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The effect of forest edges on the community structure of tropical fruit-feeding butterflies

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Abstract

Artificial edges in tropical forests are known to have profound effects on microclimate, tree mortality, forest structure, and community composition. While edges between continuous forest and clear felled stands have been well-researched, less attention has been paid to the effects of logging roads and smaller tracks. This study focuses on the effect a small (2-3m wide) road has on the community structure of the guild of fruit-feeding Nymphalidae butterflies in Sabah, Borneo. Traps were hung at ground-level along the road and 100m into the adjacent primary forest. In total, 43 individuals from 17 species were caught. Both the edge and the forest had seven species unique to that habitat, with three species found in both. Analysis of community structure found no significant difference between the two habitats. Cluster analysis placed the three forest sites and one of the edge traps within a cluster, suggesting a possible primary forest community, with the edge site relatively unaffected by edge-mediated changes. The other two edge sites bore little similarity to any other site. Species found at the edge tended to be less shade-tolerant and had generalist or grass-specialist larvae, making them more adapted to disturbed edge habitats than the forest interior. Although a couple of edge-tolerant species were caught within the forest, the forest habitat still retained a high number of tree-specialists, suggesting that any edge effects at 100m into the forest are relatively weak. The ability of fruit-feeding Nymphalidae to act as indicators of forest disturbance is reflected upon.

Keywords: Edge effects; Community structure; Nymphalidae; Tropical forest

1. Introduction

The tropical forests of South East Asia are experiencing a high rate of deforestation and habitat fragmentation to satisfy the rising demands of population expansion, agriculture, and commercial logging (Wright, 2006). Where trees are removed, the abrupt transition between forest and the surrounding habitat causes a host of changes in forest structure, microclimate, and species compositions (Laurance and Yensen, 1991).

The creation of a forest edge causes a dramatic increase in the amount of solar radiation reaching the forest understory. This rise in radiation influences other microclimatic factors, leading to higher and more variable daily temperatures and reduced humidity (Murcia, 1995). The changes to understory radiation, temperature and humidity extend at least 40m into the forest interior, which may sharply reduce the area of undisturbed interior forest in smaller forest fragments. Soil moisture levels are reduced within 20m of a forest edge, due to an increase in evapotranspiration rates as plants are exposed to higher temperatures and solar radiation (Kapos, 1989). Forest edges are subjected to significantly higher wind speed and turbulence than forest interiors, as wind speeds are able to increase whilst travelling across adjacent deforested areas (Laurance and Curran, 2008). Wind penetration is estimated to extend around three times the height of the trees into the forest, causing far-reaching disturbance to the wind profile (Kapos, 1989).

Extensive tree mortality often occurs at forest edges, with trees suffering physical damage from strong wind forces (Murcia, 1995). Many other trees remain as standing dead trees, killed by excessive desiccation as a result of drier conditions and increased light exposure (Olupot, 2009). Most trees situated along newly created edges lack the physiological adaptations required to cope with the elevated heat and wind stress (Laurance *et al.*, 2007), with edge-mediated mortalities occurring as far as 500m from the forest edge (Laurance and Curran, 2008). The reduction in foliage density in the canopy arising from tree mortalities increases the light levels reaching the forest understory, causing an increase in the density of understory vegetation (Faria *et al.*, 2009), and a rise in the abundance and diversity of saplings, shrubs and herbs (Harper *et al.*, 2005). Weedy propagules from surrounding habitats can invade the forest with greater ease, changing the species composition to favouring high-disturbance species (Laurance and Yensen, 1991). Structural parasites such as lianas and other vines thrive at forest edges, causing increased damage and reduced reproductive success to forest trees. The risk of fire becomes greater following the creation of a forest edge. Leaf litter becomes more abundant as desiccated trees shed their leaves, and raised temperatures and light penetration increase the flammability of leaf litter and fallen trees (Laurance and Curran, 2008).

Many of the early studies on the effect of edges on animals focused on birds, finding occurrences of increased diversity at edges, which led to an initial belief that edges were intrinsically beneficial to animal communities (Leopold, 1933; Johnston, 1947). This was attributed to a more heterogeneous vegetation structure at forest edges, with more vegetation layers being able to accommodate a wider range of species (Roth, 1976). Strelke and Dickson (1980) found enhanced bird diversity and abundance at a clearfelled forest edge compared to both the interior and the clearfelled stand, with more complex foliage providing foraging and singing posts for

species from both habitats. However, as interest in edge effects rose and more studies were carried out, negative effects of edges on animal communities began to be found. Declines in bird breeding success at forest edges have been documented, due to increased access for nest predators and parasites from adjacent habitats (Wilcove, 1985). Changes in microclimate leading to drier conditions at forest edges can be highly damaging to some amphibian species reliant on moist skin for respiration, forcing them further into the forest interior (Lehtinen *et al.*, 2003).

The permeability of an edge can alter an organism's ability to disperse between patches of suitable habitat. An edge's permeability consists of both the vegetation structure and composition of the habitat and surrounding matrix, and the behaviour of individuals when faced with an edge (Rittenhouse and Semlitsch, 2006). Hard edges with highly contrasting vegetation structures, such as between closed-canopy forest and clearfelled stands, can be highly impermeable to dispersal. Soft edges are less contrasting, and enable more individuals to disperse (Berggren *et al.*, 2002). Hard edges can lead to increased densities of organisms aggregating at edges, as organisms approaching the edge are unable to freely traverse through the surrounding matrix (Haynes and Cronin, 2006). In other cases edges may have lower organism densities, through the strong edge avoidance behaviour often exhibited by species dependent on a closed canopy. In highly fragmented landscapes, an inability to emigrate between remnants of suitable habitat may place small populations at risk of local or regional extinction through a lack of gene flow and a reduced chance of recolonisation of unoccupied patches (Lees and Peres, 2009).

A common finding in studies of edge effects on animals is the high degree of species specificity in the direction of response, influenced by a variety of factors such as physiology, life history and dispersal ability, highlighting the importance of assessing changes in the structure of the community instead of focusing solely on species diversity (Laurance, 1994; Baker *et al.*, 2007). Abrupt habitat edges are likely to have a strong influence on butterfly community structure. Most butterfly species have a narrow range of tolerances of light levels and humidity, with some requiring the darker, more humid conditions of the forest interior, while others are more suited to more open, drier habitats. Butterflies exhibit high levels of host plant specificity, and may be driven away from a forest edge if the host plant is unable to tolerate microclimatic changes or increased competition from invasive species (Kremen, 1992). Distinct fruit-feeding butterfly communities have been found in comparisons of disturbed and undisturbed habitats, with the data showing strong correlation with other arthropod taxa. This, along with the high degree of habitat specificity of butterfly species, suggests that butterfly community composition may function as a key indicator of tropical forest disturbance, with the ability to reflect on possible changes to other arthropod communities (Uehara-Prado *et al.*, 2009).

While other studies have focused on butterfly responses to conspicuous edges caused by clearfelling and logging roads (Cleary *et al.*, 2005), less obvious edges caused by smaller forest roads may have an impact on butterfly community structure, deterring species more adapted to the forest interior, and increasing the effects of habitat fragmentation. This study tests the hypothesis that butterfly community structure is likewise affected by softer forest edges, forming distinct edge and forest interior communities. The potential value of fruit-feeding butterfly communities as indicators of forest disturbance is also considered.

2. Materials and methods

2.1 Study site

Fieldwork took place from the 8th to the 14th of August 2008 at Danum Valley Field Centre in Sabah, Malaysian Borneo. The Field Centre is situated within Danum Valley Conservation Area (Fig. 1), which consists of 428 km² of unlogged lowland tropical forest (Dumbrell and Hill, 2005). Danum Valley Conservation Area was established within the Yayasan Sabah Forest Concession in 1981, with the aim to create a centre for conservation, research and education, protected from the high levels of commercial selective logging occurring in the surrounding area. Temperature remains fairly constant throughout the year, with a mean of 26.7°C, and mean maximum and minimum of 30.9°C and 22.5°C respectively. Rainfall is more variable, being influenced by two monsoons occurring from November to March and June to July, with drier inter-monsoon periods in April and September. The annual rainfall average at Danum Valley Field Centre is 2822mm, with rain falling on average 220 days of the year (Marsh and Greer, 1992). The forest canopy is dominated by trees in the family Dipterocarpaceae, accounting for approximately 80% of the emergent trees (Ashton, 1982), with the ability to grow to over 70m in height (Ashton and Hall, 1992).

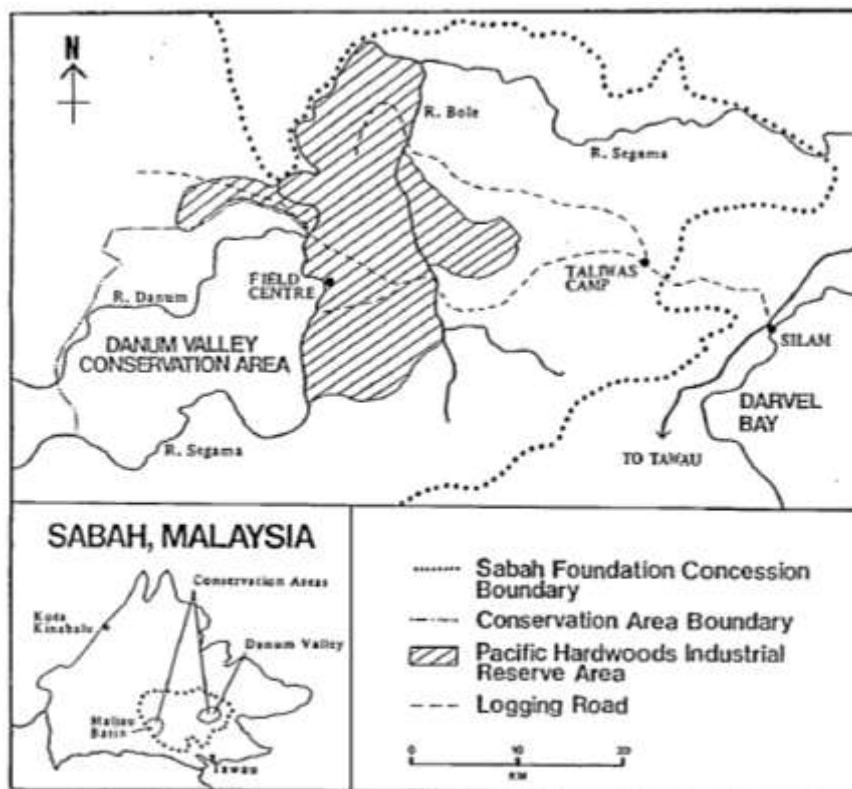


Figure 1. Map showing Danum Valley Conservation Area within Sabah Foundation's Forest Concession.

Figure 1: Map showing Danum Valley Conservation Area within Sabah Foundation's Forest Concession. Source: Marsh and Greer (1992)

2.2 Data collection

Butterflies were sampled using fruit-baited traps suspended from branches. These traps consist of a bait dish suspended below a cylinder of netting. After feeding, butterflies fly away vertically, and so become trapped within the net (K.C. Hamer, personal communication, 06/08/2008). With no prior knowledge of local butterfly species, and the difficulties involved in identifying butterflies in flight in the species-rich tropics (Walpole and Sheldon, 1999), fruit-baited traps provide a means to reliably identify individuals. Fruit-baited traps attract species in the family Nymphalidae, of which approximately 75% of species on Borneo are fruit-feeders (Hill *et al.*, 2001).

Sampling took place in an area of primary forest situated close to the field centre, in a patch of forest divided by a road approximately 2-3m wide. Three traps were placed within the primary forest 100m from the road (traps P1-P3), and three were placed along the edge of the forest and the road (traps E1-E3). Traps were situated 100m apart, to minimise butterfly dispersal between traps (J.K. Hill, personal communication, 06/08/2008). To hang the traps, a slingshot was used to send a rope over a suitable branch. The trap was then tied to the rope, and suspended approximately 1.5m above the ground.

Traps were baited with fresh banana the day before sampling commenced, with a fresh piece of banana added daily, to give a mixture of fresh and rotten fruit. Traps were checked twice daily at 8am and 4pm. Any butterflies that couldn't be identified in the field were brought back to the field centre. Butterflies were placed in the refrigerator for two hours to reduce their activity and allow for photographs to be taken of both sides of the wings. Photographs were taken using a Fugifilm Finepix A900 digital camera. All butterflies were identified to species level using Otsuka (1988) and Corbet and Pendlebury (1992), with the exception of the genus *Tanaecia*, which can only be accurately identified from the male genitalia (Hill *et al.*, 2001). Following identification, butterflies were marked with a felt-tipped pen to avoid counting recaptured individuals, and released.

2.3 Data analysis

Using Minitab, the number of species and number of individuals in primary forest and edge traps were tested for normality using the Kolmogorov-Smirnov normality test. Two-sample t-tests were used to test for differences in number of species and number of individuals between habitats.

To assess the difference in community composition between edge and primary forest sites, ANOSIM in the program PRIMER was used. This calculates the variance within and between habitats (Cleary *et al.*, 2005). A Bray-Curtis similarity matrix was then used to assess the degree of similarity between sites. The values calculated range from 0 demonstrating no common taxa between samples, to 100 for samples that are identical (Spector and Ayzama, 2003).

3. Results

3.1 Butterfly abundances

In total, 43 individuals from 17 species were collected during 7 days of sampling. All species were in the family Nymphalidae with the exception of *Graphium doson*,

which belongs to the Papilionidae (Table 1). The most common species was *Ragadia makuta*, with 7 individuals caught in the forest and 4 caught at the edge. The forest and the edge each had 7 species unique to that habitat, and 3 species were found in both habitats (Fig. 2).

Two-sample t-tests of the number of species and individuals found in primary forest compared to forest edges found that while primary forest had slightly more species and individuals, the result was not significant (Table 2).

3.2 Community structure

The ANOSIM tested for differences in community composition between the forest and the edge. The test statistic *R* lies between -1 and 1, with a value of 1 indicating all replicates within a habitat are more similar to each other than each replicate from another habitat. *R* = 0 demonstrates that there is the same degree of similarity within and between habitats. Negative values of *R* indicate higher similarities between than

Table 1: Summary of butterfly taxa collected in primary forest and edge traps

Family	Subfamily	Primary Forest		Edge	
		No. Species	No. Individuals	No. Species	No. Individuals
Nymphalidae	Nymphalinae	4	10	4	6
	Charaxinae	1	2	1	3
	Morphinae	1	1	0	0
	Satyrinae	4	11	4	9
Papilionidae	Papilioninae	0	0	1	1

Table 2: Number of species and individuals in primary forest and edge habitats

Habitat	No. Species		No. Individuals	
	\bar{x}	\pm s.e.	\bar{x}	\pm s.e.
Primary Forest	5.0	1.7	8.0	1.2
Edge	4.7	0.7	6.3	1.2

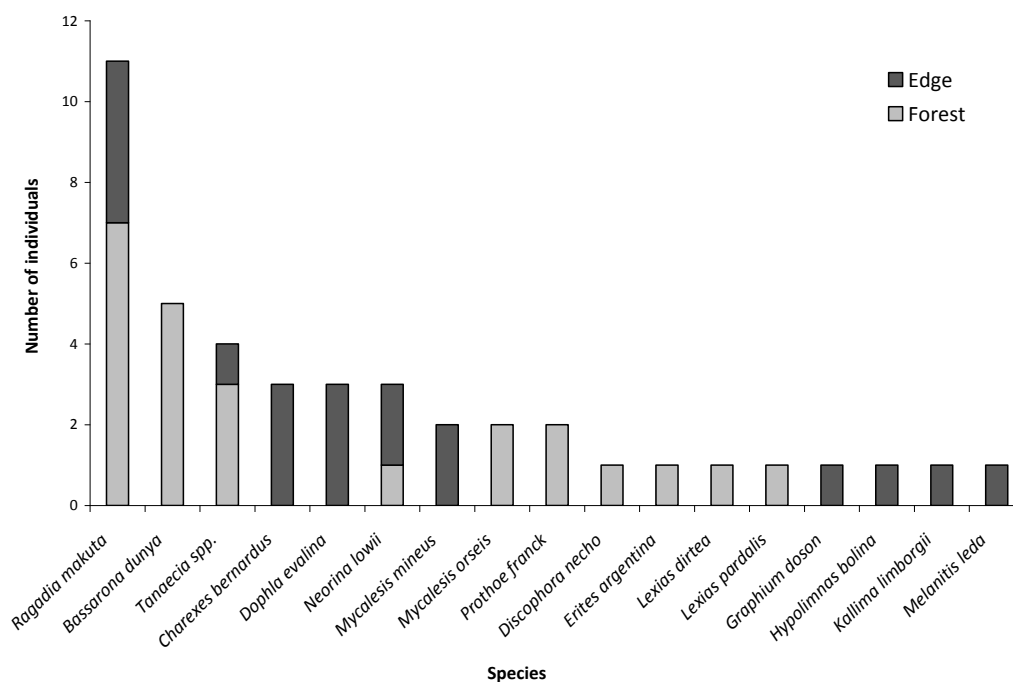


Figure 2: Species abundances in forest and edge habitats

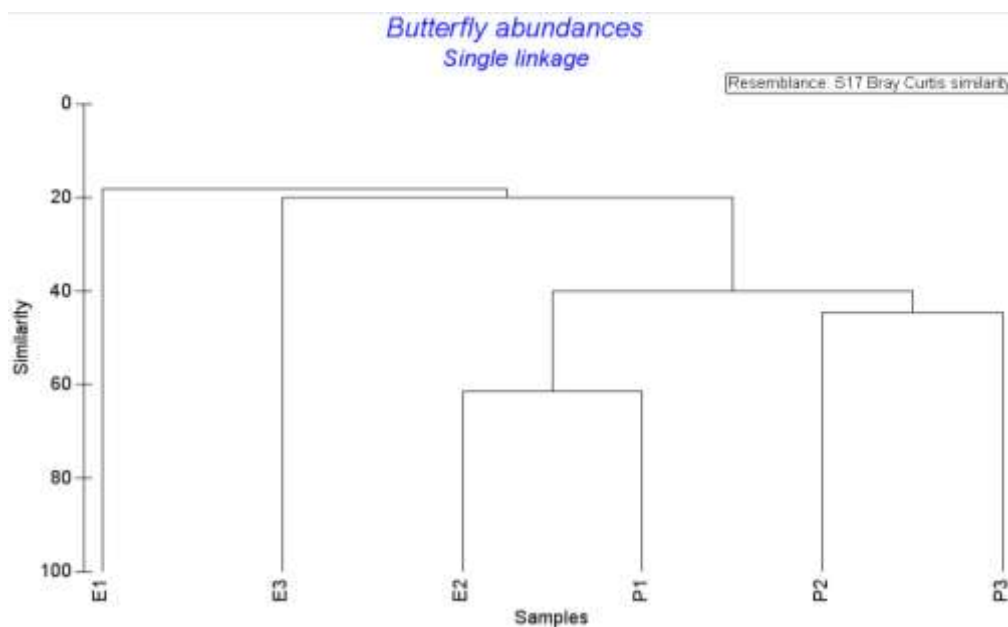


Figure 3: Dendrogram of similarity between edge and forest sites

within habitats (Clarke and Warwick, 2001). The ANOSIM produced a test statistic of $R = 0.426$, $P = 0.1$, which showed that while not significant, there was a tendency for greater similarity in community structure within than between habitats.

A Bray-Curtis similarity matrix was then calculated to assess which sites display the greatest degree of similarity in community structure. Figure 3 demonstrates that traps P1 and E2 are the most similar, followed by P2 and P3. The primary forest traps and E2 form a cluster at ~40% similarity. Traps E1 and E3 both show little similarity to other edge or forest traps.

4. Discussion

4.1 Collection of data

Fruit-baited traps have been used with great success in a number of studies at Danum Valley and throughout other areas of tropical forest (Dumbrell and Hill, 2005; DeVries *et al.*, 1999), and this technique is generally considered to be a highly effective method for sampling tropical butterflies (Sparrow *et al.*, 1994). Hill *et al.* (2001) collected 54 species of butterfly at Danum Valley Field Centre over 1,060 trap days, representing approximately 70% of the species of fruit-feeding butterflies that have been recorded at this site. During this study a total of 17 species, 30% as many as Hill *et al.* (2001), were caught over a period of just 42 trap days. Although species were readily accumulated, many of these were found in low densities, with only one individual caught for eight of the species. Over the 42 trap days, 43 individuals were caught, averaging at just over one individual per trap per day. This low rate of trapping is reflected in Hill *et al.* (2001), where 951 individuals were caught over the 1,060 trap days, with an average of less than one individual per trap per day. Tropical butterflies tend to be present in low densities, with one of the exceptions being *Ragadia makuta* (Hill, 1999), which accounted for a quarter of all individuals in this study. One problem with this method, which is not such an issue with the large sample sizes obtained in more long-term studies but that may have had more of an impact on this study, is the ability of butterflies to escape from the traps. It is estimated that around 5% of butterflies escape (Hill *et al.*, 2001), and whilst checking the traps, two were observed flying out.

4.2 Community structure

Distinct edge and forest communities have been reported for a variety of tropical forest taxa. Communities of forest-dependent birds have been found to contain lower species diversity at forest edges, with a high proportion of edge-intolerant forest specialists restricted to the forest interior. This was suggested to be driven by food resource availability, with desiccating microclimate conditions at edges reducing abundance of food for frugivores and canopy insectivores (Watson *et al.*, 2004). Alternatively, lemurs appear to show a greater tolerance to forest disturbance, with an increase in folivores at the forest edge due to increased foliar density (Harding and Gomez, 2006), with frugivores that can switch their diet to foliage having the ability to persist in both forest interiors and edges (Lehman *et al.*, 2006). Communities of web spiders are influenced by changes in vegetation structure and richness within 50m of forest edges, with an increase in spider richness and abundance towards the forest interior. Vegetation structure is important for

attachment of webs, with various species excluded from the more structurally sparse edge habitats (Baldissera *et al.*, 2004).

Whilst this study has not found significant differences in the community structure between edge and forest interior, the data do suggest a trend for primary forest sites to show greater similarity to each other than to edge sites. Cluster analysis placed the edge site E2 within the forest cluster, as it shared two of its four species with primary forest sites. Of the three edge sites along the forest path, this was the least open, with the other two sites being situated in clearings along the path. Sites E1 and E3 bore little similarity to any other site. This is in agreement with Bossart and Opuni-Frimpong (2009), where it was found that edge sites showed higher levels of variation in butterfly community structure than forest interior sites. Some edges appeared to be beneficial, while others had a detrimental effect on many forest interior species, causing them to be driven away from the edge.

Following clearfelling, light-loving butterfly species of secondary growth have been found to invade forest fragments, as far as 200-300m in some species, in response to increased penetration of light (Lovejoy *et al.*, 1986). Changes in feeding guild are also observed at forest edges, with generalists and liana specialists occurring in higher abundances and a reduction in tree specialists along disturbed road sites in response to the invasion of secondary vegetation (Cleary *et al.*, 2005). This change at habitat edges is reflected in the distribution of a number of the species found in this study. *Dophla evelina* and *Charexes bernardus* were both found exclusively at edge sites. These species are more prevalent in forest gaps than shaded forest interiors (Hamer *et al.*, 2003), and have generalist larvae with low host-plant specificity (Hirowatari *et al.*, 2007). Other generalists such as *Graphium doson* and *Kallima limborgii* (figure 4) also occurred at the forest edge (Cleary *et al.*, 2009). The larvae of *Melanitis leda* and *Mycalesis mineus*, both of which species were caught in edge traps, feed on a variety of Gramineae plants at the forest edge (Aoki *et al.*, 1982). *Melanitis leda* and *Hypolimnas bolina* are dependent on edges for mating, with males of these species patrolling along forest edges in search of a mate (Kemp, 2002). The appearance of the above species at the forest edge may indicate that the forest boundary caused by the road is affecting the composition of species. The requirements for specific microclimatic conditions, larval host plants, or mating habitats exhibited by these species may predispose them to be more suited to disturbed, secondary environments, such as those found at an anthropogenic forest edge.



Figure 4: Photograph of *Kallima limborgii* © C. Armstrong

4.3 Edge penetration distance

The presence of *Mycalesis orseis* and *Erites argentina* at forest sites suggests edge effects may penetrate at least 100m into the forest, as these species are grass-specialists whose larval host plants are unlikely to occur within an undisturbed forest interior (Cleary *et al.*, 2009). However, the forest traps contained predominantly tree-specialists (Cleary *et al.*, 2009), suggesting that the forest 100m away from the edge has been minimally affected by microclimate changes at the forest edge. Increased tree mortality, especially of large trees measuring >60cm dbh, has been found to extend 300m into the forest from an edge (Laurance *et al.*, 2000). In this study, the high proportion of tree specialists occurring 100m from the forest edge may imply that the edge effects caused by this road are less destructive than those formed from clearfelling, as high tree mortality from increased temperature and water stress would be likely to cause a decline in larval host plant availability for tree specialists. A reason for this may be that the road bisecting the forest was relatively narrow and had partial canopy cover along parts of its length. The shading provided by the canopy may lessen the impacts of increased solar radiation typically seen at abrupt forest edges (Kapos, 1989), and the narrowness of the road may prevent an increase in wind shear forces and turbulence, which can often lead to physical damage to vegetation (Laurance and Curran, 2008).

Tropical forest roads do have the ability, however, to adversely impact on understory microclimate, vegetation composition and structure, and hinder the dispersal of forest interior species (Laurance *et al.*, 2009). Linear edges such as those formed by roads can affect a substantial area of forest habitat, as any edge effects extend into the forest on either side of the road, effectively doubling the area of edge-impacted habitat (Goosem, 2007). In this study, a number of edge- and disturbance-tolerant species were found inhabiting narrow edges, suggesting that a linear clearing this size may be large enough to affect tropical forest communities. Further study should sample butterflies at a variety of distances from forest roads, in an attempt to ascertain the distance of edge penetration. Sampling across a gradient of road widths would give an insight into the relationship between the degree of openness of a linear edge and the penetration distance of edge effects. The ability of forest interior communities to recover following the creation of a road could be explored by sampling a variety of road ages.

4.4 The value of fruit-feeding butterflies as disturbance indicators

The gradient in specific microclimatic and habitat requirements that spans across the Nymphalidae family has led to the proposal that this is a key taxon to be utilised as an indicator of tropical forest disturbance (Kremen, 1992). Light levels (Hamer *et al.*, 2003), hostplant distribution, and total tree density (Cleary *et al.*, 2009) have been found to impact butterfly community structure, with species distributions closely mirroring gradients of disturbance. Disturbed forests suffer increased rates of tree mortality (Murcia, 1995), which will therefore lead to a reduced tree density and greater canopy openness, thus increasing light levels. Disturbed forests are easily colonised by grasses, lianas and other vines (Laurance and Curran, 2008), which along with the decrease in mature trees, will likely impact the distribution and abundance of butterflies through the alteration of larval host plant availability.

Other invertebrate taxa may also experience altered community structure along disturbance gradients due to habitat preferences. This is seen in litter-dwelling ants, which show interspecific variation in preference for litter depth (Carvalho and Vasconcelos, 1999). Increased desiccation at forest edges results in deeper leaf litter layers (Laurance and Curran, 2008), thus influencing the species composition of ants capable of inhabiting edge-disturbed sites (Carvalho and Vasconcelos, 1999). The requirements of these ants are however predominantly influenced by just one environmental factor, whereas the combination of a variety of microclimatic factors and host plant specificity required by butterflies may enable the community structure to provide a more detailed reflection on the state of the habitat.

Relative to many other tropical invertebrate taxa, butterflies have been thoroughly studied, with a great many of these species reliably identifiable to species level using photographic guides (Otsuka, 1988; Corbet and Pendlebury, 1992). This gives them added value as indicators, as there is less chance of incorrectly identifying cryptic species and the time and labour costs of identification are drastically reduced. The low capture rate of fruit-feeding butterflies in fruit-baited traps (on average one butterfly per trap per day, in this study and Hill *et al.*, 2001), however, may negate much of the benefits gained from the ease of identification, requiring perhaps several months to gain a reliable and representative sample size. The use of fruit-baited traps also restricts sampling to the fruit-feeding guild of Nymphalidae, accounting for 75% of the family (Hill *et al.*, 2001). Community composition among other butterfly families may demonstrate better indicator abilities, and a comparison across various Lepidopteran families and feeding guilds may be able to determine if any particular taxon is superior in indicating forest disturbance.

5. Conclusions

The findings from this study suggest that even relatively small levels of forest clearance and canopy opening may impact faunal community structure. This highlights the importance of protecting tropical forests from small-scale disturbance and limiting the construction of roads. This also has implications for actions such as selective logging, which is the predominant form of logging in South East Asian forests (Sodhi *et al.*, 2004). Gaps from tree-felling can cause microclimatic edge effects, resulting in increased canopy openness extending up to 100m into the surrounding forest (Broadbent *et al.*, 2008). Increasing the uptake of reduced impact logging, whereby the felling and extraction of trees and the location of roads are carefully planned to minimise forest disturbance (Pereira *et al.*, 2002), may help to compensate for the detrimental effects of forest edges.

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References

- Aoki, T., Yamaguchi, S., Uemura, Y., 1982. Butterflies of the South East Asian Islands Volume 3: Satyridae, Libytheidae. Plapac, Tokyo.
- Ashton, P.S., 1982. Dipterocarpaceae, Flora Malesiana Series 1. Spermatophyta 9, 251-552.
- Ashton, P.S., Hall, P., 1992. Comparisons of structure among mixed dipterocarp forests of north-western Borneo. *Journal of Ecology* 80, 459-481.
- Baker, S.C., Barmuta, L.A., McQuillan, P.B., Richardson, A.M.M., 2007. Estimating edge effects on ground-dwelling beetles at clearfelled non-riparian stand edges in Tasmanian wet eucalypt forest. *Forest Ecology and Management* 239, 92-101.
- Baldissera, R., Ganade, G., Fontoura, S.B., 2004. *Biological Conservation* 118, 403-409.
- Berggren, A., Birath, B., Kindvall, O., 2002. Effect of corridors and habitat edges on dispersal behavior, movement rates, and movement angles in Roesel's Bush-Cricket (*Metrioptera roeseli*). *Conservation Biology* 16, 1562-1569.
- Bossart, J.L., Opuni-Frimpong, E., 2009. Distance from edge determines fruit-feeding butterfly community diversity in Afrotropical forest fragments. *Environmental Entomology* 38, 43-52.
- Broadbent, E.N., Anser, G.P., Keller, M., Knapp, D.E., Oliveira, P.J.C., Silva, J.N., 2008. Forest fragmentation from deforestation and selective logging in the Brazilian Amazon. *Biological Conservation* 141, 1745-1757.
- Carvalho, K.S., Vasconcelos, H.L., 1999. Forest fragmentation in central Amazonia and its effects on litter-dwelling ants. *Biological Conservation* 91, 151-157.
- Clarke, K.R., Warwick, R.M., 2001. *Change in Marine Communities: An Approach to Statistical Analysis and Interpretation*, second ed. PRIMER-E Ltd, Plymouth.
- Cleary, D.F.R., Boyle, T.J.B., Setyawati, T., Menken, S.B.J., 2005. The impact of logging on the abundance, species richness and community composition of butterfly guilds in Borneo. *Journal of Applied Entomology* 129, 52-59.
- Cleary, D.F.R., Gennera, M.J., Koh, L.P., Boyle, T.J.B., Setyawati, T., de Jong, R., Menken, S.B.J., 2009. Butterfly species and traits associated with selectively logged forest in Borneo. *Basic and Applied Ecology* 10, 237-245.
- Corbet, A.S., Pendlebury, H.M., 1992. *The Butterflies of the Malay Peninsula*, fourth ed. Malayan Nature Society, Kuala Lumpur.
- DeVries, P.J., Murray, D., Lande, R., 1997. Species diversity in vertical, horizontal, and temporal dimensions of a fruit-feeding butterfly community in an Ecuadorian rainforest. *Biological Journal of the Linnean Society* 62, 343-364.
- DeVries, P.J., Walla, T.R., Greeney, H.F., 1999. Species diversity in spatial and temporal dimensions of fruit-feeding butterflies from two Ecuadorian rainforests. *Biological Journal of the Linnean Society* 68, 333-353.

Dumbrell, A.J., Hill, J.K., 2005. Impacts of selective logging on canopy and ground assemblages of tropical forest butterflies: Implications for sampling. *Biological Conservation* 125, 123-131.

Faria, D., Mariano-Neto, E., Zanforlin Martini, A.M., Ortiz, J.V., Montingeli, R., Rosso, S., Paciencia, M.B., Baumgarten, J., 2009. Forest structure in a mosaic of rainforest sites: The effect of fragmentation and recovery after clear cut. *Forest Ecology and Management* 257, 2226-2234.

Goosem, M., 2007. Fragmentation impacts caused by roads through rainforests. *Current Science* 93, 1587-1595.

Hamer, K.C., Hill, J.K., Benedick, S., Mustaffa, N., Sherratt, T.N., Maryati, M., Chey, V.K., 2003. Ecology of butterflies in natural and selectively logged forests of northern Borneo: the importance of habitat heterogeneity. *Journal of Applied Ecology* 40, 150-162.

Harding, E.K., Gomez, S., 2006. Positive edge effects for arboreal marsupials: an assessment of potential mechanisms. *Wildlife Research* 33, 121-129.

Harper, K.A., Macdonald, S.E., Burton, P., Chen, J., Brososky, K.D., Saunders, S., Euskirchen, E.S., Roberts, D., Jaiteh, M., Esseen, P-A., 2005. Edge influence on forest structure and composition in fragmented landscapes. *Conservation Biology* 19, 768-782.

Haynes, K.J., Cronin, J.T., 2006. Interpatch movement and edge effects: the role of behavioral responses to the landscape matrix. *OIKOS* 113, 43-54.

Hill, J.K., Hamer, K.C., Tangah, J., Dawood, M., 2001. Ecology of tropical butterflies in rainforest gaps. *Oecologia* 128, 294-302.

Hirowatari, T., Makihara, H., Sugiarto, 2007. Effects of fires on butterfly assemblages in lowland dipterocarp forest in East Kalimantan. *Entomological Science* 10, 113-127.

Johnston, V.R., 1947. Breeding birds of the forest edge in Illinois. *Condor* 2, 45-53.

Kapos, V., 1989. Effects of isolation on the water status of forest patches in the Brazilian Amazon. *Journal of Tropical Ecology* 5, 173-185.

Kemp, D.J., 2002. Visual mate-searching behaviour in the evening brown butterfly, *Melanitis leda* (L.) (Lepidoptera: Nymphalidae). *Australian Journal of Entomology* 41, 300-305.

Kremen, C., 1992. Assessing the indicator properties of species assemblages for natural areas monitoring. *Ecological Applications* 2, 203-217.

Laurance, W.F., 1994. Rainforest fragmentation and the structure of small mammal communities in tropical Queensland. *Biological Conservation* 69, 23-32.

Laurance, W.F., Curran, T.J., 2008. Impacts of wind disturbance on fragmented tropical forests: A review and synthesis. *Austral Ecology* 33, 399-408.

Laurance, W.F., Delamônica, P., Laurance, S.G., Vasconcelos, H.L., Lovejoy, T.E., 2000. Conservation: Rainforest fragmentation kills big trees. *Nature* 404, 836.

Laurance, W.F., Goosem, M., Laurance, S.G.W., 2009. Impacts of roads and linear clearings on tropical forests. *Trends in Ecology and Evolution* 24, 659-669.

Laurance, W.F., Nascimento, H.E.M., Laurance, S.G., Andrade, A., Ewers, R.M., Harms, K.E., Luizão, R.C.C., Ribeiro, J.E., 2007. Habitat fragmentation, variable edge effects, and the landscape-divergence hypothesis. *PLoS ONE* 2(10): e1017.

Laurance, W.F., Yensen, E., 1991. Predicting the impacts of edge effects in fragmented habitats. *Biological Conservation* 55, 77-92.

Lees, A.C., Peres, C.A., 2009. Gap-crossing movements predict species occupancy in Amazonian forest fragments. *Oikos* 118, 280-290.

Lehman, S.M., Rajaonson, A., Day, S., 2006. Edge effects and their influence on lemur density and distribution in Southeast Madagascar. *American Journal of Physical Anthropology* 129, 232-241.

Lehtinen, R.M., Ramanamanjato, J., Raveloarison, J.G., 2003. Edge effects and extinction proneness in a herpetofauna from Madagascar. *Biodiversity and Conservation* 12, 1357-1370.

Leopold, A., 1933. *Game Management*. Charles Scribner Sons, New York.

Lovejoy, T.E., Bierregaard Jr., R.O., Rylands, A.B., Malcolm, J.R., Quintela, C.E., Harper, L.H., Brown Jr., K.S., Powell, A.H., Powell, G.V.N., Schubart, H.O.R., Hays, M.B., 1986. Edge and other effects of isolation on Amazon forest fragments, in: Soule, M. (Ed.), *Conservation Biology: The Science of Scarcity and Diversity*. Sinauer Associates Inc., Massachusetts, pp. 257-325.

Marsh, C.W., Greer, A.G., 1992. Forest land-use in Sabah, Malaysia: an introduction to Danum Valley. *Philosophical Transactions of the Royal Society of London, Series B* 335, 331-339.

Murcia, C., 1995. Edge effects in fragmented forests: implications for conservation. *Trends in Ecology & Evolution* 10, 58-62.

Olupot, W., 2009. A variable edge effect on trees of Bwindi Impenetrable National Park, Uganda, and its bearing on measurement parameters. *Biological Conservation* 142, 789-797.

Otsuka, K., 1988. *Butterflies of Borneo, Volume 1*. Tobishima Corporation, Tokyo.

Pereira Jr., R., Zweede, J., Asner, G.P., Keller, M., 2002. Forest canopy damage and recovery in reduced-impact and conventional selective logging in eastern Para, Brazil. *Forest Ecology and Management* 168, 77-89.

Rittenhouse, T.A.G., Semlitsch, R.D., 2006. Grasslands as movement barriers for a forest-associated salamander: Migration behavior of adult and juvenile salamanders at a distinct habitat edge. *Biological Conservation* 131, 14-22.

- Roth, R.R., 1976. Spatial heterogeneity and bird species diversity. *Ecology* 57, 773-782.
- Schulze, C.H., Linsenmair, K.E., Fiedler, K., 2001. Understorey versus canopy: patterns of vertical stratification and diversity among Lepidoptera in a Bornean rain forest. *Plant Ecology* 153, 133-152.
- Sodhi, N.S., Koh, L.P., Brook, B.W., Ng, P.K.L. (2004) Southeast Asian biodiversity: an impending disaster. *Trends in Ecology and Evolution* 19: 654-660
- Sparrow R.H., Sisk D.T., Ehrlich, P.R., Murphy, D.D., 1994. Techniques and guidelines for monitoring Neotropical butterflies. *Conservation Biology* 8, 800-809.
- Spector, S., Ayzama, S., 2003. Rapid turnover and edge effects in dung beetle assemblages (Scarabaeidae) at a Bolivian neotropical forest-savanna ecotone. *Biotropica* 35, 394-404.
- Strelke, W.K., Dickson, J.G., 1980. Effect of forest clear-cut edge on breeding birds in east Texas. *Journal of Wildlife Management* 44, 559-567.
- Uehara-Prado, M., Fernandes, J.O., Bello, A.M., Machado, G., Santos, A.J., Vaz-de-Mello, F.Z., Freitas, A.V.L., 2009. Selecting terrestrial arthropods as indicators of small-scale disturbance: A first approach in the Brazilian Atlantic Forest. *Biological Conservation* 142, 1220-1228.
- Walpole, M.J., Sheldon, I.R., 1999. Sampling butterflies in tropical rainforest: an evaluation of a transect walk method. *Biological Conservation* 87, 85-91.
- Watson, J.E.M., Whittaker, R.J., Dawson, T.P., 2004. Habitat structure and proximity to forest edge affect the abundance and distribution of forest-dependent birds. *Biological Conservation* 120, 311-327.
- Wright, S.J., 2006. The future of tropical forest species. *Biotropica* 38, 287–301.
- Wilcove, D.S., 1985. Nest predation in forest tracts and the decline of migratory songbirds. *Ecology* 66, 1211-1214.