land use intensities, exclusions, times and levels.

General Predation (Exclusion A):

Predation declined along a gradient of land use intensity from 43% in old growth, 42% in logged forest, 33% in secondary forest and 33% in oil palm. Predation was significantly lower in secondary forest and oil palm than in old growth (z = -3.403, p<0.001, d.f 402). Time had no significant effect on predation but vegetation layer rates were lower than those at litter layer (z = -6.130, p<0.001, d.f 402). Across all sites rates from exclusion A were higher than either B or C (z = 5.690, p<0.001, d.f = 1003).
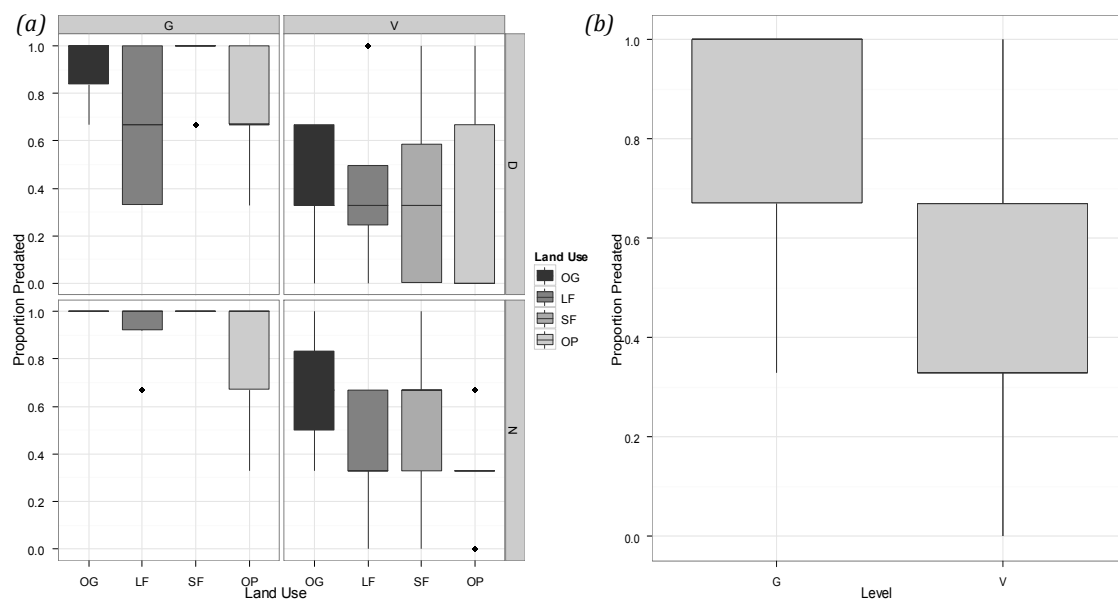

Fig.3 – (a) Land use as a predictor of predation pressure at vegetation layer (V), ground layer (G), day (D) and night (N), n=402. Land use categories: OG = Old growth, LF = Logged forest, SF = Secondary forest, OP = Oil Palm. *(b)* The effect of level (vegetation layer or ground layer) on predation pressure. Ground layer (G) rates are significantly higher than those measured at 1.5m (V) (mean rates from exclusion A), n=402.

Exclusion C:

Disturbance had a strong effect on exclusion C and all classes were significantly different to old growth. Predation was highest in old growth (38%,

z = 5.865, p<0.001, d.f 403) and decreased along a disturbance gradient to a nadir in secondary forest, oil palm rates were higher than disturbed forest sites (LF: 13%, z = -2.955, p<0.01, d.f 403, SF: 7%, z = -3.742, p<0.001, d.f 403, OP: 26%, z = 2.747, p<0.01, d.f 403). Exclusion C was not affected by time, but vegetation layer had a negative effect (z = -9.689, p<0.001, d.f 403).
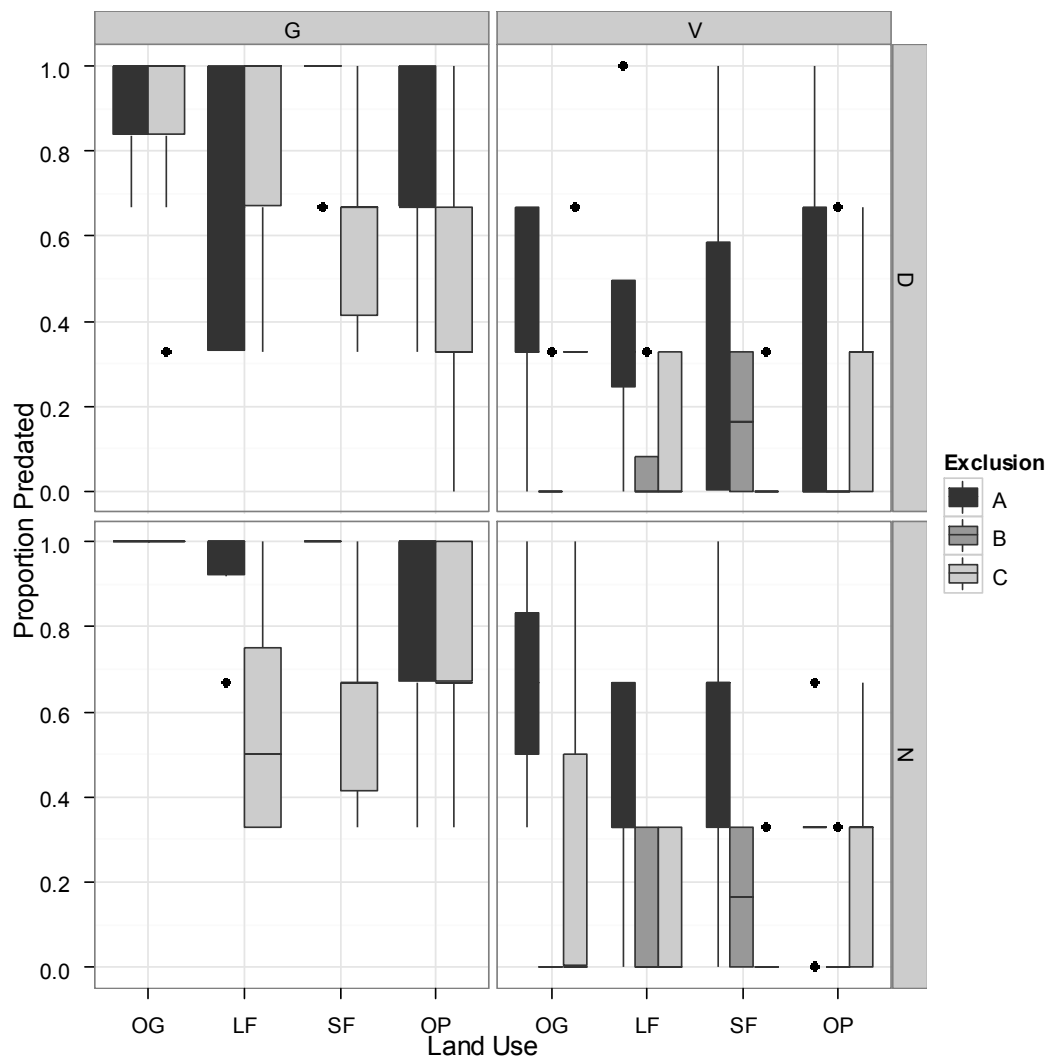

Fig. 4 – Land use as a predictor of predation pressure from each exclusion at vegetation layer (V), ground layer (G), day (D) and night (N), n=402. Land use categories: OG = Old growth, LF = Logged forest, SF = Secondary forest, OP = Oil Palm.

Exclusion B:

Proportions of rates on exclusion B were not significantly affected by time. Predation was significantly lower in old growth compared to other sites (5%, z = -3.669, p<0.001, d.f 200), and secondary forest experienced significantly

higher levels predation on exclusion B than other sites (17%, z = 1.967, p<0.05, d.f 200).

Habitat features:

The most influential environmental feature on overall predation was canopy height (z = 3.209, p<0.01, d.f 402). Vegetation cover at 1.5m had a negative effect on exclusion C (z = -2.742, p<0.01, d.f 404). No habitat features measured had any significant effect on predation when terrestrial predators were excluded.
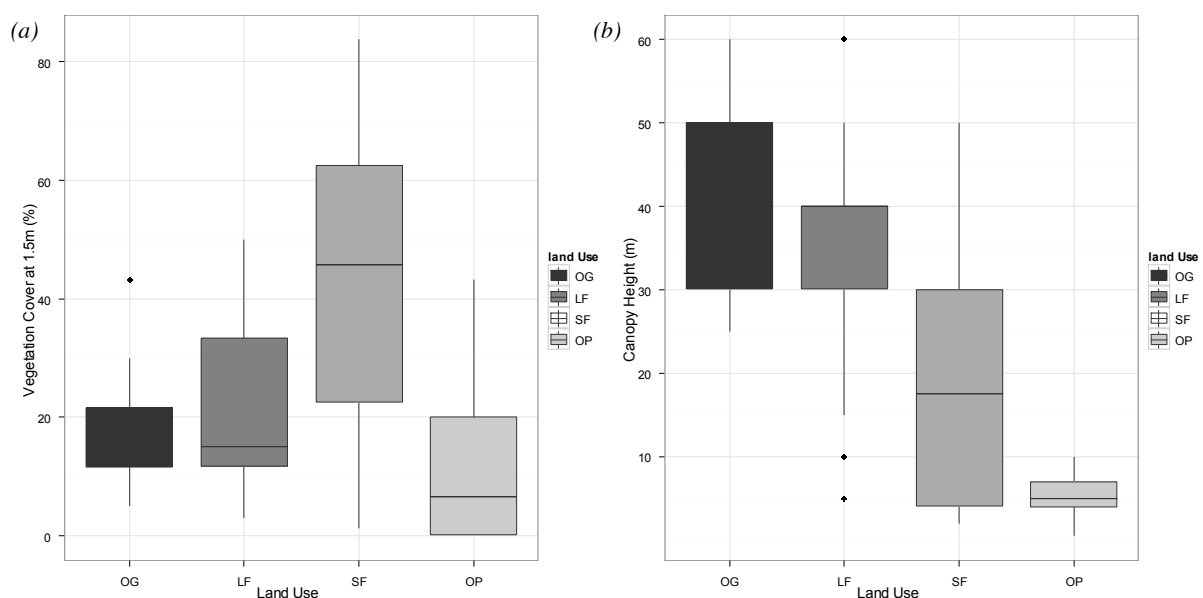
Fig. 5 – Land use as a predictor of habitat features (a) vegetation cover at 1.5m and (b) canopy height. N=1020. Land use categories: OG = Old growth, LF = Logged forest, SF = Secondary forest, OP = Oil Palm.

Discussion

Overall predation rates declined as land use intensity increased. Patterns of predation changed however as highlighted by results obtained from the exclusions. Predation rates from exclusion C declined with disturbance and then rose again within oil palm. Exclusion B rates had the opposite pattern, rising with disturbance and then falling again within oil palm sites. Predation at

ground layer was higher than vegetation layer and time (nocturnal or diurnal period) had no significant effect.

Old Growth:

Predation pressure was significantly higher in old growth forest compared to secondary forest and oil palm. Predation in undisturbed forest has been shown to be largely driven by invertebrates (Koh & Menge 2006; Loiselle & Farji-Brener 2002; Posa et al. 2008). The more diverse invertebrate community structure within old growth compared to other forest types is likely to be the cause of the higher rates observed in this study. Old Growth forest has been shown to contain a higher abundance and diversity of invertebrate species than other forests (Basset et al 1998). Lepidopteran larvae have been shown to exist in higher abundance in the understory of unlogged forest in Northern Borneo as compared to regenerating forest (Edwards 2012), and it is likely that there is consequently a higher abundance of invertebrate natural enemies. Plants under herbivory stress release volatiles that have been shown to attract natural enemies that then exert top-down control to regulate populations of herbivores (Bergelson & Lawton 1988). The mealworms in this experiment at 1.5m were probably experiencing similar predation pressure to natural externally feeding phytophagous larvae. Structural characteristics of the forest are also likely to have played a role, in the more open understory that is characteristic of old growth forest it may be easier to locate prey items. Results contrast with those reported by Posa et al. (2008) and Tvardikova & Novotny (2012) who observed higher predation rates in disturbed environments. Faveri et al (2008) however recorded slightly higher predation rates in continuous forest as compared to disturbed patches in the Amazon.

Logged Forest and Secondary Forest:

The predation patterns in both once and twice logged forest were similar to each other but both significantly different to those observed in primary forest and oil palm. Predation rates generally were lower, but the proportion of predation on exclusion B was significantly higher in secondary forest than in old growth. The differences between rates from exclusion C and A were also much larger than in old growth or oil palm, suggesting that there is a large

amount of overall predation pressure from a predator type not able to take prey from exclusion C. An analysis of the current available literature on attempts to quantify predation identified arthropods, birds, and small mammals as the three main drivers of predation in experiments of this type (Remmel et al. 2011). While the exclusions in this study could not be said to be taxa specific it is justified to assume that the majority of predation from exclusion B was from birds and exclusion C from arthropods. This implies that one of the reasons for an increased difference between exclusion C and exclusion A is increased predation from small mammals. Certain foraging guilds of birds have been shown to respond positively to logging within the forests of Northern Borneo, particularly understory generalists (Edwards 2009). Structural changes brought about after disturbance can increase nesting possibilities for certain understory birds and increase their relative abundance (MacArthur & MacArthur 1961). Similarly logging tracks and canopy gaps can enable non-forest and edge generalists easier access to the forest interior (Tvardikova & Novotny 2012). Generalist small mammal species have shown to exist in significantly higher densities in logged forest compared to primary forest (Bernard & Mohamed 2009). This could again be related to structure, as small mammals are shown to favor dense patches of undergrowth over open areas as a means of predator avoidance (Shadbolt & Ragai 2011).

Oil Palm:

Oil palm predation rates were significantly lower than old growth and logged forest but had higher proportions of arthropod predation (if it is assumed that predation events from exclusion C were mostly arthropod driven). Oil palm has been shown to be depauperate, with assemblages typically dominated by a few abundant generalists, non-forest species (including invasives) and pests (Fitzherbert et al 2008). Species that disappear when forest is converted to oil palm tend to include those with the most specialised diet, or those reliant on habitat features not found in plantations (Aratrakorn et al 2006). The generalists that survive in oil palm plantations are abundant (Fitzherbert et al 2008), and potentially exert quite significant predation pressure. The physical structure of plantations is also extremely homogenous, with very little

understory or vertical complexity. These features could make it easier for invertebrate predators to locate prey items.

Level:

Predation rates were significantly higher at ground level than at vegetation level across all sites. Predation pressure is highest at canopy level and ground level in most systems, as this is where the greatest abundance of fauna exists (Loiselle & Farji-Brener 2002). The difference in the observed rates imply that ground layer and vegetation layer are quite distinct microhabitats, and even within a system as homogenous as oil palm plantation there exists a certain amount of habitat stratification. Carnivorous insect guilds decline at litter layer along a gradient of land use (Edwards 2012), and this is reflected in the results obtained from exclusion C. Overall ground layer rates were highest in secondary forest sites however, and this could be due to added pressure from generalist small mammals that are shown to be abundant in more disturbed sites (Bernard & Mohamed 2009).

Habitat Features:

The only habitat features that showed significant relationships with predation were canopy height, which had a positive effect on overall predation rates, and vegetation cover, which had a negative effect on exclusion C. Other studies have failed to directly associate any habitat variables with predation rates (Koh & Menge 2006; Loiselle & Farji-Brener 2002; Posa et al. 2008; Tvardikova & Novotny 2012) and thus the significance of these variables should be approached with caution. It is possible that rather than having a direct effect on predation rates, canopy height and vegetation cover were the most diagnostic components of habitats that either experienced high or low predation rates due to a vast variety of interacting features

Summary

Holistically the results showed a decrease in overall predation pressure from old growth forest to logged forest sites, and identified a possible taxa shift from invertebrate driven predation to vertebrate driven predation. Structural

differences in forests may lead to altered species assemblages that exert different predation pressures on invertebrate larvae. Tropical forests are incredibly complex and it is difficult to highlight specific characteristics that directly affect predation rates. It may be more appropriate to focus on defining characteristics of forest types in order to highlight differences when conducting short-term studies. Oil palm sites do not conform to trends seen amongst forest sites, and should be considered functionally distinct in terms of predation processes. The study used live prey items rather than model caterpillars in an attempt to reduce some of the biases associated with the model method. This proved a successful experimental procedure although it lacked some of the resolution of the model method in terms of taxa identification, meaning that some assumptions had to be drawn from the data in order to form conclusions. These problems could be rectified via the use of more specific exclusion treatments. Conflicting results between this study and others in old growth forest could be explained by the higher degree of specialism associated with old growth faunal communities. Specialist predators may respond better to the cues given off by live prey items, meaning that methods using models would report lower incidences of predation in pristine forest environments compared to disturbed sites where more generalists occur. This would imply that the live prey method gives a more accurate representation of natural predation rates, although a direct comparison is required to verify these suggestions.

Conclusion

The world is facing a biodiversity crisis owing in part to the fragmentation and conversion of tropical forests (Achard 2002). Due to poor management of timber concessions and the lucrativeness of the oil palm industry secondary forests are becoming a more common feature of the tropical landscape, and they have plausible value in terms of wildlife conservation (Gardner et al. 2008). While studies have highlighted the potential for secondary forests in their assemblages of faunal taxa (Chazdon et al. 2009; Dent 2009; Edwards 2009; Woodcock et al. 2011), functional and process based studies are still lacking. Functional diversity and ecological processes such as herbivory,

predation, pollination and seed dispersal are key for maintaining community structure in a complex system (Crawley 1983). High levels of disturbance can generate a community dominated by closely related species with disturbance-adapted traits, where biotic interactions play a relatively minor role (Ding et al. 2012). Old growth forest communities are governed by fine-scale biotic interactions often mediated by invertebrates. Predation pressure has the ability to change the community ecology of invertebrates, which could in turn have implications for the overall ability of a system to self regulate. Differing patterns in basic processes also have the potential to create 'ecosystem traps', which may lead to species declines and extinctions (Schlaepfer 2002). Secondary forests are functionally different systems, and more research should be directed towards the processes underpinning the ecology of disturbed and secondary forests to gauge their long-term potential for wildlife conservation.

Bibliography

Achard, F., Eva, H. D., Stibig, H., Mayaux, P., Gallego, J., Richards, T., Malingreau, J-P. (2002) Determination of deforestation rates of the world's humid tropical forests. *Science*. 297 (5583), 999-1002.

Aratrakorn, S., Thunhikorn, S. & Donald, P. (2006) Changes in bird communities following conversion of lowland forest to oil palm and rubber plantations in southern Thailand. *Bird Conservation International*. 16 (1), 71-82.

Barlow, J., Gardner, T. A., Araujo, I. S., Avila-Pires, T. C., Bonaldo, A. B., Costa, J. E., Esposito, M. C., Ferreira, L. V., Hawes, J., Hernandez, M. M., Hoogmoed, M. S., Leite, R. N., Lo-Man-Hung, N. F., Malcolm, J. R., Martins, M. B., Mestre, L. A. M., Miranda-Santos, R., Nunes-Gutjahr, A. L., Overal, W. L., Parry, L., Peters, S. L., Ribeiro-Junior, M. A., da Silva, M. N. F., Motta, C. d. S. & Peres, C. A. (2007) Quantifying the biodiversity value of tropical primary, secondary, and plantation forests. *Proceedings of the National Academy of Sciences of the United States of America*. 104 (47), 18555-18560.

Barlow, J., Peres, C., Henriques, L., Stouffer, P. & Wunderle, J. (2006) The responses of understorey birds to forest fragmentation, logging and wildfires: An Amazonian synthesis. *Biological Conservation*. 128 (2), 182-192.

Basset, Y., Novotny, V., Miller, S. & Springate, N. (1998) Assessing the impact of forest disturbance on tropical invertebrates: some comments. *Journal of Applied Ecology*. 35 (3), 461-466.

Bergelson, J. M. & Lawton, J. H. (1988) Does foliage damage influence predation on the insect herbivores of birch? *Ecology*. 69, (2), 434-445

Bernard, H., Fjeldsa, J. & Mohamed, M. (2009) A case study on the effects of disturbance and conversion of tropical lowland rain forest on the non-volant small mammals in north Borneo: Management implications. *Mammal Study*. 34 (2), 85-96.

Bihn, J. H., Gebauer, G. & Brandl, R. (2010) Loss of functional diversity of ant assemblages in secondary tropical forests. *Ecology*. 91 (3), 782-792.

Brodie, E. (1993) Differential Avoidance of Coral Snake Banded Patterns by Free-Ranging Avian Predators in Costa-Rica. *Evolution*. 47 (1), 227-235.

Crawley, M. J. (1983) *Herbivory: the dynamics of animal-plant interactions*. Blackwell Science Publications, Oxford. 437.

Chazdon, R. L., Peres, C. A., Dent, D., Sheil, D., Lugo, A. E., Lamb, D., Stork, N. E. & Miller, S. E. (2009) The Potential for Species Conservation in Tropical Secondary Forests. *Conservation Biology*. 23 (6), 1406-1417.

Dent, D. H. & Wright, S. J. (2009) The future of tropical species in secondary forests: a quantitative review. *Biological Conservation*. 142 (12), 2833-2843.

Didham, R., Ghazoul, J., Stork, N. & Davis, A. (1996) Insects in fragmented forests: A functional approach. *Trends in Ecology & Evolution*. 11 (6), 255-260.

Ding, Y., Zang, R., Letcher, S. G., Liu, S. & He, F. (2012) Disturbance regime changes the trait distribution, phylogenetic structure and community assembly of tropical rain forests. *Oikos*. 121 (8), 1263-1270.

Edwards, D. P., Ansell, F. A., Ahmad, A. H., Nilus, R. & Hamer, K. C. (2009) The Value of Rehabilitating Logged Rainforest for Birds. *Conservation Biology*. 23 (6), 1628-1633.

Edwards, D. P., Backhouse, A. R., Wheeler, C., Khen, C. V. & Hamer, K. C. (2012) Impacts of logging and rehabilitation on invertebrate communities in tropical rainforests of northern Borneo. *Journal of Insect Conservation*. 16 (4), 591-599.

Edwards, D. P., Larsen, T. H., Docherty, T. D. S., Ansell, F. A., Hsu, W. W., Derhe, M. A., Hamer, K. C. & Wilcove, D. S. (2011) Degraded lands worth protecting: the biological importance of Southeast Asia's repeatedly logged forests. *Proceedings of the Royal Society B-Biological Sciences*. 278 (1702), 82-90.

Ewers, R. M., Didham, R. K., Fahrig, L., Ferraz, G., Hector, A., Holt, R. D., Kapos, V., Reynolds, G., Sinun, W., Snaddon, J. L. & Turner, E. C. (2011) A large-scale forest fragmentation experiment: the Stability of Altered Forest Ecosystems Project. *Philosophical Transactions of the Royal Society B-Biological Sciences*. 366 (1582), 3292-3302.

Faveri, S. B., Vasconcelos, H. L. & Dirzo, R. (2008) Effects of Amazonian forest fragmentation on the interaction between plants, insect herbivores, and their natural enemies. *Journal of Tropical Ecology*. 24, 57-64.

Feeny, P., Blau, P. & Kareiva, P. M. (1985) Larval growth and survivorship of the Black Swallowtail Butterfly in Central New York. *Ecological Monographs*. 55 (2), 167-187.

Fitzherbert, E. B., Struebig, M. J., Morel, A., Danielsen, F., Bruehl, C. A., Donald, P. F. & Phalan, B. (2008) How will oil palm expansion affect biodiversity? *Trends in Ecology & Evolution*. 23 (10), 538-545.

Gardner, T. A., Hernandez, M. I. M., Barlow, J. & Peres, C. A. (2008) Understanding the biodiversity consequences of habitat change: the value of secondary and plantation forests for neotropical dung beetles. *Journal of Applied Ecology*. 45 (3), 883-893.

Hill, J. K., Gray, M. A., Khen, C. V., Benedick, S., Tawatao, N. & Hamer, K. C. (2011) Ecological impacts of tropical forest fragmentation: how consistent are patterns in species richness and nestedness? *Philosophical Transactions of the Royal Society B-Biological Sciences*. 366 (1582), 3265-3276.

Howe, A., Gabor, L. L. & Gosta, N. (2009) Dummy caterpillars as a simple method to assess predation rates on invertebrates in a tropical agroecosystem. *Entomologia Expermimentalis et Applicata*. 131 (3), 325-329.

Jones, C. G., Lawton, J. H. & Shachak, M. (1994) Organisms as ecosystem engineers. *Oikos*. 69 (3), 373-386.

Kareiva, P. (1987) Habitat Fragmentation and the Stability of Predator Prey Interactions. *Nature*. 326 (6111), 388-390.

Kielty, J., AllenWilliams, L., Underwood, N. & Eastwood, E. (1996) Behavioral responses of three species of ground beetle (Coleoptera: Carabidae) to olfactory cues associated with prey and habitat. *Journal of Insect Behavior.* 9 (2), 237-250.

Koh, L P. (2008) Can oil palm plantations be made more hospitable for forest butterflies and birds? *Journal of Applied Ecology.* 45, 1002-1009.

Koh, L. P. & Menge, D. (2006) Rapid assessment of Lepidoptera predation rates in neotropical forest fragments. *Biotropica.* 38 (1), 132-134.

Koh, L. P. & Wilcove, D. S. (2009) Oil palm: disinformation enables deforestation. *Trends in Ecology & Evolution.* 24 (2), 67-68.

Krauss, J., Bommarco, R., Guardiola, M., Heikkinen, R. K., Helm, A., Kuussaari, M., Lindborg, R., Ockinger, E., Partel, M., Pino, J., Poyry, J., Raatikainen, K. M., Sang, A., Stefanescu, C., Teder, T., Zobel, M. & Steffan-Dewenter, I. (2010) Habitat fragmentation causes immediate and time-delayed biodiversity loss at different trophic levels. *Ecology Letters.* 13 (5), 597-605.

Kruess, A. & Tscharntke, T. (1994) Habitat Fragmentation, Species Loss, and Biological Control. *Science.* 264 (5165), 1581-1584.

Lewinsohn, T. M., Novotny, V. & Basset, Y. (2005) Insects on plants: diversity of herbivore assemblages revisited. *Annual Reviem of Ecology, Evolution and Systematics.* 36, 597-620.

Loiselle, B. A & Farji-Brener, A. G (2002) What's up? An experimental comparison of predation levels between canopy and understory in a tropical wet forest. *Biotropica.* 38, 132-134.

MacArthur, R. H. & MacArthur, J. W. (1961) On bird species diversity. *Ecology.* 42, 594-598.

McMorrow, J. & Talip, M. (2001) Decline of forest area in Sabah, Malaysia: Relationship to state policies, land code and land capability. *Global Environmental Change-Human and Policy Dimensions.* 11 (3), 217-230.

Morris, D. (2003) Shadows of predation: habitat-selecting consumers eclipse competition between coexisting. *Evolutionary Ecology.* 17 (4), 393-422.

Myers, N., Mittermeier, R., Mittermeier, C., da Fonseca, G. & Kent, J. (2000) Biodiversity hotspots for conservation priorities. *Nature.* 403 (6772), 853-858.

Posa, M. R. C., Sodhi, N. S., & Koh, L. P. (2007) Predation on artificial nests and caterpillars across a disturbance gradient in Subic Bay, Phillipines. *Journal of Tropical Ecology.* 23, 27-33.

Remmel, T., Davison, J. & Tammaru, T. (2011) Quantifying predation on folivorous insect larvae: the perspective of life-history evolution. *Biological Journal of the Linnean Society.* 104 (1), 1-18.

Richards, L. A. & Coley, P. D. (2007) Seasonal and habitat differences affect the impact of food and predation on herbivores: a comparison between gaps and understory of a tropical forest. *Oikos.* 116, 31-40.

Schlaepfer, M. A., Runge, M. C. & Sherman, P. W. (2002) Ecological and evolutionary traps. *Trends in Ecology and Evolution*. 17, 474-480.

Shadbolt, A. B. & Ragai, R. (2010) Effects of habitat fragmentation on the movement patterns and dispersal ability of the brown spiny rat (Maxomys rajah) in the Planted Forest Zone of Sarawak, Eastern Malaysia. *Biodiversity and Conservation*. 19 (2), 531-541.

Shiojiri, K. & Takabayashi, J. (2003) Effects of specialist parasitoids on oviposition preference of phytophagous insects: encounter-dilution effects in a tritrophic interaction. *Ecological Entomology*. 28 (5), 573-578.

Sih, A., Jonsson, BG & Luikart (2000) Habitat loss: ecological, evolutionary and genetic consequenses. *Trends in Ecology & Evolution*. 15 (4), 132-134.

Sodhi, N. S. & Brook, B. W. (2006) *Southeast Asian Biodiversity in Crisis*. Cambridge Tropical Biology Series. The Pitt Building, Trumpington st, Cambridge.

Sodhi, N. S., Koh, L. P., Brook, B. W. & Ng, P. K. L. (2004) Southeast Asian biodiversity: an impending disaster. *Trends in Ecology & Evolution*. 19 (12).

Stork, N. E., Coddington, J. A., Colwell, R. K., Chazdon, R. L., Dick, C. W., Peres, C. A., Sloan, S. & Willis, K. (2009) Vulnerability and Resilience of Tropical Forest Species to Land-Use Change. *Conservation Biology*. 23 (6), 1438-1447.

Tscharntke, T., Steffan-Dewenter, I., Kruess, A. & Thies, C. (2002) Characteristics of insect populations on habitat fragments: A mini review. *Ecological Research*. 17 (2), 229-239.

Tvardikova, K. & Novotny, V. (2012) Predation on exposed and leaf-rolling artificial caterpillars in tropical forests of Papua New Guinea. *Journal of Tropical Ecology*. 28, 331-341.

Walker, M. & Jones, T. (2001) Relative roles of top-down and bottom-up forces in terrestrial tritrophic plant-insect herbivore-natural enemy systems. *Oikos*. 93 (2), 177-187.

Woodcock, P., Edwards, D. P., Fayle, T. M., Newton, R. J., Khen, C. V., Bottrell, S. H. & Hamer, K. C. (2011) The conservation value of South East Asia's highly degraded forests: evidence from leaf-litter ants. *Philosophical Transactions of the Royal Society B-Biological Sciences*. 366 (1582), 3256-3264.